Table 6. — Expected genetic gain (%) at family level for *P. strobus* × *P. peuce* hybrids as compared to their mean and parents mean (in brackets).

Characters	Genetic gain if selected the best ... families			
	3	6	12	18
Resistance	23	2o	11	4
	(4r	(1o)	(6)	(2)
Height growth	7	5	3	1
	(8)	(6)	(4)	(1)

populations to utilize in a selective breeding program for resistance and growth.

Some parents had positively and some negatively significant GCA effects for growth. No one parent combines significantly favourably the resistance to *C. ribicola*.

Growth seems to be under polygenic control, but the question of whether or not resistance is under single gene or polygenic control remains to be answered.

Narrow-sense heritabilities had moderate values both for resistance and growth, but if the hybrids are planted on a large scale a substantial genetic gain should be achieved, particularly in resistance.

Acknowledgements

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Age-to-Age Correlations in Growth Processes with fixed and random Effects

By S. MAGNUSSEN[1]

Summary

A model to predict phenotypic single tree age-to-age correlations is developed. Correlations are predicted from variance ratios and a factor d which depicts the relative proportion of size dependent growth in a quantitative juvenile trait. Observed age 10 to age 35 correlations of stem volume in a *Pinus resinosa* (AIT.) spacing trial indicated that the model is a good first approximation at a spacing of 2 m × 2 m. Correlations were underestimated at closer spacings and overestimated at wider spacings. Prediction bias could be explained by spacing dependent changes in d. With time, d approached an upper limit asymptotically. Accurate predictions were possible once d was close to its limit. Examples from the literature illustrated the potential for predicting age-to-age correlations of tree height. An application of the model as a tool for tree breeders to settle questions about selection age is demonstrated.

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Introduction

Age-to-age correlation of a trait or a trait index is a principal tool in forest genetics, used in calculating gain arising from juvenile selections of a future breeding population (NAMKOONG, 1979; ZOBEL and TALBERT, 1984). Frequently, breeders pursue the objective of a maximum rate of genetic gain (FOSTER, 1986; FRANKLIN, 1979; HATCHEL *et al.*, 1972; KANG, 1985; LAMBETH, 1980; ROBINSON and VAN BUIJTENEN, 1979; SQUILLACE, 1974; WAKELY, 1971) that invariably leads to selections before economic maturity of the trait. Age-to-age correlations are then needed to make downward adjustments to the expected genetic gain in the mature trait, in order to reflect the uncertainties of juvenile selections. Further details of the theory and applications of juvenile selection are found in, for example, BECKER (1984), COCHRAN (1951), FALCONER (1981), KANG (1985), NAMKOONG (1979), and NANSON (1976).

Age-to-age correlations will, for a fixed age interval, increase over time as a result of the cumulative nature of tree growth. A partitioning of age-to-age correlations into contributions by size and growth has shown that the correlations are largely determined by the former (LAMBETH *et al.*, 1983). Other factors that influence age-to-age correlations are growth rates (BENJAMIN and HARDWICK, 1986; CLARK and DISNEY, 1970; HARA, 1984; FOSTER, 1986; NAMKOONG and CONKLE, 1976), site (BOYLE, 1986; BONGARTEN and HANOVER, 1986), experimental design (LIBBY and COCKERHAM, 1980; WILLIAMS *et al.*, 1983), and stocking and competition (FRANKLIN, 1979; GÄRTNER, 1982; HÜHN, 1976; MITCHELL-OLDS, 1987), among others. In all, these factors, which may make predictions of future genetic gain difficult, stress a need for models of juvenile-mature correlations based on the dynamics of tree growth rather than time (LAMBETH, 1980).

Model derivation

A quantitative trait X is observed at two points in time in a tree population. It is assumed that X is normally distributed, with mean μ_x and variance σ^2_x. Let X_t denote the trait value of an individual tree at time t, and let $X_{t} + \triangle_t$ be the trait value at time $t + \triangle t$. In the absence of any growth constraints or growth disturbances a simple size dependent relationship would exist between X_t and $X_t + \triangle_t$.

[1] $X_{t+\Delta t} = (1 + k_{\Delta t})X_t$ where $k_{\Delta t}$ is an intrinsic (non-observable)

maximum growth rate ($k_{\Delta t} > 0$) of trait X during the time Δt.

It is assumed that $k \triangle_t$ is constant for all population members. In the presence of growth constraints and disturbances, a tree will grow at a lower rate. Hence, realized growth can be considered to be the difference between maximum growth and the amount "lost" due to extraneous factors. This relationship is expressed as:

[2] $X_{t+\Delta t} = (1 + k_{\Delta t})X_t - L_{\Delta t} \cdot k_{\Delta t}X_t = (1 + k_{\Delta t}(1-L_{\Delta t}))X_t$ where $L_{\Delta t}$ is the

fraction of growth "lost" in an individual tree during the period Δt

$(0 < L_{\Delta t} < 1)$.

At the population level, equation [2] describes a growth process of fixed (size dependent) and apparently random deviations. The size dependent fraction of growth is equal to the amount not "lost" by extraneous factors, i.e. it is equal to 1-L $\triangle_t$ or simply d $\triangle_t$ ($0 <$ d $\triangle_t <$ 1).

Equation [2] can now be written as:

[3] $X_{t+\Delta t} = (1 + k_{\Delta t} \cdot d_{\Delta t})X_t$

The variance of $X_t + \triangle_t$ is found by a Taylor series expansion of [3] (for example, NAMKOONG, 1979).

[4] $\sigma^2_{x_{t+\Delta t}} = (1+k_{\Delta t} \cdot \bar{d}_{\Delta t})^2 \sigma^2_{x_t} + (\mu_x k_{\Delta t})^2 \sigma^2_{d_{\Delta t}} + 2(\mu_{x_t} k_{\Delta t})(1+k_{\Delta t} \cdot d_{\Delta t}) \cdot$

cov($d_{\Delta t}, x_t$) where $\bar{d}_{\Delta t}$ is the mean fraction of size dependent growth

during Δt and $\sigma^2_{d_{\Delta t}}$ is the variance of $d_{\Delta t}$.

In order to arrive at an expression suited for predictions of correlations, a simplification of [4] is needed. Assume, therefore, that cov (d $\triangle_t$, X_t) = O and that $\sigma^2_d \triangle_t$ = 1-$\bar{d}^2 \triangle_t$. Given these assumptions σ^2_x $t + \triangle_t$ can be expressed as:

[5] $\sigma^2_{x_{t+\Delta t}} = (1+k_{\Delta t} \cdot \bar{d}_{\Delta t})^2 \sigma^2_{x_t} + (\mu_x k_{\Delta t})^2 \cdot (1-d^2_{\Delta t})$

Taking the ratio σ^2_x $t + \triangle_t / \sigma^2_x$ t leads to

[6] $VR_{\Delta t} = \sigma^2_{x_{t+\Delta t}} / \sigma^2_{x_t} = (1+k_{\Delta t}\bar{d}_{\Delta t})^2 + CV^{-2}_{x_t} \cdot k^2_{\Delta t} \cdot (1-\bar{d}^2_{\Delta t})$ where CV_{x_t} denotes

the coefficient of variation of trait X at time t ($CV_{x_t} = \sigma_{x_t} / \mu_{x_t}$).

To find the covariance between X_t and $X_t + \triangle_t$ an application of the "delta"-technique (for example, BECKER, 1984) on equation (3) yielded the following result (given the above assumption).

[7] $cov(X_{t+\Delta t}, X_t) = (1+k_{\Delta t}\bar{d}_{\Delta t}) \sigma^2_{x_t}$

From [7] and [6] we obtain the following expression for the Pearson correlation coefficient (r $\triangle_t$) between X_t and $X_t + \triangle_t$:

[8] $r_{\Delta t} = (1+k_{\Delta t}\bar{d}_{\Delta t}) \cdot VR^{-\frac{1}{2}}_{\Delta t}$

According to [8] a $\bar{d}$ $\triangle_t$ value of 1.0 (a completely size dependent growth process) leads to r $\triangle_t$ = 1, and for $\bar{d}$ $\triangle_t$ = 0 (a completely random growth process) we obtain r $\triangle_t$ = VR$^{-1/2}\triangle_t$ as required. Also, r $\triangle_t$ will increase with $\bar{d}$ $\triangle_t$ for any given VR $\triangle_t$. Equations [6] and [8] provide the necessary framework for predicting age-to-age correlations from variance ratios and sample estimates of $\bar{d}$ $\triangle_t$ and CV_{x_t} obtained from measurements of X at time t and $t + \triangle t$.

Model Verification

To test whether the model in [8] provides realistic predictions of phenotypic age-to-age correlations from "known" variance ratios and a sample estimate (juvenile) of the d $\triangle_t$ factor, comparisons between observed and predicted correlations were made with data from a red pine (*Pinus resinosa* AIT.) spacing trial, and with published results from three forest genetics trials. Single tree phenotypic age-to-age correlations are used in all examples.

Verification proceeded in the following way:
1. Calculate sample estimates of $\sigma^2_{x_1}$, $\sigma^2_{x_2}$, μ_{x_1}, μ_{x_2}, CV_{x_1}, CV_{x_2}, $VR_{1:2}$, and $r_{1:2}$ from two juvenile measurements of X (here denoted by subscripts 1 and 2; 1:2 is used in place of $\triangle_t$).

2. Insert the appropriate estimates in [6] and [8] and solve for $\bar{d}_{1:2}$ and $k_{1:2}$, respectively.

3. Obtain for all available older measurements (i) the variance ratios VR $_{2:i}$ (i = 3, 4, 5, . . . , n).

4. Insert VR $_{2:i}$, $\bar{d}_{1:2}$, and CV $_{x_2}$ in [6] and [8] and solve for r $_{2:i}$ (for all i).

Data from the red pine spacing trial consist of single tree stem volumes at ages 10, 15, 20, 25, 30, and 35 years measured in permanent sample plots (0.1 ha to 0.2 ha) in the Research Forest of the Petawawa National Forestry Institute, Chalk River, Ontario. A detailed description of the trials in published elsewhere (STIELL and BERRY, 1977; BRAND and MAGNUSSEN, 1988). Data from measurements at age 10 and at age 15 served to estimate the parameters listed in steps one and two of the verification process. Further details of these data are given in *Table 1*. Spacing exerted no apparent influence on $\bar{d}_{1:2}$. Values close to one were seen in all spacings. Variance ratios VR $_{1:2}$ tended to increase with increased spacing as a result of accelerated growth in the wider spacings (BRAND and MAGNUSSEN, 1988). *Figure 1* shows the actual observed Pearson correlation coefficients plotted against the sample variance ratio VR$_{\triangle t}$. A clear effect of spacing emerges from this diagram. For any given variance ratio, the age-to-age correlation r$_{\triangle t}$ increased with decreasing initial tree spacing. The average predictions are illustrated by a dashed line. A good agreement between observed and the average expected values appears only at intermediate spacings ($\gtrsim$ 2 m). *Figure 2* shows in more detail the deviations between individual predictions of r$_{\triangle t}$ and the observed sample estimates. Again, spacing was the decisive factor in the accuracy of predictions. Predictions for closely spaced (< 1.8 m) plots were, as a rule, too low whereas the opposite was true for wider spaced plots (> 2.4 m). The error of prediction increased with the magnitude of VR$_{\triangle t}$. Reliable ($|r_{pred}-r_{obs}|$ < 0.05) predictions under the stated model assumptions appear only possible at

Figure 1. — Observed age-to-age correlations of stem volume in 13 red pine plots. VR$_{\triangle t}$ = ratio of variance at age t_i to variance at age 15. t_i = 20, 25, 30, 35 (spacing > 1.2 m), t_i = 20, 25 (spacing = 1.2 m). Dashed line depicts the average prediction model ($\bar{d}$ 10:15 = 0.96 CV 15% = 36.8). See *Table 1* for further plot details.
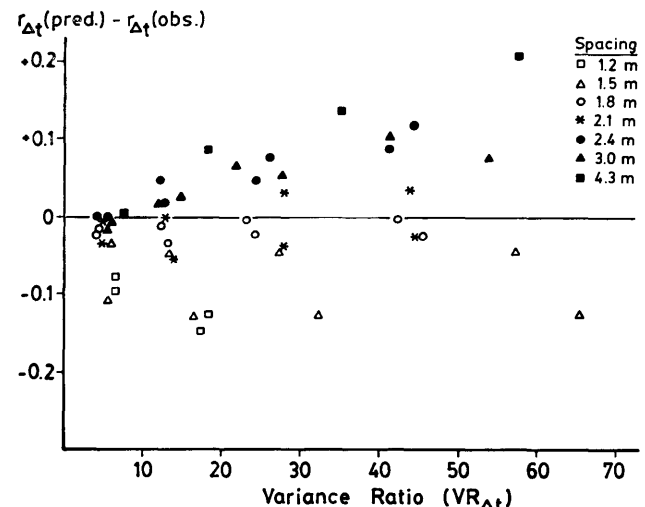
Figure 2. Deviations of individual plot predictions of stem volume age-to-age correlations (r$_{\triangle t}$(pred.)) from observed correlations (r$_{\triangle t}$(obs)) in the red pine spacing trial.

VR$_{\triangle t}$ = ratio of variance at age t_i to variance at age 15
t_i = 20, 25, 30, 35 (spacing > 1.2 m)
t_i = 20, 25, (spacing = 1.2 m)

a spacing of approximately 2 m and for variance ratios below 20.

Prediction bias can be explained by violation of the assumption of a constant $\bar{d}_{\triangle t}$ value throughout the prediction period. *Table 2* provides the actual sample estimates of $\bar{d}_{\triangle t}$. Actual $\bar{d}_{\triangle t}$ values above the model-value will lead to an underestimation of correlations and vice versa. Use of the d $_{15:20}$ values as a basis for predicting correlation r$_{20:i}$ (i = 25, 30, 35) would have reduced the average prediction error to less than 5% for the 1.2 m to 3.0 m spacing plots. Accurrate predictions were not possible for the 4.3 m plot due to the persistent instability of $\bar{d}_{\triangle t}$. In the 1.8 m and 2.1 m spaced plots $\bar{d}_{\triangle t}$ varied far less over time than in any other plots. This explains why the model did relatively well in these plots.

Table 1. — Average stem volume, coefficients of variation, variance and d-factor in 13 permanent sample plots (PSP) of *Pinus resinosa* (AIT.).

PSP	Spacing m	Trees in plot	μ_{10} dm³	μ_{15} dm³	CV$_{10}$%	CV$_{15}$%	VR$_{10:15}$	$\bar{d}_{10:15}$
364	1.2	501	4.9	19.4	54.3	44.0	10.32	.90
365	1.2	521	4.7	18.4	54.2	41.9	9.21	.90
373	1.5	379	6.3	24.8	41.9	32.9	9.43	.97
374	1.5	374	6.4	25.8	40.2	31.7	9.77	.94
371	1.8	289	6.9	31.1	42.2	31.5	11.48	.98
372	1.8	283	6.6	30.2	44.4	33.1	11.72	.98
368	2.1	200	8.4	39.6	43.5	30.6	10.99	.96
375	2.1	207	7.3	37.7	47.8	35.8	14.85	.98
376	2.4	156	6.3	35.8	52.1	38.8	18.30	.98
377	2.4	150	6.7	38.5	53.3	37.1	15.99	.98
366	3.0	102	7.4	44.0	53.4	36.4	16.48	.97
378	3.0	96	7.1	45.6	51.6	34.8	18.80	.97
369	4.3	102	6.0	30.9	55.2	49.8	21.84	.98

μ_{10} = plot average of stem volume at age 10
μ_{15} = plot average of stem volume at age 10
CV$_{10}$% = coefficient of variation of stem volume at age 10
CV$_{15}$% = coefficient of variation of stem volume at age 15
VR$_{10:15}$ = variance ratio (σ^2_2/σ^2_1) of stem volume variance at age 15 to stem volume variance at age 10
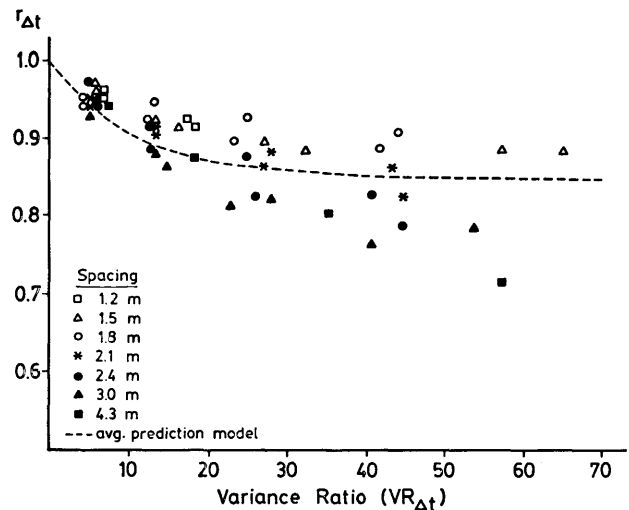$\bar{d}_{10:15}$ = average fraction of maximum growth that is size dependent

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Figure 3 illustrates the predicted and observed age-to-age correlations of tree height in two forest genetics trials, one with Douglas-fir (NAMKOONG *et al.*, 1972), and the second with ponderosa pine (NAMKOONG and CONKLE, 1976). On an average the model predictions differed by 0.08 from the observed sample estimates. In one case (Douglas-fir) the predictions were too low, in the other (ponderosa pine) the predictions were too high. Prediction errors did not seem to increase beyond a variance ratio of approximately 20. Application of LAMBETH's formulae (LAMBETH, 1980) would have generated predictions similar to those of the model presented herein for the ponderosa pine study, whereas predictions for the Douglas-fir trial would have been much closer to the observed correlations.

Lack of fit in the given examples was traceable to temporal changes in $\bar{d}\triangle_t$ (*Table 3*), just as we saw in the case of red pine. In the Douglas-fir pine, trial $\bar{d}\triangle_t$ actually increased between age 12 and 53 and this led to an underestimation of the actual correlations. In ponderosa pine the used d-value and the predicted r-values coincided only in the 7:20 years prediction period. All other predictions were too high because the actual $\bar{d}\triangle_t$ value was less than assumed (*Table 3, Figure 3*). Predictions of correlations ap-
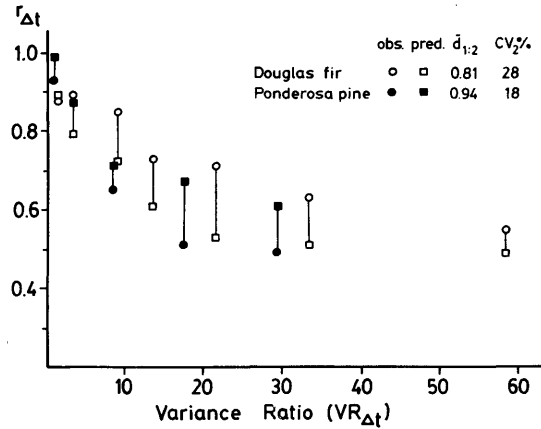

Figure 3. — Observed and predicted age-to-age correlations of tree heights (within plot) in open pollinated progenies of Douglas-fir (NAMKOONG *et al.*, 1972) and ponderosa pine (NAMKOONG and CONKLE, 1976).

$\bar{d}_{1:2}$ = average fraction of size dependent growth during time t_1 to t_2,
$CV_2\%$ = coefficient of variation at time t_2,
Douglas-fir: $t_1 = 10$, $t_2 = 12$
Ponderosa pine: $t_1 = 5$, $t_2 = 7$
$VR\triangle_t$ = ratio of variance at age t_i to variance at age t_2
Douglas-fir: $t_i = 15$, 18, 23, 28, 33, 40, 53
Ponderosa pine: $t_i = 8$, 12, 20, 25, 29

pear feasible from age 18 in Douglas-fir and from age 8 in ponderosa pine. Beyond these ages, $d\triangle_t$ is stable enough to allow predictions within 5% of the actual values. Apparent growth disturbances, which cause the size dependent growth factor d to decline, are evident in the ponderosa matrix of $\bar{d}\triangle_t$ values. In years 3 and 8 growth was only loosely related to current tree size.

The last example of verification illustrates that anomalies in the data (growth disturbances) may, in certain cases, render predictions next to impossible. *Figure 4* shows how these anomalies can cause age-to-age correlations to fluctuate wildly. Instead of the expected regular decline with age, correlations first drop rapidly to a minimum level more than 80% below predictions and they then recover to values predicted by the model; finally they decline much more rapidly than predicted. Drought years

Table 2. — Fraction (d$\triangle_t$) of size dependent stem-volume growth in 13 permanent sample plots (PSP) of red pine. Circled values were used for the prediction purposes.

AGE	15	20	25	30	30	15	20	25	30	35
	PSP=364, spacing=1.2m.					PSP=365, spacing=1.2m.				
10	(.90)	.88	.87	-	-	(.90)	.87	.86	-	-
15		.97	.97	-	-		.98	.98	-	-
20			.99	-	-			.99	-	-
25				-	-				-	-
30					-					-
	PSP=373, spacing=1.5m.					PSP=374, spacing=1.5m.				
10	(.97)	.95	.94	.94	.93	(.94)	.93	.91	.91	.91
15		.99	.98	.98	.98		.99	.98	.98	.98
20			.99	.99	.99			.98	.99	.99
25				.99	.99				.99	.99
30					.99					.99
	PSP=371, spacing=1.8m.					PSP=372, spacing=1.8m.				
10	(.98)	.97	.96	.96	.95	(.98)	.97	.96	.95	.94
15		.98	.99	.99	.98		.98	.99	.98	.98
20			.99	.99	.99			.99	.99	.99
25				.99	.99				.99	.99
30					.99					.99
	PSP=368, spacing=2.1m.					PSP=375, spacing=2.1m.				
10	(.96)	.93	.92	.90	.89	(.98)	.96	.94	.93	.92
15		.96	.98	.97	.97		.98	.98	.97	.97
20			.99	.98	.98			.99	.99	.98
25				.99	.99				.99	.99
30					.98					.98
	PSP=376, spacing=2.4m.					PSP=377, spacing=2.4m.				
10	(.98)	.96	.94	.92	.90	(.98)	.95	.92	.90	.87
15		.98	.97	.96	.95		.97	.96	.95	.94
20			.98	.98	.98			.98	.98	.98
25				.98	.98				.98	.98
30					.98					.97
	PSP=366, spacing=3.0m.					PSP=378, spacing=3.0m.				
10	(.97)	.94	.89	.85	.82	(.97)	.94	.89	.87	.85
15		.98	.96	.94	.93		.98	.96	.95	.95
20			.98	.97	.97			.98	.98	.98
25				.98	.98				.99	.99
30					.99					.99
	PSP=369, spacing=4.3m.									
10	(.98)	.95	.91	.88	.83					
15		.97	.93	.90	.86					
20			.95	.94	.92					
25				.96	.96					
30					.97					

Table 3. — Estimates of $\bar{d}\triangle_t$ for tree height in the Douglas-fir study (NAMKOONG *et al.*, 1972) and ponderosa pine study (NAMKOONG and CONKLE, 1976). See *Figure 3* and text for details. Circled values were used for prediction purposes.

Douglas-fir

Age	12	15	18	23	28	33	40	53
10	(.92)	.92	.94	.96	.95	.96	.95	.93
12		.92	.97	.98	.98	.98	.97	.96
15			.98	.99	.99	.99	.98	.98
18				.99	.99	.99	.98	.97
23					.99	.99	.98	.96
28						.99	.99	.99
33							.99	.99
40								.97

Ponderosa pine

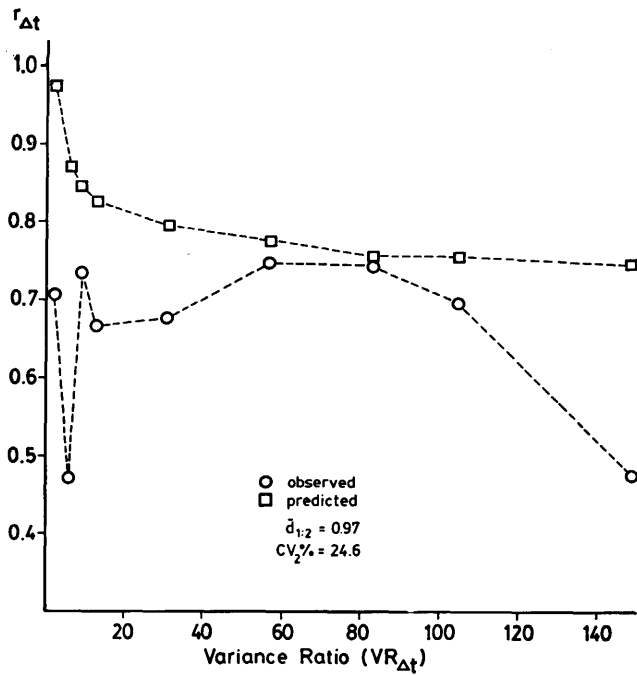| Age	5	7	8	12	20	25	29
3	.24	.18	.24	.30	.04	-.42	-.56
5		(.94)	.92	.92	.80	.79	.74
7			.55	.95	.90	.90	.90
8				.98	.95	.95	.94
12					.92	.97	.97
20						.97	.98
25							.96

Figure 4. — Observed and predicted age-to-age correlations of clonal mean (7 ramets per clone) tree heights in Norway spruce (ROULUND et al., 1985). Age min. = 2 (base year), Age max. = 13.

$r_{\triangle t}$ = age two to age t correlation coefficient (t = 3, 4, 5, 6, 7, 8, 9, 10, 13

$\bar{d}_{1:2}$ = average fraction of size dependent growth between age 1 and age 2

$CV_2\%$ = coefficient of variation of tree height at age two.

and differential loss of leader growth are speculated causes for this seesaw pattern of correlations. Many longterm field trials can be expected to suffer from similar growth disturbances, with lasting disruptive effects on otherwise regular trends in age-to-age correlations. A look at the $\bar{d}_{\triangle t}$ values in Table 4 confirms the source of inconsistencies in observed correlations. An apparent reversal of the normal growth pattern took place in the third year and somewhere between ages 10 and 13, when height growth became less deterministic. To use a $\bar{d}_{\triangle t}$-value of 0.97 to predict $r_{2:i}$ (i = 3 (1) 10, 13) correlations was appropriate only for the $r_{2:8}$ and $r_{2:9}$ predictions (see Figure 4). Reasonable predictions (error less than 10%) are only possible after the sixth growing season.

It is concluded that the model yields acceptable results only at intermediate levels of intertree spacing and that predictions should be restricted to variance ratios below 20. Predictions should also be limited to cases where growth anomalies have been negligible in the past. Due to a large error of prediction, the results obtained can only

Table 4. — Estimated $\bar{d}_{\triangle t}$ values of tree height growth in a field test of Norway spruce clones (ROULUND et al., 1985). Circled $\bar{d}_{\triangle t}$-value was used for prediction purposes.

Age	2	3	4	5	6	7	8	9	10	13
1	(.97)	.29	.09	.84	.77	.83	.90	.91	.90	.78
2		-.37	.16	.92	.90	.94	.97	.97	.96	.88
3			.96	.98	.98	.96	.98	.99	.99	.92
4				.81	.96	.96	.97	.98	.99	.93
5					.91	.98	.99	.99	.99	.97
6						.98	.99	.99	.99	.94
7							.99	.99	.97	.86
8								.99	.95	.79
9									.93	.61
10										.55

be indicative and should not form the sole basis for deciding selection age.

Application

In a typical application, the model can be used to assist the breeder in settling the following question: Has a juvenile progeny trial reached a stage where juvenile-mature correlations can be expected to be sufficiently strong to make juvenile selections more attractive than selections for the same trait at "maturity"? A 12-year-old progeny trial with open-pollinated jack pine (*Pinus banksiana* LAMB.) progenies tested on two sites ("A" and "S") shall serve as a representative example of model application. Details of this trial are published elsewhere (MAGNUSSEN and YEATMAN, 1986). Tree height (measured at ages 8 (HT_8) and 12 (HT_{12})) is the trait considered for improvement. The following results were obtained (symbols as defined in the Model Derivation section).

Site	HT_8	HT_{12}	$CV_8\%$	$CV_{12}\%$	$VR_{8:12}$	$r_{8:12}$	$\bar{d}_{8:12}$
"A"	3.8 m	6.0 m	12.7	10.3	1.72	0.764	0.02
"S"	4.1 m	7.0 m	11.7	9.5	1.96	0.798	0.76

Site "S" had better height growth, was relatively less variable, and showed a stronger age 8 to age 12 correlation than site "A". Consequently, height growth between ages 8 and 12 on site "A" can be characterized as an almost completely random process ($\bar{d} \cong 0$), whereas the growth fraction determined by size was above 70% on site "S". Maturity of the trait (height) is assumed to be 25 m. Trees on site "A" are expected to reach this height at age 50 whereas the trees on site "S" are expected to reach the same height at age 40. In order to obtain estimates of the ratio of the variance at maturity to the variance at age 12, low and high "guesses" were obtained by raising the ratios of the mature heights to the heights at age 12 (selection age) to the power of 1.5*) and 2.0*), respectively. (Alternative assumptions about a constant $CV\%$, for example, appear equally reasonable (BRAND and MAGNUSSEN, 1988)). For site "A" these ratios were 8.5 and 17.4, whereas the ratios for site "S" were 6.7 and 12.8. Using the above estimates of $\bar{d}_{8:12}$ and $CV_{12}\%$ the desired age 12-to-maturity correlations were derived from equations [6] and [8].

	"low" estimate		"high" estimate	
Site	$VR_{12:maturity}$	$r_{12:mat.}$	$VR_{12:maturity}$	$r_{12:mat.}$
"A"	8.4	.35	17.4	.24
"S"	8.8	.51	18.2	.41

In turn, these correlations were used to calculate the expected response in tree height at maturity (m), given juvenile (j) selections at age 12. Assuming constant heritabilities (h^2) over age, the expected response (R) can be expressed as $R_{m|j} = i \cdot h^2 \cdot \sigma_p \cdot r_{j:m}$ (FALCONER, 1981) where i denotes the selection intensity, σ_p the phenotypic standard deviation of the trait at maturity, and $r_{j:m}$ the juvenile-mature correlation of the trait (the theoretical correct genetic correlation has been replaced here by the more conservative phenotypic correlation). The direct selection response at maturity is $R_m = i \cdot h^2 \cdot \sigma_p$. For juvenile selection to be more efficient than mature selection we must require that

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*) Powers obtained empirically from analysis of several data sets.

the genetic gain per unit time is higher than the rate of improvement arising from selections at maturity, i.e. that

$$r_{j:m} > \frac{T_j + \delta}{T_m + \delta}$$

where T stands for time in years (subscripts refer to selection age), and δ is a delay factor between selection and actual seed production. Using the above values of T_j (12), T_m (40, 50), and letting $\delta = 5$ years, we obtain a minimum value of 0.31 for the juvenile-mature correlation on site "A" and a minimum value of 0.38 for site "S". From the expected $r_{j:m}$ values we tentatively conclude that age 12 selections appears to be favourable to mature selection at site "S" but questionable at site "A". A two to three year postponement of selections at the latter site appears the most reasonable recommendation.

Discussion and Conclusions

The proposed model, for predicting age-to-age correlations via variance ratios and a factor of relative size-dependent growth, is the simplest possible. Three important assumptions were needed to reach a simple model. First, a constant maximum periodic intrinsic growth rate $k\triangle_t$ common to all individuals in a population contradicts findings of competition-influenced functional relationships between tree size and relative growth rate (BENJAMIN and HARDWICK, 1986; FORD, 1975; HARA, 1984; WEINER and TOMAS, 1986). However, for the stated purpose of the model these relationships are too complex and specific in nature to be cast into a single prediction model. Often, predictions of age-to-age correlations will have to be based on data collected prior to the onset of competition. Without any data on how the future competition among trees will develop, it appears futile to develop a model which has a built-in relationship between $k\triangle_t$ and tree size save for the proposed constancy of $k\triangle_t$. Another important and questionable model assumption relates to the cov $(d\triangle_t, X_t) = 0$ restriction. Again, competition and size related disturbances will tend to invalidate this restriction. Further, violation of the first assumption will obscure the true nature of this covariance. It should be mentioned that improved model fit could be obtained in all the shown examples provided certain assumptions were made about this covariance. However, such assumptions can only be verified when data are available for which predictions are made. When predictions are based on past data, it becomes virtually impossible to ascertain the magnitude of cov $(d\triangle_t, X_t)$. The assumption cov $(d\triangle_t, X_t) = 0$, therefore, is reasonable within the framework of the model. Given the hypothetical nature of the size dependent growth factor $d\triangle_t$, assumptions concerning its variance were needed. The assumption $\sigma^2 d_{\triangle_t} = d^2\triangle_t$ was chosen somewhat arbitrarily. However, the advantage of the chosen form is the consistency of the model output with known results of $r\triangle_t$, when $\bar{d}\triangle_t$ is either one or zero.

Relating correlations to the associated variances and to the amount of fixed growth provides an integrated framework for interpretations and comparison of results. Traditionally, correlations have been displayed as a function of time (LAMBETH, 1980). However, with the known effects of growth rates, spacing, and competition on variances (YODA et al., 1957), it becomes clear that time itself is a poor scale for comparing and predicting correlations (BENJAMIN and HARDWICK, 1986; CAMPBELL et al., 1986; FORD, 1975; HARA, 1984; YODA et al., 1957). In fact, LAMBETH's time dependent

model proved less satisfactory than the proposed variance ratio-model. Realistic predictions (within 5% of the sample estimate) with the presented model depends obviously on a stable fraction of size-dependent growth. It is, of course, not possible to judge from two measurements whether the fraction $\bar{d}\triangle_t$ has stabilized or not. Stand development and dynamics exert an influence on $\bar{d}\triangle_t$. Wide spacings and growth disturbances clearly delay the stabilizing of $\bar{d}\triangle_t$. Information from three or four juvenile measurements may make it possible to infer about the stability of $\bar{d}\triangle_t$ and, hence, the prospect of accurate predictions.

For variances increasing monotonically over time, computing the variance ratio is straightforward. In other situations an integral solution is needed. Examples of variances that fluctuated with age have been used to formulate a theory of distinct ontogenetic growth phases, with phase transitions and low age-to-age correlations occurring during periods with diminishing variances (FRANKLIN, 1979; NAMKOONG et al., 1972). Situations like that are by no means rare, but they are considered aberrations to more general and lasting trends of variances to increase with tree size (BRAND and MAGNUSSEN, 1988; DANIELS, 1976, FORD, 1975; HAMILTON, 1969; MARTIN and EK, 1984; WEINER and THOMAS, 1986). Sudden declines in the variance of an increasing variable may simply be biological artifacts caused by diverse factors such as mortality, competition, experimental design, or even sampling errors. The latter factor, combined with the extreme sensitivity of the correlation coefficient to outliers (DEVLIN et al., 1975), is believed to be a major cause of irregularities in published correlation matrices. Performance of the model was illustrated by comparing observed and predicted correlations. Strictly numerical considerations seem to indicate that the model should be used only when the fraction of deterministic growth has become stable. On the other hand, given the lack of any alternative prediction model of single tree**) juvenile-mature correlations, the proposed model may serve as a first interim approximation until more appropriate models become available. Such approximations are often needed in practice where detailed information is lacking. Used with prudence, the presented framework for predicting age-to-age correlation could benefit the breeder in decisions about selection age. To protect against ineffective (premature) juvenile selections, a minimum age-to-age correlation standard based on actual juvenile correlation has been developed by MAGNUSSEN (1988). This minimum standard, combined with predictions based on the model presented herein, may assist in optimizing the rate of genetic improvement in trees.

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**) LAMBETH's model (LAMBETH, 1980) predicts correlations at the family/provenance level.

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Demographic Processes in Pinus sylvestris Populations from Regions under strong and weak Anthropogenous Pressure

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Summary

In two naturally regenerating populations of Pinus sylvestris, one under strong influence of pollution from smelting work and the second from an area under relatively weak anthropogenous pressure the isoenzyme variability in the age groups was studied. Some of the alleles and genotypes showed directional changes of frequencies in the studied age groups. This phenomenon may point to selection processes taking place in the studied populations. In the case of the population subjected to industrial pollution the changes of genetic structure are more intense in the groups of embryos and young individuals. In the population from an area without pollution changes in the genetic structure in the older groups of trees are observed. Adaptation strategy of the studied populations is connected with the increased level of genetic variability.

Zusammenfassung

Die Variabilität von Isoenzymen in verschiedenen Altersgruppen von zwei Pinus sylvestris Populationen wurde untersucht. Eine Population ist im oberschlesischen Industriegebiet in unterschiedlichem Maße Luftverunreinigungen, die andere ist neben Poznan, ausgesetzt. Eine der beiden Populationen wurde stark, die andere nur gering durch Immissionen belastet.

Es wurden Allele und Genotypen gefunden, die eine gesicherte Selektion in Altersgruppen anzeigen. Sie scheint in schwer belasteten Populationen mehr an frühe Entwicklungsstadien (Embryos und junge Pflanzen) gebunden zu sein. In Populationen geringer Immissionsbelastun-