Theor Appl Genet (1992) 85:152–158

THEORETICAL AND APPLIED GENETICS

Predictions of age-age correlations of total height based on serial correlations between height increments in Maritime pine (*Pinus pinaster* Ait.)

A. Kremer

Laboratoire de Génétique et d'Amélioration des Arbres Forestiers,
Laboratory of Genetics and Forest Tree Improvement, INRA, B.P. 45, 33611 Cestas Cedex, France

Received March 27, 1992; Accepted May 7, 1992
Communicated by P. M. A. Tigerstedt

Summary. Successive annual height increments (AHIs) are considered to be elements of a time series. Empirical data in Maritime pine (*Pinus pinaster* Ait.) show that genetic correlations between successive AHIs (serial correlation) decrease when the lag between corresponding growing seasons increases. When separated by more than 13 years AHIs are no longer genetically correlated. It is shown that age-age correlations between total heights depend on three components: the serial correlation structure between AHIs, the genetic coefficient of variation of AHIs, and the phenotypic growth curve of AHIs. Age-age correlations are computed in various combinations of the three components. Serial correlation structure and the genetic coefficient of variation had the more pronounced effect on age-age correlations. The genetic correlation between height at age 10 and height at age 50 varies between 0.764 and −0.136 according to the different combinations. Results obtained by simulations are comparable to those issued from previous empirical methods. Implications on early selection procedures and on optimal selection age are discussed.

Key words: Juvenile-mature correlation – Serial correlations – Early selection – Growth model – *Pinus pinaster* (Ait.)

Introduction

The phenotypic expresion of any given trait of a perennial plant can take different forms in response to time: discrete, repetitive, or cumulative. Height of a tree is a typical cumulative trait, since successive annual height increments (AHIs) add up to obtain the final height. The genetic value for size of a given genotype is the result of gene action during all previous seasons. From a biological point of view, an analysis of growth should therefore address the elementary unit, which is the annual height increment.

Silviculturists and tree breeders, however, are focusing their attention on total height, and not on single increments. In breeding programs and silviculture, volume production is an important goal. Among the two components of stem volume, total height is less sensitive to environmental conditions than diameter and has therefore been used as a selection criterion for volume growth. The objective of this paper is to build a model of genetic age-age correlation of total height based on information originating from single AHIs, reconciling, as a consequence, both approaches.

Empirical models of age-age correlations have already been established (Lambeth 1980); these remarkably constant results across species have been confirmed in later studies (Foster 1986; McKeand 1988). A further step has consisted of separating the two components of the correlation of height between age t′ and t: variance of height at age t and covariance between height at age t′ and increment between t′ and t (Lambeth et al. 1983; Kang 1991). The approach here subdivides total height into all its annual components. Age-age correlations are then expressed as a function of variances and covariances of and between all single AHIs. Their calculation requires the following information: (1) correlation between successive AHIs or serial correlations; (2) evolution of the genetic coefficient of variation of AHI as a function of age; (3) phenotypic values of AHIs derived from growth curves. In addition to the computation of age-age correlations this approach provides specific insights into the genetic architecture of height growth.

Description of the model

Total height of trees is a cumulative trait, the result of successive annual height increments. If Y_t is the total height at age t, then

$$Y_t = X_1 + X_2 + X_3 + \ldots + X_t \tag{1}$$

where X_t is the annual height increment during growing season t.

Consequently, the genetic correlation between two different total heights at age t and t′ depends strictly on the correlation between the different annual increments that compose Y_t and $Y_{t'}$. The model that will be developed is exclusively based on correlations between annual height increments. It comprises three different components.

1) The serial genetic correlation structure, i.e., the variation of $r(X_t, X_{t'})$ as a function of age (t) and of lag between both increments $(t-t')$. $r(X_t, X_{t'})$ is the genetic (additive) correlation between annual height increments at age t and t′.
2) The variation of the genetic coefficient of variation of the annual height increments $(CV(X_t))$ with age t.

$$CV(X_t) = (V_{At})^{1/2} / \bar{X}_t \,. \tag{2}$$

V_{At} is the genetic (additive) variance of the annual height increment at age t. $\bar{X}_t$ is the phenotypic mean value of the annual height increment at age t.
3) A phenotypic growth model providing the evolution of $\bar{X}_t$ as a function of t.

For construction of the model we will assume that the values of the three components are known. The covariance between genetic values of height increment t and t′ can then be written as:

$$\mathrm{Cov}(X_t, X_{t'}) = \bar{X}_t \bar{X}_{t'} \, CV(X_t) \, CV(X_{t'}) \, r(X_t, X_{t'}) \,. \tag{3}$$

As a result the covariance between total heights at different ages t and t′ $(t' < t)$ is:

$$\begin{aligned} \mathrm{Cov}(Y_t, Y_{t'}) = {} & \sum_{i=1}^{t'} V(X_i) + \sum_{i=1}^{t'} \sum_{\substack{j=1 \\ i \neq j}}^{t'} \mathrm{Cov}(X_i, X_j) \\ & + \sum_{i=1}^{t'} \sum_{j=t'+1}^{t} \mathrm{Cov}(X_i, X_j) \,. \end{aligned} \tag{4}$$

The matrix of genetic correlation between any pair of total heights can now be calculated from the matrix of covariances given by (4).

Observed data of serial correlation and coefficient of genetic variation in Maritime pine

Material

A progeny trial comprising 100 open-pollinated families was used to obtain data on annual height increments. The test was established in the fall of 1965. Plantation rows were separated by 3 m, and individual trees were separated in the rows by 1.1 meters. The experimental design was a triple lattice 10*10 repeated 3 times. Each plot comprised 10 trees and was established in two adjacent plantation rows (5 trees/row). A systematic thinning was done in 1976 eliminating every second tree in each row of the plantation. A second systematic thinning was done in 1987, in which trees in every second row were all cut. The number of trees per plot that were cut during the second thinning varied between 2 to 3 depending on the number of trees left after the first thinning. Trees cut during the second thinning were used to assess all annual height increments from the 3rd to the 22nd growing season.

These increments were measured retrospectively on felled trees from the 22nd to the 6th growing seasons. The whorls of branches were used as morphological markers of the different annual shoots. Intermediate total heights measured during the fall of 1976 (12th growing season) were available and used as reference marks for retrospective measurements of the different annual height increments. Heights at the end of the 2nd, 3rd, 4th, and 5th growing seasons were available from contemporary measurements and used to derive height increments.

Data analysis

The experimental design was interpreted as a complete block design comprising nine blocks. A multivariate two-way analysis of variance (family and block effects) was run to obtain the genetic variances and covariances between the different AHIs. Sibs within the open-pollinated families were assumed to be half-sibs. Genetic correlations between the different AHIs and the genetic variation coefficient were estimated from family variances obtained by the analysis of variance:

$$r(X_t, X_{t'}) = \mathrm{Cov}_F(X_t, X_{t'}) / (V_F(X_t) \, V_F(X_{t'}))^{1/2}$$
$$CV(X_t) = (4 * V_F(X_t))^{1/2} / \bar{X}_t \,.$$

$\mathrm{Cov}_F(X_t, X_{t'})$ is the covariance between family values of AHI at age t and t′; $V_F(X_t)$ is the variance of the family values of AHI t. These variances and covariances were estimated in a non-orthogonal multivariate ANOVA (general least square method, model Henderson 3; Searle 1971). $\bar{X}_t$ is the overall mean value of AHI_t in the progeny test.

Results

Serial correlation. The genetic correlation coefficients between annual increments were calculated between all combination of t and t′ from the 3rd to the 22nd growing season. Mean values of the correlation coefficients were

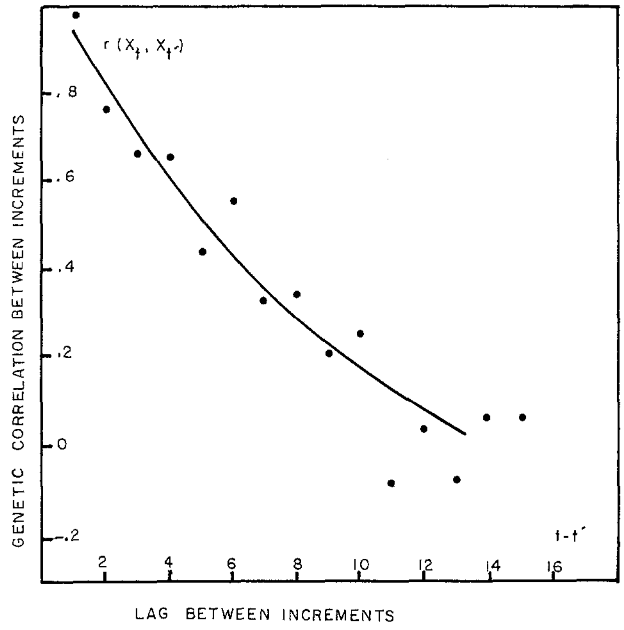

Fig. 1. Genetic correlation values between successive AHIs as a function of the lag separating them (from lag 1 to 15). *Dots* represent observed mean values: for lag 1 the dot represents 19 values; for lag 15, only 4 values. Observed values were fit to a polynomial function (see text)

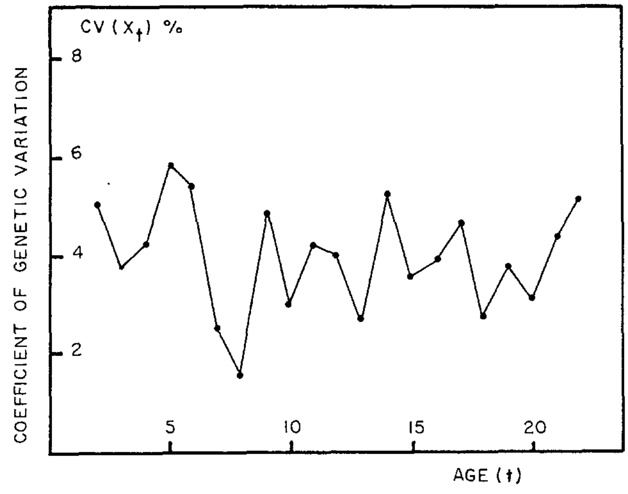

Fig. 2. Evolution of the genetic (additive) coefficient of variation of successive AHIs

then computed for the different lag values between increments, i.e., from $t-t'=1$ to $t-t'=15$. For lag 1, 19 different combinations were available; the number of combinations decreased to 4 for lag 15. The mean values obtained are plotted versus lag in Fig. 1. Genetic correlation values can be seen to decrease constantly with lag, from 0.98 for lag 1 to 0.03 for lag 12. For larger intervals between increments, the coefficients stabilized near zero. Annual increments separated by more than 13 years are no longer genetically correlated.

Genetic coefficient of variation of annual height increments. The genetic coefficients of variation of annual height increments do not follow a particular trend of variations with age (Fig. 2). The mean value over the 20 annual observations was 3.99%; extreme values were 1.8% and 6%, and these extreme values both occurred before age 8.

Predictions of age-age correlation for total height

Case study

A series of specific situations corresponding to various combinations of serial correlation structures, growth curves, and evolution of additive variance are tested. The main emphasis is put on the calculation of genetic correlations between total height at age t and total height at rotation age (50).

Serial correlation structure. Three cases are considered. In each one we will assume that the value of the genetic correlation between different annual height increments depends only on the lag separating the two respective growing seasons: $r(X_t, X_{t'})$ is independent of t, but depends only on $(t-t')$.

Case 1 corresponds to the structure observed in the data set of the progeny test (Fig. 1) and is applied during the whole rotation age. Genetic correlations between AHIs separated by more than 16 years are assumed to be zero.

$$r(X_t, X_{t'}) = 0.0039^* (t-t')^2 - 0.132^* (t-t') + 1.079 .$$

Case 2 is identical to case 1 during the first 16 years; serial correlations are assumed to be zero during the next 18 years, and then decrease during the rest of the rotation symmetrically to the first period of 16 years (Fig. 3). This case refers to the situation where genotypes have a contrasting growth pattern between the young and adult stage. Rapid growers during the first 16 years would systematically tend to be the poorest growers during their last 16 years.

Case 3 is a hypothetical pessimistic situation (Fig. 3) relative to the observed data set. Genetic correlation between annual height increments reach negative values according to the following model:

$$r(X_t, X_{t'}) = 0.00056^* (t-t')^2 - 0.056^* (t-t') + 0.7 .$$

Evolution of additive variance. Three different cases are considered:

- coefficient of genetic variation constant (0.04);
- coefficient of genetic variation linearly increasing over the whole rotation from 0.02 to 0.06;

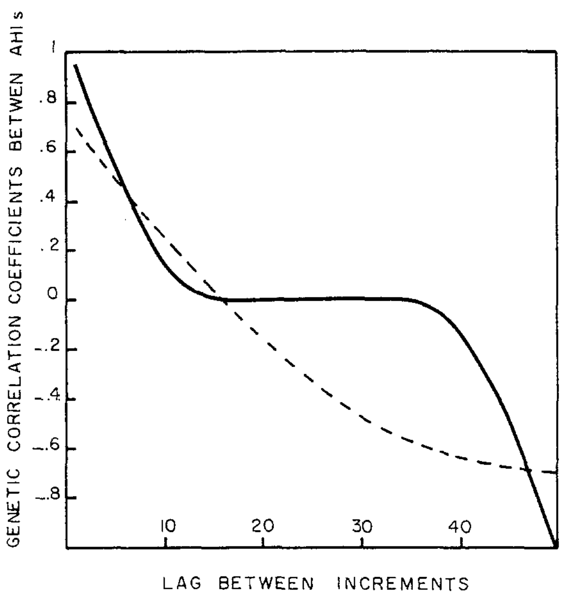

Fig. 3. Theoretical serial genetic correlations between successive AHIs. —— case 2, identical to case 1 during the first 16 years, ---- case 3

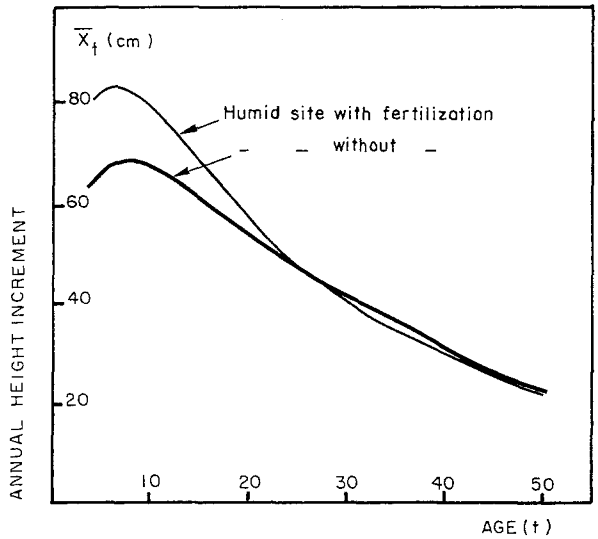

Fig. 4. Phenotypic annual height increments derived from growth models (Lemoine, 1981, 1991)

- coefficient of genetic variation linearly decreasing over the whole rotation from 0.06 to 0.02;

Phenotypic growth model. A growth model developed by Lemoine (1981, 1991) was used and applied to two different ecological and silvicultural situations: (1) humid sandy moor with fertilization and (2) humid sandy moor without fertilization (Fig. 4). These two cases are representative of the growing conditions of Maritime pine in the Landes area in the southwest of France.

Results of predictions (Fig. 5)

Genetic correlation between total height at any age and height at rotation age remains positive in most cases, as illustrated on Fig. 5. Age-age correlations are negative only when the additive variance decreases with age and when the serial correlations attain negative values rapidly (Fig. 5d–f). Even in these extreme situations, positive values appear after age 15 (Fig. 5f). The general form of the curves is convex; as a result, except in the three aforementioned cases, the values of correlations are higher than those given by the linear relation between age-age correlations and age. For example, correlations between age 10 and 50 are always higher than 0.20. Age-age correlations reach their asymptotic value after age 22 in the most optimistic situation (Fig. 5a) and after age 42 in the most pessimistic case (Fig. 5f).

Among the three causes of variation, serial correlation structure and evolution of additive variance have the more pronounced effects on age-age correlations.

Variation due to the serial correlation structure. Important differences in age-age correlations can be observed depending on the different serial correlation structures used in the simulations. The range of variation depends on the level of additive variance and the phenotypic growth model. In the most optimistic situation, corresponding to the combination of decreasing genetic variance with age and favorable environment (Fig. 5a), correlations between age 10 and age 50 vary between 0.616 and 0.764. On the contrary, in the most pessimistic situation (Fig. 5f), corresponding values range between −0.339 and 0.446.

The differences in age-age- correlations between case 1 and 2 of the serial correlation structure are rather minor, whatever the value of the other parameters. Negative correlations between increments during the extreme early and late growth phases (case 2, Fig. 3) reduce only slightly the age-age correlations compared to the situation where correlations between extreme phases are zero (case 1). In general, differences are more important between the two first cases (Fig. 1, case 2 in Fig. 3) and the third case (case 3, Fig. 3) of the serial correlation structure.

Variation due to the evolution of additive variance. Age-age correlations rapidly reach high values when genetic variance is decreasing with age. The correlation between height at age 10 and 50 is 0.764 when the serial correlation structure corresponds to our data set (case 1) and is on the fertilized site (Fig. 5a). Corresponding values in similar situations are 0.672 when the additive variance remains constant (Fig. 5c) and 0.501 when the additive variance increases with age (Fig. 5e). Differences are more important when serial correlations become negative rapidly (case 3, Fig. 3): values of correlations between

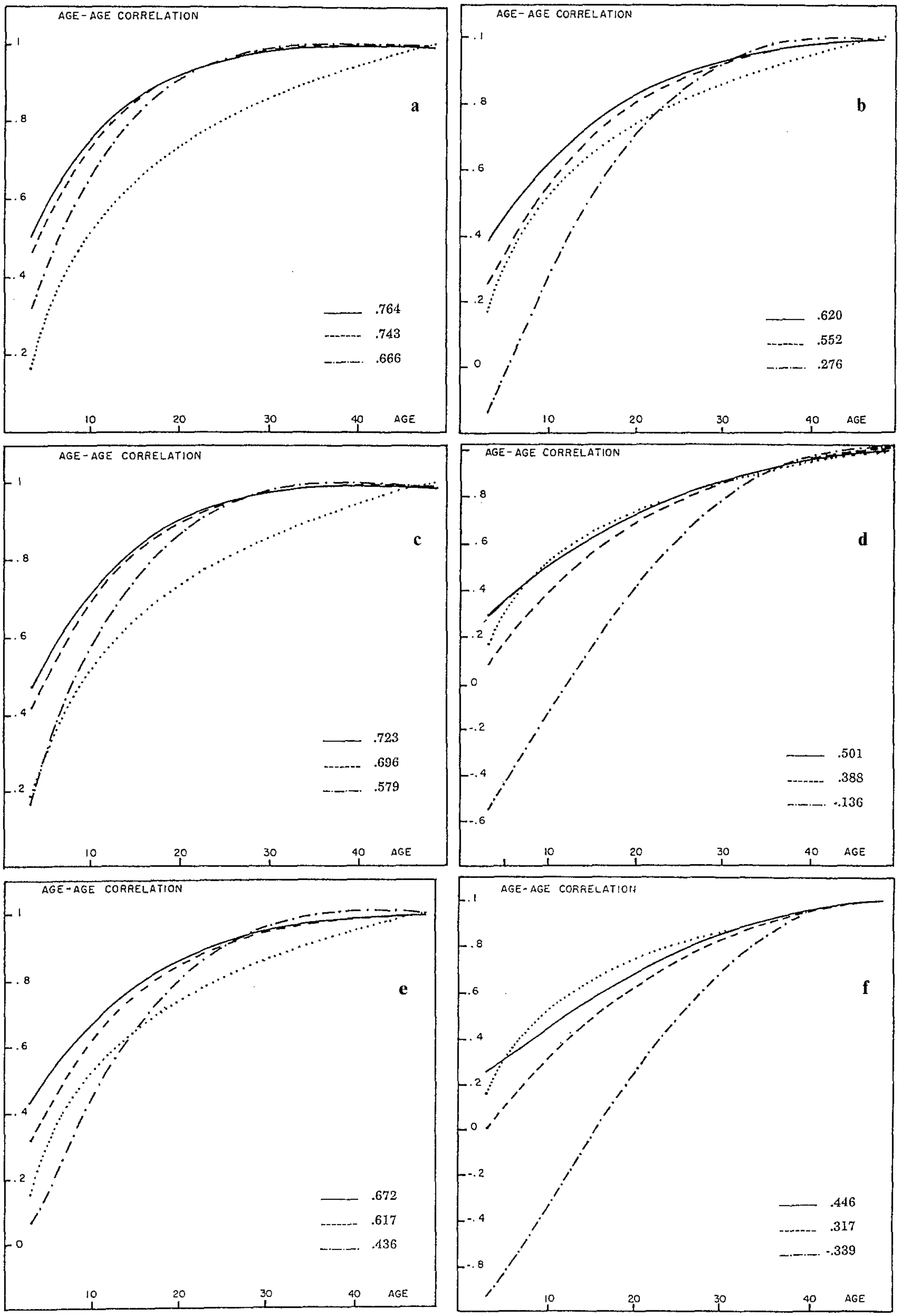

Fig. 5a–f. Genetic correlations between total height at current age and total height at rotation age. **a**, **c** and **e** Humid site with fertilization; **b**, **d** and **f** humid site without fertilization; **a** and **b** genetic variation decreasing with age; **c** and **d** genetic variation constant; **e** and **f** genetic variation increasing with age. —— Serial correlation (case 1, see Fig. 1), ---- serial correlation (case 2, see Fig. 3), –·–·– serial correlation (case 3, see Fig. 3), ···· Lambeth's empirical law. *Numbers* in each graph represent genetic correlations between height at age 10 and height at rotation age (50)

height at age 10 and 50 are respectively 0.666, 0.436, and −0.136 when the additive variance is successively decreasing, constant, and increasing with age (Fig. 5a, c, e).

Variation due to the phenotypic growth model. Age-age correlations are systematically higher in the more favorable environment, although the differences remain small (compare between Fig. 5a, c, e with Fig. 5b, d, f, respectively). This is due to the higher yearly growth increment during the first 20 years in the fertilized sandy moor (Fig. 4). If juvenile growth is improved by silvicultural means and other factors do not vary (serial correlation structure and genetic control), age-age correlations will tend to be increased.

Comparison with Lambeth's empirical law. Age-age correlations derived from Lambeth's empirical law (Lambeth 1980) generally reach their asymptotic values less rapidly than our curves. The former tend to be lower when the additive variance is decreasing with age (Fig. 5a, b), higher when the additive variance is increasing with age (Fig. 5e, f), and intermediate to ours when the additive variance is constant with age (Fig. 5c, d).

Discussion

Serial correlation structure

Genetic correlation between successive annual height increments decrease with the lag separating the increments, reaching zero after 13 years. A similar pattern has been observed at the phenotypic level (Lemoine 1981). It has been suggested that positive genetic correlations between height growth in successive seasons are due to pleiotropy rather than linkage (Atchley 1984). A given set of genes affects growth and is progressively modified with time; after each season a portion of the set is replaced. As a result, after 13 years in the case of maritime pine, the original set has been totally modified. The results we obtained may be interpreted by this scenario.

No negative genetic correlations between annual height increments were observed during 16 successive years, indicating the absence of compensatory growth (Atchley 1984). Therefore, a strong inertia in the growth process exists in pines compared to other organisms. Riska et al. (1984) found no significant relationship between successive weekly weight gains in mice. Compensatory growth may exist, but only between growth separated by more than 16 years. The present study lacks the data to evaluate compensatory growth between extreme phases of the growth curve as has been observed in other organisms (Riska et al. 1984). However, results at the phenotypic level show that serial correlations remain positive in maritime pine even in the extreme case when the lag extends the whole rotation period (Lemoine 1981).

Evolution of the additive variance

Additive variance of AHI did not exhibit any particular time trend when expressed as a coefficient of variation. Over the first 22 seasons, the variation observed was rather random. While numerous references exist on time trends on genetic parameters on total height (Kremer 1981; Foster 1986; Cotterill and Dean 1988; Kremer and Lascoux 1988), observations on increments are scarce. In most of these studies time trends were analyzed during the early phase of growth until age 20. The results were consistent and showed a constant increase in additive variance and heritability of total height. This would be expected if the coefficients of variation of additive effects of single AHIs remain constant over successive years.

Results over a longer period of time (Namkong et al. 1972; Namkong and Conkle 1976) were summarized by Franklin (1979). Time trends were interpreted to be consequences of stand development. On four different species (*Pinus ponderosa*, *Pseudotsuga menziesii*, *Pinus taeda*, and *Pinus elliottii*) heritability values and additive variance of total height remained low during the early phase of a stand when no competition existed between the trees. They then constantly increased while the trees developed and competition for light occurred between the crowns. Later on during the last phase, the growth curves of the different genotypes reached their asymptotic value and heritability values decreased as a result of compensatory growth. In Franklin's interpretation the decrease in heritability values is due to the decrease in additive effects rather than to the increase in the phenotypic variance. As a result one would expect that, on an annual increment level, the additive genetic variance diminishes during the end phase of the stand.

Selection for height growth

The model that was developed can be used as a guideline for identifying selection age in tree breeding programs. The results show that genetic correlations between heights assessed after age 15 and height at rotation age are always positive. However, in most of the cases considered, the values were already high when assessments were made at age 10, which corresponds to the routine assessment deadline in Maritime pine (Baradat and Pastuzka 1990). Previous determinations of optimum selection ages were based on empirical results. Values varied between 6 and 8 years in rapidly growing pines [McKeand (1988) for *Pinus taeda*; Cotterill and Dean (1988) for *Pinus radiata*]. For species cultivated over a 40-year rotation the optimum selection age was found to be 8 years (Lambeth 1980).

Age-age correlations derived by the proposed model support earlier results based on empirical methods (Lambeth 1980). In addition, because the model identifies three important components contributing to the age-age correlations, further improvements in early selection procedures can be suggested. It is shown that age-age correlations are mostly dependent on the serial correlation structure and on the evolution of additive variance with age. The phenotypic growth model has only a slight impact. However, the effect of the serial correlation structure can be efficiently reduced when experiments are conducted under optimal conditions (fertilized sites) and when the additive variance is decreasing with age. Our results therefore suggest the establishment of progeny tests in favorable environmental conditions and with sophisticated experimental designs where high heritability values can be obtained.

Although particular attention was addressed to genetic correlations between height at any age and height at rotation age, the model can also be applied for predicting correlations between heights at any two stages. Extension of the model could be derived to include genotype-environment interaction. The introduction of G* E effects could be accomplished by computing serial correlations between couples of environment as developed by Yamada (1962) and Burdon (1976). As a result correlation could be computed between height at age a in environment e with height at age a′ in environment e′.

References

Atchley WR (1984) Ontogeny, timing of development, and genetic variance-covariance structure. Am Nat 123:519–540

Baradat Ph, Pastuzka P (1990) Stratégie d'amélioration et diversification variétale du pin maritime. In: Actes du 3ème Colloque Sciences et Industries du Bois, Arbora, Editions Bergeret, Bordeaux, France, pp 375–390

Burdon RD (1977) Genetic correlation as a concept for studying genotype*environment interaction in forest tree breeding. Silvae Genet 26:168–175

Cotterill PP, Dean CA (1988) Changes in the genetic control of growth of radiata pine to 16 years and efficiencies of early selection. Silvae Genet 37:138–146

Foster GS (1986) Trends in genetic parameters with stand development and their influence on early selection for volume growth in Loblolly pine. For Sci 32:944–959

Franklin EC (1979) Model relating levels of genetic variance to stand development of four North American conifers. Silvae Genet 28:207–212

Kang H (1991) Components of juvenile-mature correlations in forest trees. Theor Appl Genet 81:173–184

Kremer A (1981) Déterminisme génétique de la croissance en hauteur du Pin maritime (*Pinus pinaster* Ait.). 3. Evolution des composantes de la variance phénotypique et génotypicque. Ann Sci For 38:355–375

Kremer A, Lascoux DM (1988) Genetic architecture of height growth in Maritime pine (*Pinus pinaster* Ait.). Silvae Genet 37:1–8

Lambeth CC (1980) Juvenile-mature correlations in Pinaceae and implications for early selection. For Sci 26:571–580

Lambeth CC, Van Buijtenen JP, Duke SD (1983) Early selection is effective in 20-year-old progeny tests in Loblolly pine. Silvae Genet 15:76–84

Lemoine B (1981) Application de l'analyse factorielle à l'étude de la croissance en hauteur des arbres: exemple du Pin maritime. Ann Sci For 38:31–54

Lemoine B (1991) Growth and yield of Maritime pine (*Pinus pinaster* Ait.): the average dominant tree of the stand. Ann Sci For 48:593–611

McKeand SE (1988) Optimum age for family selection for growth in genetic tests of Loblolly pine. For Sci 34:400–411

Namkoong G, Conkle MT (1976) Time trends in genetic control of height growth in Ponderosa pine. For Sci 22:2–12

Namkoong G, Usanis RA, Silen RR (1972) Age related variation in genetic control of height growth in Douglas-fir. Theor Appl Genet 42:151–159

Riska B, Atchley WR, Rutledge JJ (1984) A genetic analysis of targeted growth in mice. Genetics 107:79–101

Searle SR (1971) Linear models. John Wiley and Sons, New York

Yamada Y (1962) Genotype by environment interaction and genetic correlation of the same trait under different environments. Jpn J Genet 37:498–509