MORPHOGENETIC SUBDIVISION OF HEIGHT GROWTH AND EARLY SELECTION IN MARITIME PINE.

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Abstract As part of ongoing studies on early selection in maritime pine, we have summarized the major points so far analyzed namely (i) optimal age for selection with traditional technics (ii) identification of potential early selection criteria (iii) choice of juvenile testing environments. When total height is used as criteria, experimental results and simulations show that selection should be done later than 12 years. Subdivision of height into components shows that gene action may vary with components and that there is a high degree of genetic plasticity in height growth. As a result identification of a single component as selection criteria is doubtful. Explicative approaches show that raising first season seedlings in continuous days accelerates the maturation of the seedlings. This treatment exhibits genetic differences among different families that are associated with adult performances.

Keywords: *Pinus pinaster* Ait., height growth, early selection, morphogenetic components

INTRODUCTION

The maritime pine breeding program was started in the late fifties by the pioneer work of G.Illy (1966). Continued by Baradat (Baradat and Pastuzka, 1990), it has nowadays reached the third generation. The experience has shown that the generation duration is varying between 12 and 15 years. As data have accumulated on the older progeny tests, it has become clear that early evaluation is among the greatest challenge of the actual tree improvement program.

The present review attempts to summarize the research conducted in the field of early selection for height growth. Facts and results will be presented refering to the three major issues associated to early selection: (i) optimal age for selection based on traditional technics, (ii) identification of potential early selection criteria, (iii) choice of juvenile environmental conditions for testing.

The general strategy followed in this research program is the subdivision of height growth in different additive and multiplicative components. Besides the perspective of early selection, this approach has the advantage to afford basic information on the height growth process *per se.* The lack of this information is still a major drawback which has limited progress in physiological genetics of height growth in forest trees. Concerning early selection strictly, two specific features of the subdivision of height growth have been stressed: the cumulative and sequential nature of growth on the one hand and the genetic architecture of height growth on the other hand.

1.JUVENILE-MATURE CORRELATION: A CHALLENGE FOR MARITIME PINE BREEDING.

The data presented here report on the important effects of juvenile-mature correlation on tree improvement efficiency. They are based on age-age correlation estimated in one of the oldest open pollinated.progeny test established in the Landes **area**. The progeny test comprises 100 open pollinated of trees selected in natural stands of maritime pine during the late fifties. These parental trees originated from various natural stands and were older than 40 years and close to rotation age. Among the 100 families, 88 belong to 44 pairs of families choosen as follows (Illy, 1966):

* one member of a pair corresponds to the offspring of plus trees, selected on the basis of its relative superiority over the 30 nearest trees in the stand.

* the second member corresponds to the offspring harvested on the control tree among the nearest neighbours: the control tree has its total height closest to the overall mean of the neighbours.

Data available on the parental trees were the standardized value of total height (relative to the population of the 30 nearest neighbours). Successive total heights between age 2 and age 22 were measured on the offsprings in the progeny test. Figure 1 shows the evolution of the proportion of pairs in which the offspring of the plus tree were superior to the offspring of the control tree. At age 2 of the progeny test, this proportion was only 50%, which would be expected if there was no correlation between age 2 and the adult stage. This proportion constantly increased with age of the progeny test reaching 70% at age 22. Correlation coefficients between standardized values of total height of the parental trees and mean values of their offspring provide a similar picture of JM correlation (figure 2). These correlation coefficients can be considered as the best estimates actually available on genetic JM correlation. They include GE interactions, since the parental trees came from different forests. There is a definitive trend of increase with the age of the progeny test, starting from -.1 at age 2 and reaching .33 at age 22.

From these results, one may conclude that (i) phenotypic selection of adult trees for height growth was effective and that (ii) selection earlier than 12 years based on total heights may lead to genetic gain close to zero.

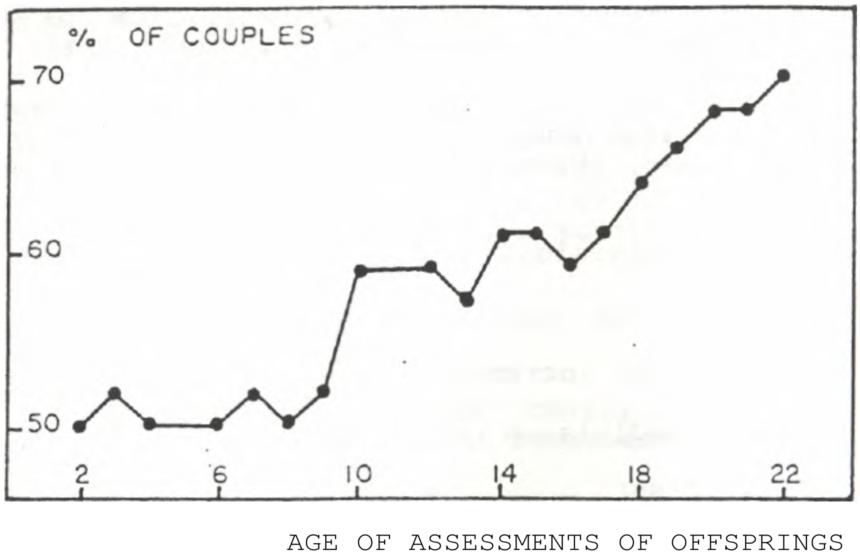


Figure 1. Percentage of pairs (plus and control tree) for which the offsprings of the plus trees are higher than the offsprings of the control tree. The progenies are measured every year from the second to the 22nd growing season.

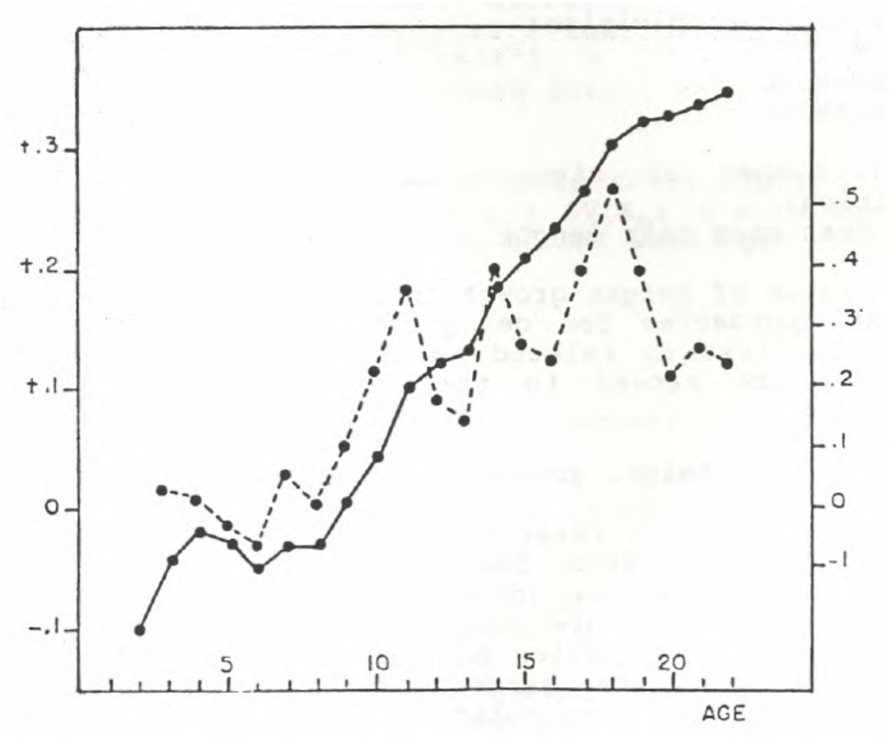


Figure 2. Evolution of the correlation coefficient between the parental standardized values at harvest age and the mean of total height or AHI) of the open pollinated families. Scale of correlation with TH is on the left y axis of the diagram, on the right y axis for AHI.

2. A STRATEGY FOR EARLY EVALUATION: SUBDIVISION OF TOTAL HEIGHT INTO MORPHOLOGICAL AND MORPHOGENETICAL COMPONENTS.

Total height (TH) of a tree is a cumulative trait that can be subdivided in various components from the total height up to the cellular level (Cannell, 1978; Kremer and Lascoux, 1988).

(1) First level of subdivision:

TH = AHI

AHI : Annual height increment

(2) Second level of subdivision

AHI = PSL + AESS*SSL

PSL : Primary shoot length, corresponding to the first morphogenetic cycle (for definition of a cycle see Debazac, 1963)
AESS: ability to express additionnal cycle (yes or no response)
SSL : length of shoots corresponding to additional cycles.

(3) Third level of subdivision:

SSL= NSU*MSUL

NSU : Number of stem units (see Doak, 1935 for definition)
MSUL: Mean stem unit length

The subdivision of height growth into components can lead to two different approaches for designing a strategy for early evaluation. The first is related to the cumulative nature of height growth, the second to the genetic architecture of height growth.

Cumulative nature of height **growth.**

There is a mechanistic relationship between components and the composite traits. This feature can be used in the definition of a strategy for identifying the optimal age for selection. For example, since components at a given age are part of total height at rotation age, how many components over how many years should be summed to provide an adequate prediction of total height at rotation age? We report here on the results obtained with this strategy applied at the first level of subdivision.

Genetic architecture of height growth.

By subdividing total height into components, one may ask if some components benefit of genetic parameters at a high level: heritability, contribution and genetic correlation with the composite trait. This approach may lead to identify potential early selection criteria. The estimation of these genetic parameters in the frame of the subdivision is called "genetic architecture of height growth".

3. CUMULATIVE NATURE OF HEIGHT GROWTH AND OPTIMAL AGE FOR SELECTION

3.1. A model of age-age correlations based on serial correlations of annual height increments.

Since height growth is a cumulative trait, it is obvious that the genetic correlation between two different total heights at age t and t' depends strictly on the correlation between the different annual height increments comprised in the total heights. The model that will be developed is based on the correlation between annual height increments. For simplicity of the formulas total height at age t (TH_t) is now written as Y_t and AHI_t as X. Three different informations are needed to construct the model.

(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, i.e. the variation of genetic control of AHI with age.

$$CV(X_t) = \frac{\sqrt{V_{At}}}{\overline{X}_t}$$

V_{At} is the genetic (additive) variance of the annual height increment at age t.

$\overline{X}_t$ is the phenotypic mean value of the annual height increment at age t.

(3) A phenotypic growth model of total height providing the evolution of X_t as a function of t.

The covariance between genetic values of annual height increment t and t' can then be written as :

$$Cov(X_t , X_{t'}) = \overline{X}_t \, \overline{X}_{t'} \, CV(X_t) \, CV(X_{t'}) \, r(X_t , X_{t'})$$

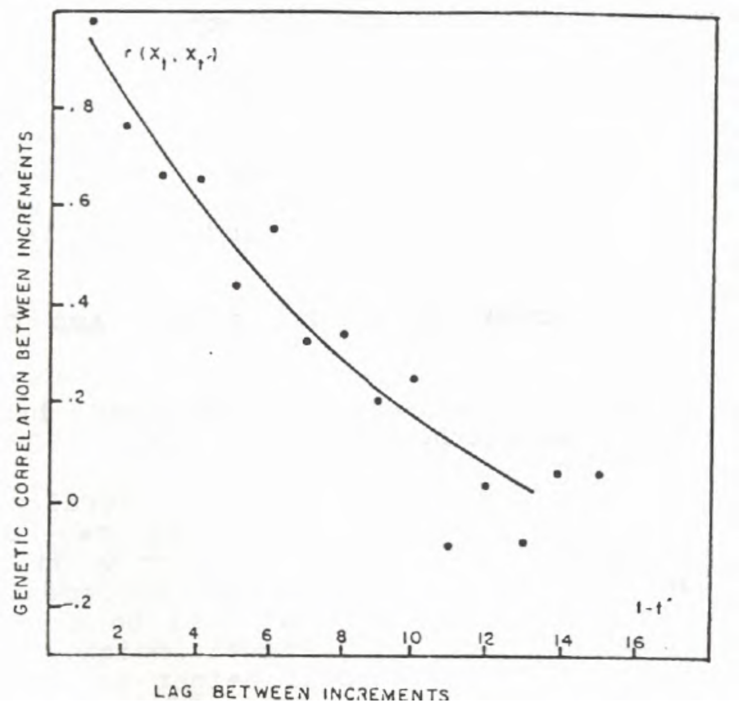


Figure 3a, Genetic correlation values between successive AHis as a function of the lag separating them (from lag 1 to lag 15). Dots represent observed points. The data come from the progeny test outlined in paragraph 1. For lag 1, the dot represents the mean of 20 values of coefficient of correlation between AHIs separated by only one year. For lag 15 a mean of only 6 values are available. The line drawn is fitted with polynomial function. This serial correlation structure is refered on figure 4a and 4b as casel.

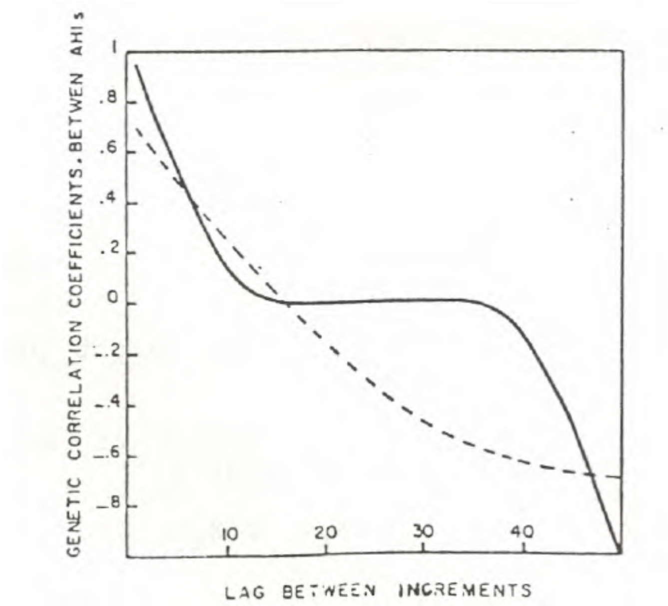


Figure 3b. Two examples of theoretical serial correlation structure tested in the age-age correlation model. (
case2; - • : case)

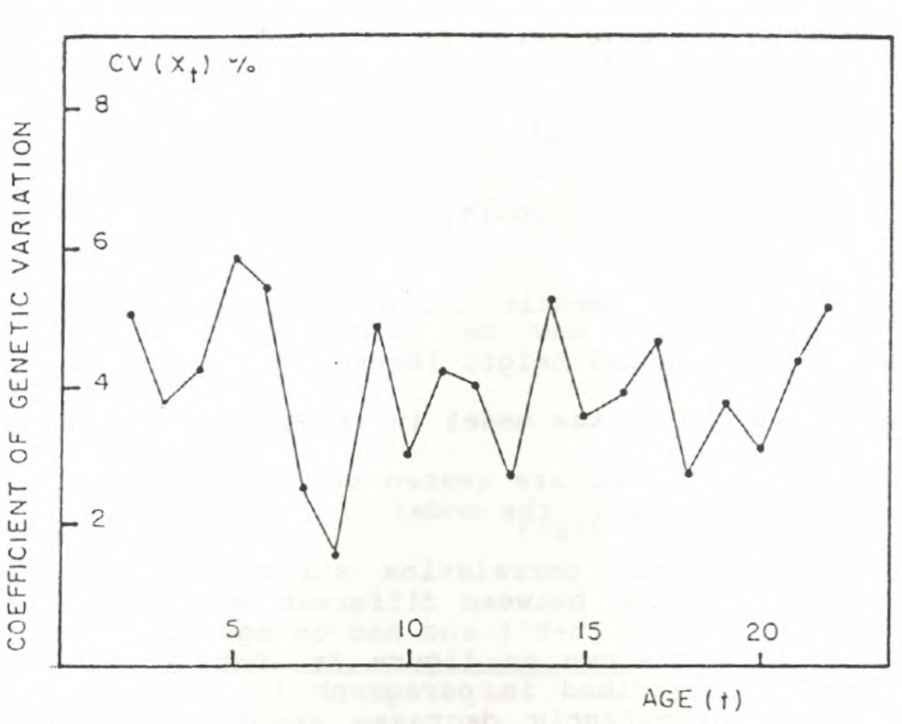


Figure 3c. Evolution of the genetic (additive) coefficient of variation of successive AHIs. Data come from the progeny test described in paragraph 1.

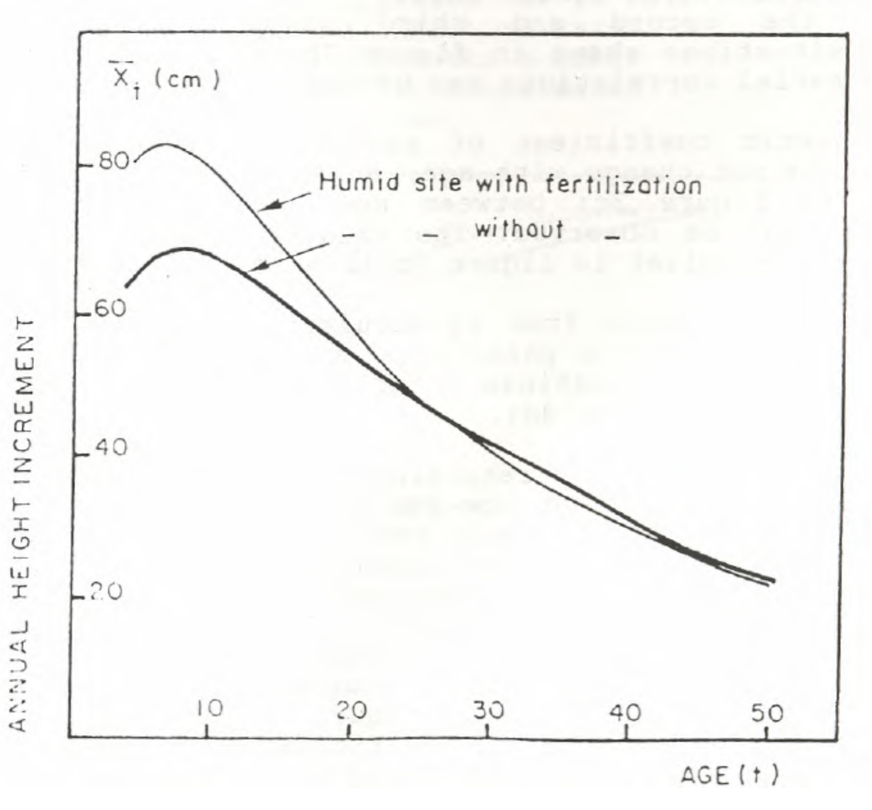


Figure 3d. Phenotypic height growth model in two different forest situations. Data **are** kindly provided *by* B. Lemoine.

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

$$\mathrm{Cov}(Y_t\ ,\ Y_{t'}) = \sum_{i=1}^{t'} V(X_i) + 2\sum_{i=1}^{t'}\sum_{j=1}^{t'} \mathrm{Cov}(X_i\ ,\ X_j) + \sum_{j=1}^{t'}\sum_{i=1}^{t} \mathrm{Cov}(X_i\ ,\ X_j)$$

The matrix of genetic correlation between any couple of total heights can now be calculated from the matrix of covariances of annual height increments.

3.2. Application of the model in various situations.

Various situations are tested according to different values of the three inputs in the model.

(1) Serial genetic correlation structure. We assumed that genetic correlations between different ages depend only on the lag separating them (t-t') and not on age (t). Observed serial correlations are shown on figure 3a. Data originate from the progeny test described in paragraph 1 . Genetic correlations between AHIs constantly decrease reaching 0 when then are separated by more than 13 years. Three situations are tested:

- serial correlations as observed in figure 3a. We further assume that when lag is superior to 13 years the correlations remain null.
- the second and third situations are theoretical situations shown in figure 3b. Compared to situation 1, serial correlations can become negative .

(2) Genetic coefficient of variation. We assume that their values do not change with age, as suggested by observed values shown on figure 3c: between age 2 and 22 no definite age pattern can be observed. The value of .04, corresponding to the average values in figure 3c is used in the model.

(3) Data available from sylviculturists (Lemoine, 1981) are used to construct a phenotypic growth model correponding to two contrasting situations : humid sandy moor with and without fertilization (figure 3d).

Curves of figure 4, resulting from calculations outlined in paragraph 2.1 show that age--age correlation based on the model of serial correlation are rather optimistic. Interestingly they follow the pattern of Lambeth's empirical law (Lambeth, 1980). Even in the case when AHIs are negatively correlated over large lags (situation 3 of serial correlation structure), the correlation of total height between age 10 and 50 varies between .20 and .6. However these values are higher than those represented in figure 2. Several reasons may explain the discrepancy: simplification of the assumptions in the model of age-age correlation, GE interaction...From figures 2 and 4, one may conclude that selection based on total height should be achieved when trees are older than 12 years.

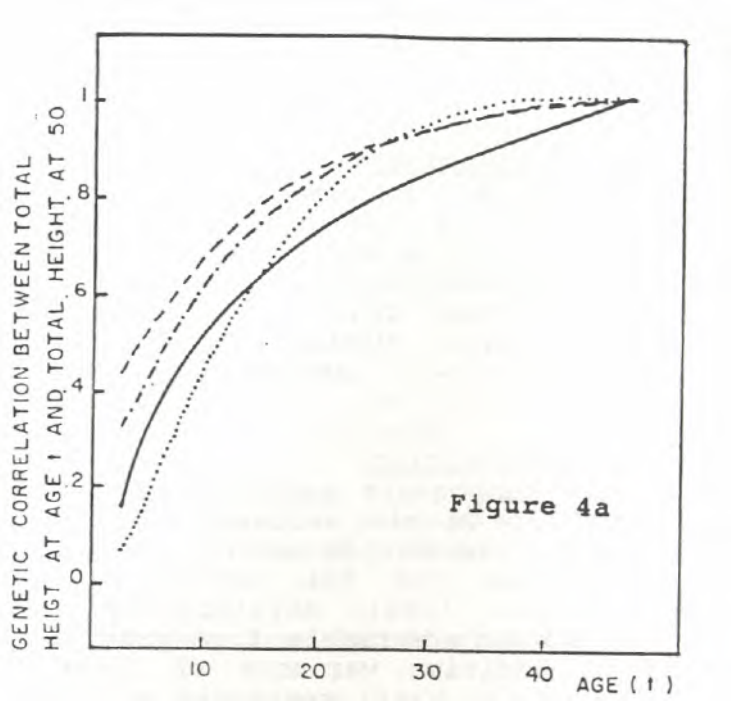
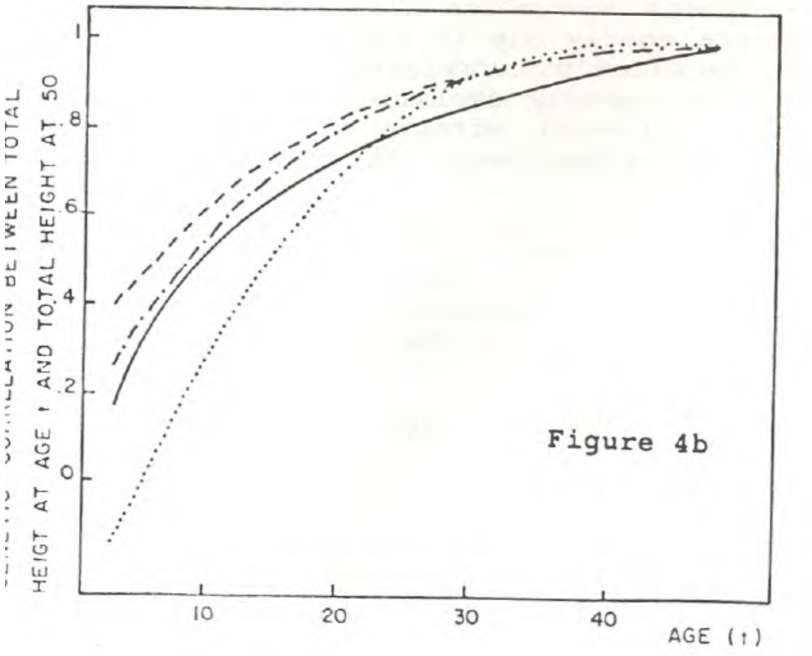


Figure 4 Simulated age-age genetic correlation between total height at age t and height at rotation age (age 50) . Calculations are made for humid sandy moor with (figure 4a) and without (figure 4b) fertilization. CV is held constant at .04.

- - - - : serial correlation structure case1
-·-·-·- : serial correlation structure case2
········ : serial correlation structure case3
——— : Lambeth's empirical law



3. GENETIC ARCHITECTURE OF HEIGHT GROWTH AND IDENTIFICATION OF SELECTION CRITERIA.

Genetic control

First level of subdivision.

Additive variance of single AHIs represents generally between 60 to 90 % of the total genotypic variance. Heritability values of sums of successive AHIs increase with the number of increments reaching between .3 to .5 when several AHIs are summed. This variation is due to the decrease of the environmental variance (relative to the total phenotypic variance) when several succesive AHIs are added (Kremer, 1981b).

Second level of subdivision

Among all the components assessed PSL exhibits the highest heritability value. On six successive AHIs, the heritability values of AHI varied between .06 and .12, whereas corresponding values for PSL varied between .14 and .28 (Kremer and Lascoux, 1988). Heritability values of AESS and SSL are lower and more variable from year to year (Kremer and Lascoux, 1988). Additive variance of these traits represent from 60 to 90 % of the total genotypic variance.

Third level of subdivision

Compared to the other components NSU and MSUL are more affected by non additive gene effects. Additive variance of theses traits represent less than 40 % of the total genotypic variance reaching values of 20% for MSUL (Lascoux, 1984). As a result their heritability values are lower than corresponding values of other components.

Comparisons between the proportion of genotypic variance explained by additive variance provide pertinent information on gene effects controling height growth (table 1). Since NSU and MSUL are mostly due to non additive gene effects and are generally negatively correlated, and because their resulting trait (PSL) is mostly explained by additive effects, one may conclude on epistatic effects between genes of NSU and MSUL loci affecting primary shoot length.

Growing season	Height growth components		
	PSL	NSU	MSUL
9th season	56	28	18
10th season	74	37	12

Table 1 Ratio of additive variance on total genotypic variance for different height growth components (in percentage). These variances were estimated in a factorial

mating design (15 male parents and 15 female parents comprising 112 full sib families (Kremer and Lascoux, 1988).

Genetic correlations between components.

Components are never genetically independent. Refering to the different levels of subdivision , results are as follows:

First level of subdivision.

Successive AHIs are positively genetically correlated as shown on figure 3a; the correlation decrease with the lag separating AHIs.

Second level of subdivision.

PSL and AESS (and SSL) are generally negatively correlated (Kremer , 1981a; Kremer and Lascoux, 1988).

Third level of subdivision

The genetic correlation between NSU and MSUL varies, but are in most cases negative (Lascoux, 1984; Kremer and Lascoux, 1988).

Contribution of components to the composite traits.

First level of subdivision

Successive AHIs have similar contribution coefficients (Kremer , 1984) to the total height (Kremer and Lascoux, 1988). We are lacking data on comparisons between AHIs assessed during the juvenile stage and older AHIs.

Second level of subdivision

PSL shows systematically higher contribution to AHI than SSL: contribution coefficient values range between .7 and .8 for PSL and .2 to .3 for SSL (Kremer , 1984; Kremer and Lascoux, 1988).

Third level of subdivision

In most cases studied so far NSU has a larger contribution to PSL (or SSL): In general differences between contribution coefficient values are important (.8 for NSU versus .2 for MSUL) (Kremer, 1984). Interestingly results of age-age correlation relative to these morphogenetical components have shown that MSUL has a higher stability than NSU (Kremer and Li , 1989).

The analysis of genetic architecture of height growth shows that only PSL may be an alternative selection criteria for total height to AHI, mainly because of its higher heritability value (Boissieras, 1984; Kremer, 1988). Although we are lacking data on age-age correlation of components, there is a low chance that morphogenetical components (NSU or MSUL) will prove to be better early selection criteria, since they are mostly affected by non additive gene effects (table 1).

These results show also that there is an important genetic plasticity of height growth as revealed particularly by the variation of the genetic correlation between components indicating either compensation or cooperation between components (Kremer, 1984). Similar performances in height growth can be obtained by various pathways. As a result search mating design (15 male parents and 15 female parents comprising 112 full sib families (Kremer and Lascoux, 1988).

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These results show also that there is an important genetic plasticity of height growth as revealed particularly by the variation of the genetic correlation between components indicating either compensation or cooperation between components (Kremer, 1984). Similar performances in height growth can be obtained by various pathways. As a result search of early selection should take into account components *per se* but also relationships between components or pathways followed to reach the final level of height growth. Due to the plasticity of height growth, expectations to identify single component as early selection criteria are questionable. One may find in specific studies that one component at a juvenile stage exhibits a high JM correlation with total height in the field (Kremer and Li, 1989). In this cited study MSUL in the first season has shown the highest correlation with total height at age 6. There is a definite repeatability problem: in a different study another component may show a better correlation. Several reasons may explain the discrepancy of the results:

- sampling of families and seedlings in retrospective tests has a strong effect on JM correlation (Lambeth, 1983).
- genes controlling growth may have pleiotropic effects and alternatively affect different components.
- relationships between components may be modified in different environments. As stated earlier these relationships are to be taken into account in early evaluation studies.

The conclusion of the analysis of the "genetic architecture of height growth" is that (i) only a multivariate approach revealing expression of a great number of genes involved in growth process would lead to the identification of potential criteria (ii) the plasticity has an important impact on the expression of growth; therefore more efforts should be devoted to basic research on height growth based on explicative approaches.

4. RESULTS FROM **EXPLICATIVE APPROACHES: CHOICE OF TESTING ENVIRONMENT.**

The low juvenile mature correlation of height growth may be due to several biological or genetic reasons:

(i) Existence of maternal effects. These have often been attributed to the importance of the reserves contained in the endosperm of conifer seeds, which is exclusively of maternal origin.

(ii) Genotype-interaction effects. These can he attributed to the differences between environmental conditions during the juvenile stage (nursery environment) and the adult stage (field or forest conditions), especially levels of drought.

(iii) Maturation effects. Height growth may be controlled by different genes at different ages. This hypothesis would fit with the serial correlation structure illustrated on figure 3a. The trend of variation of genetic correlation may be intrepreted by a progressive change with age of the subset of loci controlling the expression of height growth.

The first hypothesis was tested in a full diallel cross. The 6 parents of the mating scheme were of contrasting height growth pattern, 3 expressed mainly several growth cycles at an adult stage, and the 3 others only one cycle. Results obtained on the 5 first growing seasons showed that reciprocal effects were only significant during the first growing season (Guignard, 1983; table 2).

Growing season	Height growth component	GCA	SCA	GRE	SCE
1st	AHI	28.5**	2.0*	24.3**	6.6 **
	NSU	12.6**	1.1	9.9**	2.4**
	MSUL	18.8**	2.0*	8.7**	6.2**
3rd	AHI	4.9**	1.4	.6	1.0
	NSU	5.5**	1.5	.6	.5
	MSUL	1.8	2.2**	1.0	.7
4th	AHI	6.0**	2.3*	1.7	.4
	NSU	9.4**	1.1	1.6	.7
	MSUL	5.4**	2.1*	2.2	1.1
5th	AHI	6.0**	1.9	2.6	1.6
	NSU	6.9**	1.1	1.1	1.0
	MSUL	6.4**	1.0	.8	.8

Table 2 F test values corresponding to the different sources of variation for height growth components.
* : F test significant at the 5% level
**: F test significant at the 1% level
GCA, SCA : General, specific combining ability
GRE, SRE : General, specific reciprocal effects
Data originated from a full diallel mating design with 6 parents (see text), data were not availiable for the second growing season.

The two other hypothesis were tested on a retrospective test comprising 18 open pollinated families. These were subdivided in 3 classes according to height growth performances of the parents (high, average and low performance). Each class was again subdivided in 2 subsets comprising families expressing mostly polycyclic shoots and monocyclic shoots. General combining abilities for height growth and polycyclism estimated in older progeny tests (between age 10 and 18) and clonal values estimated in grafted clonal tests were used as criteria to select the 18 parent trees of the retrospective progeny test.

Genotype*environment interaction

The 18 families were raised in the nursery in standard conditions during the two first growing seasons. At the end of the second growing season (August 30 to October 25) when the apical meristem was still initiating cataphylls, the material was separated in two treatments. The first consisted to induce drought by watering only with half of the water consumption of non stressed plants (treatment 2). The same treatments were again applied during the entire third season. Predawn water potential of stressed and non stressed plants was respectvely -.09 and -.04 MPa when the difference was maximum. There were no significant differences of water potential between families.

The trees formed up to 5 cycles, but significantly less in the stress treatment. No association between adult height growth class and length of the different cycles was found except for the first cycle (table 3) in the treatment where drought stress was applied. It is clear from that table that the stress treatment revealed a variation pattern corresponding to the different adult classes. Results of the non stress treatment did not reveal any family differences associated with adult height growth subdivision (Nguyen, unpublished data).

drought stress				no stress			
family	class a)	PSL b)	duncan grouping	family	class a)	PSL b)	duncan grouping
155		248		156		327	
156		243		150	0	318	
157		232		154	0	313	
158		231		136		290	
144		230		151	0	288	
142	0	221		155		280	
136		216		139		273	
151	0	211		157		277	
139		205		159		267	
150	0	204		142	0	258	
154	0	199		153	0	248	
147		194		144		247	
152		193		149	0	242	
149	0	186		158		228	
153	0	181		141		226	
148		171		147		226	
141		156		148		223	
159		144		152		197	

Table 3 Ranking of the families in two different treatments (with drought stress (S) and without (T))
a) height growth class according to adult performances (+ : top ranking families, 0 : mid ranking ; - : bottom ranking)
b) length of the first shoot of the third growing season (in millimeters)

Maturation

The 18 families were grown during their first season in two controlled environment rooms that differed in temperature and mainly in photoperiod. The experiments were conducted in the frame of a cooperation with the Swedisd University of Agricultural Sciences (The Phytotron, D. Ingegerd Dormling). Temperatures regimes were 25°C/20°C and 25°C/15°C during 16 and 8 hours respectively, and photoperiods were 24h and 16h. Seedlings raised in the continuous day treatment exhibited shorter duration of growth. 35% of the seedlings formed adult-like buds whereas seedlings in the discontinuous day treatment formed only rosettes. Adult-like buds were associated with a higher percentage of stem units bearing axillary short shoots (15% versus 7 % between the two treatments). Seedlings in the continuous day treatment exhibited morphological traits characterizing mature trees, particularly the development of secondary needles (Lascoux, unpublished data)

Eighteen traits related to growth of the seedlings were assessed during the first growing period: height growth curve parameters (4), growth components (3), morphological traits (5), above ground dry weights of different components (6). Among these traits, six showed significant differences between the adult height growth classes in the continuous day treatment. These traits reduced to only one in the discontinuous day treatment (table 4).

In the case of forest trees, accelerated maturation in controlled environments can induce the expression of genes that would normally be expressed only at an older stage. In this respect our results obtained in maturation experiments can be compared to other studies conducted in loblolly pine (Williams, 1987). In this study, height at the first bud was negatively correlated with eight-year height, whereas height accrued after first bud set was positively correlated. By inducing secondary needle development in continuous days we obtained already significant relation between components and later field growth.

The results obtained in the drought stress and the photoperiod experiments support the hypothesis that different loci are involved in different environments or at different ages. Interestingly there are now some experimental data based on QTL that have lead to the these conclusions in tomato (Paterson et *al,* 1991): among 29 QTLs underlying phenotypic variation, only 4 are detected in all three environments, other QTLs are specific to two or one environment only. Comparative QTL studies conducted in different environments or at different ages can therefore contribute to identify sets of loci specific to these conditions. As a consequence, one may use these results to identify optimal growing conditions during the juvenile phase for early evaluation. Therefore there is still a need of further research to identify optimal juvenile environmental conditions which reveal genetic differences associated to adult height growth performances.

These research should associated molecular approaches with morphophysiological approaches, which both are currently going on in maritime pine.

Component	Class + c)	 0	 -
Continuous light			
AHI (mm.)	175 a	196 b	181 a
NSU	250 a	279 b	269 b
DWG d)	118 a	168 b	176 b
UDWPRIM d)	.28 a	.28 a	.26 b
DWST d)	51 b	64 a	55 b
NSU PREF d)	72 a	79 b	77 b
Discontinuous light			
DWB d)	90 a	123 b	130 b

Table 4. Mean values of the different classes for various first season traits. Means are only represented for criteria showing significant differences between the classes.
c) height growth classes according to adult performances (+ top ranking families; 0 : mid ranking ; - : low ranking).
d) DWB : dry weight of branches at the bas of the epicotyl on first season seedlings (10 gr.)
UDWPRIM : mean dry weight of a primary needle (10 gr.
DWST dry weight of the stem (10^{-2} gr.)
NSU PREF : number of primary needles preformed in the **bud** or the rosette.

Class means not significantly different (Tukey and LSD test at p=.05) are underlined with identical letters.

CONCLUSION

Results obtained so far have pratical implications in the genetic tree improvement program. First, if traditional technics are used (total height as selection criteria), selection can only be achieved when trees are older than 12 years. These results are obtained with experimental data and with simulations of age-age correlation. Selection at earlier stages requires to use different selection criteria, among which PSL may be an interesting alternative, provided it is assessed over several successive years.

Although some morphogenetic components (especially MSUL, Kremer and Li, 1989) in their first season are significantly correlated with later field performance, it is to early to decide on their definite use in practical breeding, because of the plasticity of height' growth which can dramatically affect the repeatability of this first result obtained in one experiment. A first solution to the problem of repeatability is to use several components as selection criteria (multivariable approach).

As the analysis of genetic architecture of height growth and the explicative approaches have shown, the lack of JM correlation lies probably in the versatility of gene action at loci affecting growth:

- additive (for some components) versus non additive (for other components), epistatic effects between genes at loci controling NSU and MSUL.
- expression of regulation genes that can explain the plasticity of height growth.
- alternate sets of loci affecting growth at different ages or different environments

Therefore there is a need toward basic knowledge on genetic control of height growth. Molecular markers can be used to identify QTL involved in different situations (environments or stage of development). We expect that these analysis will lead, by comparing the different sets of loci, to the identification of optimal testing conditions at a juvenile stage, where early evaluation can be achieved with traditional compoments.

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