

Genetic Architecture of Height Growth in Maritime Pine (*Pinus pinaster* Ait.)

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Abstract

Height increment (HI) of maritime pine (*Pinus pinaster* AIT) over six successive growing seasons (5th to 10th) is subdivided into several different components at three levels: annual height increment (AHI), ability to express a second shoot (AESS), primary shoot length (PSL), secondary shoot length (SSL), number of stem units (NSU) and mean stem unit length (MSUL).

Measurements of these components were made on trees originating from an incomplete factorial mating design comprising 15 male and 15 female parents and 112 crosses. The objective is to evaluate the contribution of each component to its corresponding resultant character and its genetic control.

There is an even contribution of each AHI to HI; heritability of HI is superior to heritability of the different AHIs. Genetic correlation coefficients between AHIs are always higher than phenotypic correlation coefficients.

PSL has always a greater contribution to AHI than SSL. PSL and SSL are negatively correlated: the genetic correlation is lower than the phenotypic correlation.

NSU has a greater contribution to PSL or SSL than MSUL. Both components are negatively correlated at the phenotypic and the genetic levels.

The consequences of these results on the research of early selection criteria for height growth are discussed.

Key words: height growth, stem unit, polycyclism, path coefficient, component analysis, maritime pine.

Zusammenfassung

Bei *Pinus pinaster* AIT wurde der Höhenzuwachs (HI) über 6 aufeinanderfolgende Vegetationsperioden (5.—10.) hinweg in verschiedene Komponenten auf drei Niveaus unterteilt: in den jährlichen Höhenzuwachs (AHI), die Fähigkeit, einen zweiten Trieb zu machen (AESS), die primäre Trieblänge (PSL), die sekundäre Trieblänge (SSL), die Anzahl der Stammeinheiten (NSU) und die mittlere Länge der Stammeinheit (MSUL).

Messungen dieser Komponenten wurden an Bäumen eines unvollständigen faktoriellen Kreuzungsschemas mit 15 männlichen und 15 weiblichen Eltern und 112 Kreuzungen durchgeführt. Das Ziel ist, den Beitrag der einzelnen Komponenten und ihrer damit verbundenen Merkmale und deren genetische Kontrolle zu schätzen.

Jedes AHI hat gleichmäßig zum HI beigetragen. Die Heritabilität des HI ist höher als die der verschiedenen AHIs. Die Koeffizienten der genetischen Korrelationen zwischen den AHIs sind immer höher als die der phänotypischen Korrelationen.

Die PSL lieferte jedesmal einen größeren Beitrag zum AHI und zur Heritabilität als die SSL. PSL und SSL waren negativ korreliert: Die genetische Korrelation ist niedriger als die phänotypische Korrelation.

NSU lieferte einen größeren Beitrag zur PSL oder SSL als die MSUL. Beide Komponenten waren negativ auf der

phänotypischen und genotypischen Ebene korreliert.

Die Konsequenzen dieser Resultate auf die Erforschung von Kriterien zur Frühselektion auf Höhenzuwachsleistung werden diskutiert.

Résumé

Titre de l'article: *Architecture génétique de la croissance en hauteur chez le pin maritime (Pinus pinaster Ait.)*

L'accroissement en hauteur (HI) chez le pin maritime durant six saisons successives de végétation a été décomposé à trois niveaux en différentes composantes: accroissement annuel en hauteur (AHI), aptitude à exprimer une seconde pousse (AESS), longueur de la pousse primaire (PSL), longueur de la pousse secondaire (SSL), nombre d'entre-noeuds (NSU), longueur moyenne d'une entre-noeud (MSUL). Ces composantes ont été mesurées sur des arbres issus d'un plan de croisement factoriel incomplet, comprenant 15 pères et 15 mères et 112 croisements. L'objectif de l'étude est d'évaluer la contribution de chaque composante au caractère résultante correspondant et son contrôle génétique. Des coefficients de contribution ont été estimés au niveau phénotypique et génétique.

Les accroissements en hauteur annuels ont une contribution égale à l'accroissement global; l'héritabilité du dernier caractère est cependant supérieure à celle des accroissements annuels. Les coefficients de corrélation génétique entre accroissements annuels sont toujours supérieurs aux coefficients de corrélation phénotypique.

Au niveau annuel, l'accroissement primaire (PSL) contribue pour une part plus grande à l'accroissement annuel (AHI) que l'accroissement secondaire (SSL). Les accroissements primaire et secondaire sont corrélés négativement. Les coefficients de corrélation génétique sont inférieurs aux coefficients de corrélation phénotypique.

Le nombre d'entre-noeuds (NSU) contribue pour une plus large part à PSL ou SSL que la longueur moyenne d'un entre-noeud. Les deux composantes sont corrélées négativement au niveau génétique et phénotypique.

Les conséquences de ces résultats sur la recherche de prédicteurs précoces de la croissance en hauteur sont discutées.

1. Introduction

Total height or height growth is usually the selection criterion for stem volume in tree improvement programs. In pine breeding assessment of height between 5 and 10 years seems to be adequate for selection in the breeding populations (SQUILLACE and GANSEL, 1974 in slash pine; LAMBETH, 1980 in loblolly pine; BOISSIERAS 1984 in maritime pine). This period corresponds also for these species to the onset of flowering.

The required characteristics of a selection criterion in the context of indirect selection, as is the case in forest trees, are high heritability and good genetic correlation with the goal of selection that should be improved (FALCONER, 1974).

Height growth in pines is a composite character including different additive or multiplicative components (CANNELL, 1978). It can be subdivided into three levels. The first cor-

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responds to the yearly level: height increment (HI) over successive years is the addition of several annual height increments (AHI). The second refers to the morphogenetic composition of AHI. Maritime pine can develop within each growing season, one or two morphogenetic cycles (KREMER, 1981). The third level relates to the anatomy of each cycle; one cycle corresponds to the sequence of stem units bearing sterile bracts, fertile bracts with axillary short shoots and bracts with axillary long shoots or cones (DEBAZAC, 1963). After DOAK (1935) a stem unit is an internode, together with the node and nodal appendages at its distal extremity. A cycle can therefore be subdivided in number of stem units (NSU) and mean stem unit length (MSUL) (LANNER, 1968).

The subdivision described above can give important information for breeding purposes particularly in the search for optimal selection criteria. It is the objective of this paper to answer the following questions. (1) Is heritability greater for an elementary component than for composite traits like HI? (2) Is there an even contribution of each component to its respective resultant character?

The study material consists of progenies of *Pinus pinaster* originating from a factorial mating design. Assessments of height growth components are made from age 5 to 10. A particular methodology, based on path coefficient analysis, is developed to estimate the contribution of the components to the resultant character.

2. Material and Methods

2.1. Material

The study material consists of 112 full sib families from a factorial mating design including 15 male and 15 female parents (Figure 1). Parents of the progenies were selected according to earlier results obtained in previous experimental plantations comprising open pollinated progenies of the same parents. The full sib families were established during the fall 1974 in a test located on a sandy moor site representative of the local soil conditions. The experimental design is a complete block design, with 10 blocks. Each plot comprises from 2 to 4 trees and is split into 2 sub plots (split plot). Half of a plot (1 or 2 trees) consists of bare root planted trees. The second half consists of container-planted trees. During the fall 1983 when the trees were 10 years old, a systematic thinning was done in the test. One out of two trees was cut, the thinned tree of each plot was measured. The tree was selected so that all the attributes mentioned below could be efficiently measured. Using this procedure, 1009 trees were cut and analysed for this study.

2.2. Measurements

Annual height increments (AHI) were measured over six successive years from the fifth to the tenth growing season. An annual height increment corresponds to either one or two morphogenetic cycles (DEBAZAC, 1963; KREMER, 1981).

This polycyclic habit can be analysed in terms of three different characters:

- (1) the ability to express a second shoot (AESS). This is a dichotomous character.
- (2) the length of the second shoot measured on all the trees (SSL1). SSL1 of the trees that did not express a second shoot was 0. Within each year, SSL1 has a skewed distribution.
- (3) the length of the second shoot (SSL2) measured on the subset of trees that expressed a second shoot. In this case SSL2 has a normal distribution within this

♀	♂	0003	1307	5301	0205	0125	3812	0004	0158	0007	0221	1312	5308	0011	5306	1305
0147	■	■	■	■	■	■	■	■	■							
0232		■	■	■	■	■	■	■	■	■						
0054			■	■	■			■	■	■	■					
0131				■	■	■	■	■	■	■	■	■				
5302					■	■	■	■	■	■	■	■	■			
0052						■	■		■	■			■			
0133							■	■	■	■	■	■	■	■	■	■
0116								■	■	■	■	■	■	■	■	■
1308	■								■	■	■	■	■	■	■	■
0243	■	■									■	■	■	■	■	■
0286	■	■	■									■	■	■		■
0157	■	■	■	■									■	■	■	■
0138	■	■	■	■	■									■	■	
3115	■	■	■	■	■	■									■	■
3102		■	■	■	■	■	■									

Figure 1. — Diagram of the mating design.

subset. SSL2 refers therefore to a different population than SSL1 or AESS.

Within each season AHI was therefore subdivided into primary shoot length (PSL) and secondary shoot length (SSL1).

Pseudoverticilles of long shoots separating the first from the second cycle are morphologically different from pseudoverticilles separating cycles of different years, and this morphological difference was used to identify the cycles.

The last two annual shoots, where needle fascicles were still present were harvested for further measurements in the laboratory. Number of stem units (NSU) was determined on each cycle by counting needle fascicles, and the corresponding mean stem unit length (MSUL) was estimated by taking the ratio between the length of the shoot where fascicles were present and NSU. Therefore on each cycle of the last two annual shoots, the "sterile bract" zone was neglected, and PSL and SSL1 refer only to the "foliar" part of the cycle.

A more rapid method of counting needle fascicles was tested for measuring NSU on first cycles, the number of which was generally over 400. A subset of 60 randomly sampled fresh fascicles and the total set of all the fascicles on a given cycle were separately weighed. The ratio between both weights was then used to estimate the total number of fascicles of a cycle. This method was tested on the two first cycles of the two last annual shoots on 90 trees of the experimental plantation. Estimates with this method were then compared with values of NSU and MSUL determined by counting all the fascicles. Results (Table 1) show that NSU is slightly overestimated and MSUL is slightly underestimated. But the bias and its standard deviation are low. The indirect method was therefore used on the study material for measuring the total number of stem units and mean stem unit length on first cycles of annual shoots.

For second cycles, counting of fascicles based on phyllotactic arrangements was used to measure NSU. However phyllotactic arrangements could not be efficiently identified on the second shoot of the ninth growing season. This cycle was therefore discarded.

Table 1. — Bias and standard deviation of the deviation due to indirect estimates of NSU and MSUL.

Component	shoot cycle	Bias	Standard ^b deviation
NSU	first cycle 9 th season	1.49	9.81
	first cycle 10 th season	1.28	9.40
MSUL ^a	first cycle 9 th season	- 0.027 ^a	0.091
	first cycle 10 th season	- 0.009 ^a	0.072

a) in millimeters

b) of the difference between observed and estimated values

2.3. Methods

Analysis of the experimental design

All data were adjusted to account for the block and method of planting effects (container or bare root) before further analysis.

$$(1) \quad Y_{ijk} = \mu + b_i + m_j + (bm)_{ij} + \varepsilon_{ijk}$$

(b_i : bloc effect; m_j : plantation method effect; $(bm)_{ij}$: interaction effect; b_i and m_j are fixed effects).

Linear adjustments were made and all subsequent calculations were made on the adjusted data.

$$(2) \quad Y'_{ijk} = Y_{ijk} - b_i - m_j$$

Interaction effects were not significant.

Analysis of the mating design

The mating design was analyzed by the HENDERSON III method (SEARLE, 1971).

$$(3) \quad Y'_{ijk} = \mu + F_i + M_j + (FM)_{ij} + \varepsilon_{ijk}$$

(F_i : female parent effect; M_j : male parent effect; $(FM)_{ij}$: interaction effect; F_i and M_j are considered as random effects).

This method, is also known as the method of fitting constants. It uses reduction in sum of squares due to fitting different subgroups of factors in the model. The expectations of the reduction of the sum of squares are linear in the variance components. This gives unbiased estimates of the variance components even in the case of non-orthogonal or unbalanced mating designs, as in our example (Figure 1).

Genetic components of variance are then estimated using estimates of covariances between relatives in the mating design. A common additive variance is estimated by weighing variance estimates of male and female effects.

$$(4) \quad \hat{V}_A = \frac{4(f-1)\hat{V}_F + 4(m-1)\hat{V}_M}{(f+m-2)}$$

\hat{V}_A : estimate of the additive variance

\hat{V}_F : estimate of the variance due to the female parent

\hat{V}_M : estimate of the variance due to the male parent

f: number of female parents

m: number of male parents

For most attributes listed in paragraph 2.2, male \times female interaction effects were not significant. Estimates of dominance variance are therefore not reported (LASCoux, 1984).

Genetic component analysis of height growth

Subdivision of height growth can be summarized by a set of equations, relating the resultant characters to their additive or multiplicative components.

- (A) $HI = \sum AHI$ } First level of subdivision
 (B) $AHI = PSL + SSL1$ }
 (C) $SSL1 = AESS \times SSL2$ } Second level of subdivision
 (D) $PSL = NSU \times MSUL$ }
 (E) $SSL2 = NSU \times MSUL$ } Third level of subdivision

Multiplicative components are reduced to additive components by logarithmic transformations. Equation (C) cannot be analyzed with the same methodology as the other equations, since $SSL2$ is not defined when $AESS = 0$.

Phenotypic, or additive variances of a resultant character can be subdivided into contributions of corresponding variances due to each component.

$$(5) \quad V_P = \sum_{i=1}^n V_{Pi} + 2 \sum_{i \neq j}^n cov(P_i, P_j)$$

$$(6) \quad V_A = \sum_{i=1}^n V_{Ai} + 2 \sum_{i \neq j}^n cov(A_i, A_j)$$

P_i, A_i : phenotypic and additive value of component i .

V_{Pi}, V_{Ai} : phenotypic and additive variance of component i

V_P, V_A : phenotypic and additive variance of the resultant character

n : number of components.

Equations 5 and 6 can be interpreted in terms of path coefficient analysis (WRIGHT, 1968). The effect of the component on the resultant character can be analysed with the aid of three parameters (KREMER, 1984).

— the path coefficient $\sqrt{\frac{V_{Pi}}{V_P}}$, which estimates the relative variation of the component compared to the variation of the resultant character

— the correlation coefficient between a component and the resultant character ($r_{Pi, P}$)

— the contribution coefficient of a component to the resultant character ($C_{Pi, P}$)

$$(7) \quad C_{Pi, P} = \sqrt{\frac{V_{Pi}}{V_P}} r_{Pi, P}$$

The contribution coefficient, which is also a regression coefficient represents the part of the standard deviation of the resultant character due to a component. A similar methodology was used by MOLL, KAMPATH and JACKSON (1982) for the analysis of factors contributing to efficiency of nitrogen utilization in corn.

$$(8) \quad \sum_{i=1}^n C_{Pi, P} = 1$$

This coefficient is called the phenotypic contribution coefficient. Similar coefficients can be estimated for the additive variances (additive or genetic contribution coef-

ficient). Finally the phenotypic variance of the resultant character can be subdivided into additive, dominance and environmental variances of the components.

$$(9) \quad V_P = \sum_{i=1}^n V_{A_i} + \sum_{i=1}^n V_{D_i} + \sum_{i=1}^n V_{E_i} + 2 \sum_{i \neq j}^n (\text{cov}(A_i, A_j) + \text{cov}(D_i, D_j) + \text{cov}(E_i, E_j))$$

where D_i and E_i represent the dominance and environmental value of component i and V_{D_i} and V_{E_i} their corresponding variances.

In this study, we are mainly concerned with the additive variance relative to the phenotypic variance. Equation (9) can therefore be interpreted in terms of path coefficient analysis and the same three parameters can be estimated.

- the path coefficient $\sqrt{\frac{V_{A_i}}{V_P}}$
- the correlation coefficient $r_{A_i, P}$
- the contribution coefficient $C_{A_i, P}$

$$(10) \quad C_{A_i, P} = \sqrt{\frac{V_{A_i}}{V_P}} \quad r_{A_i, P}$$

$$= \frac{\text{Cov}(A_i, A)}{V_P}$$

In this case, the contribution coefficient has also the form of a regression coefficient. Indeed it is used in this form for prediction purposes of A using P as predictor. It was referred to as "generalized heritability" by GALLAIS (1973)

$$(11) \quad \sum_{i=1}^n C_{A_i, P} = \frac{V_A}{V_P}$$

The contribution coefficient, in this case, also estimates the contribution of the additive variance of component i to the heritability of the resultant character (additive to phenotypic contribution coefficient).

3. Results

3.1. First Level of Subdivision

Heritability estimates

Heritability estimates of annual height increments (Table 2) show that estimates did not change much from year to year, except for the eight growing season. However, heritability of the sum of annual AHIs are higher than any other values, by up to three times. Comparisons of heritability values of a resultant character and components lead to the comparisons of the left and right terms of equations (5) and (6), and especially to comparisons of the correlation matrices between phenotypic values on the one hand, with correlation matrices between additive values on the other hand (Table 3). Correlation coefficients of successive AHI phenotypic values (Table 3) are always inferior to corresponding coefficients of additive values. As a result, additive variance of a resultant character increases "faster" than phenotypic variances when additional components are added.

Table 2. — Heritability and contribution coefficients of annual height increments of six successive years.

AHI	Heritability of raw data	Heritability of log. transformed data	$C_{P_i, P}$	$C_{A_i, A}$	$C_{A_i, P}$
5 th growing season	.097	.081	.185	.154	.050
6 th growing season	.089	.062	.209	.179	.058
7 th growing season	.082	.067	.203	.186	.060
8 th growing season	.191	.173	.156	.239	.077
9 th growing season	.072	.054	.124	.082	.027
10 th growing season	.128	.125	.123	.160	.052
Sum of the six growing seasons	.325	.303	1	1	.325

Contribution coefficient estimates

Consistency of contribution coefficients of years varied, depending on the level where coefficients are estimated (Table 2).

- phenotypic contribution coefficients show a constant decrease from the fifth to the tenth growing season.
- variation of additive contribution coefficients is higher and does not follow a definite pattern. The values obtained in two successive years (8th and 9th growing season) are extreme values.
- additive-phenotypic contribution coefficient follow the same pattern of variation as the additive contribution coefficients.

No particular year contributed significantly more or less to the additive or phenotypic variance of the height increment over successive years (Table 2).

3.2 Second Level of Subdivision

An annual shoot in maritime pine is usually composed of one or two morphogenetic cycles (DEBAZAC, 1963).

Expression of a second cycle may or may not occur. Therefore SSL1 may be further subdivided on the basis of its ability to express a second cycle (AESS) and the length of the second shoot (SSL2). AESS decreased with age while SSL2 stayed rather constant from season to season (Table 4).

Table 3. — Genetic and phenotypic correlation matrices between annual height increments over six successive growing seasons.

	5 th growing season	6 th	7 th	8 th	9 th
6 th growing season	1.122 ^a **				
	.288 ^b **				
7 th	.583 **	.745 **			
	.011 NS	.187 **			
8 th	.483 **	.749 **	.956 **		
	-.041 NS	.053 NS	.142 **		
9 th	-.069 NS	.313 NS	.478 **	.674 **	
	-.048 NS	.019 NS	-.004 NS	.135 **	
10 th	.675 NS	.996 **	1.106 **	.665 **	.259 NS
	.162 **	.140 **	.127 **	.032 NS	-.001 NS

a) correlation coefficient between additive values

b) correlation coefficient between phenotypic values

** significant at the 1% level
* " " " 5% level

NS not significant at the 5% level

Table 4. — Overall mean values of annual height increment components over six successive growing seasons.

Growing season	AHI ^a	PSL ^a	SSL1 ^a	AESS ^b	SSL2 ^a
5 th	90.25	65.99	24.26	.790	30.71
6 th	102.89	81.84	21.05	.707	29.78
7 th	107.20	84.42	22.78	.663	34.36
8 th	110.97	98.51	12.46	.386	32.28
9 th	110.13	93.36	16.77	.564	29.73
10 th	100.74	87.02	13.72	.516	26.59

a) in centimeters

b) proportion of trees expressing a second shoot

Heritability estimates

Heritability estimates of dichotomous characters can be determined by the method described by GIANOLA (1979).

This method assumes an underlying continuous normal variable, which at a given threshold point changes the outward observable variable into a yes or no response. The following equation relates the heritability of the outward scale (h^2_o) to the heritability of the continuous underlying scale (h^2).

$$(12) \quad h^2_o = \frac{h^2 z^2}{\pi (1 - \pi)}$$

π : frequency of trees exhibiting a second cycle

$1-\pi$: frequency of trees exhibiting only one cycle.

z : ordinate of the density function of the underlying variable at the threshold point corresponding to the fraction π of the population having a second shoot.

A simulation study was done by VAN VLECK (1971) to test this theory. Data were generated from a normal distribution; and the distribution was truncated at different threshold points to generate yes or no classes. Comparisons of heritability estimates of the two variables determined from covariances between relatives showed that the method is satisfactory when h^2_o is not larger than 0.7 and π not lower than 0.2. In the latter two cases, h^2 is overestimated. In our study, h^2_o ranged between 0 and .252 and π varied from .4 to .8 (Table 4). In our example GIANOLA'S method can therefore be applied without any substantial bias to estimate heritability values of the underlying variable.

Heritability estimates give some general results (Table 5).

For any component, there is a general trend of increasing of heritability estimates with age. This trend was not obvious for AHI (Table 2).

Heritability of PSL is always superior to heritability of SSL1 in any growing season.

The ability to express a second shoot (AESS) is more strongly genetically controlled than the length of the second shoot (SSL1 or SSL2).

Comparisons of Table 5 and Table 2 reveal that heritability of PSL is systematically higher than heritability of the resultant character AHI within each year. As for the first level of subdivision, the fact that the heritability value of components is different from heritability of the resultant character is due to the differences between the phenotypic and genetic correlations between components (Table 6). As shown on Table 6 both correlation coeffi-

Table 5. — Heritability and contribution coefficient estimates of annual height increment components over six successive growing seasons.

growing season	AHI component	Heritability	C _{Pi,P}	C _{Ai,A}	C _{Ai,P}
5 th	PSL	.148	.602	1.059	.100
	SSL1	.024	.335	-.059	-.005
	AESS	.000			
	SSL2	.037			
6 th	PSL	.167	.618	1.040	.097
	SSL1	.021	.382	-.040	-.004
	AESS	.054			
	SSL2	.069			
7 th	PSL	.151	.526	.817	.068
	SSL1	.057	.475	.183	.015
	AESS	.145			
	SSL2	.069			
8 th	PSL	.242	.624	.728	.127
	SSL1	.202	.377	.272	.047
	AESS	.337			
	SSL2	.123			
9 th	PSL	.285	.517	.920	.066
	SSL1	.199	.483	.080	.006
	AESS	.310			
	SSL2	.114			
10 th	PSL	.351	.858	1.721	.230
	SSL1	.232	.138	-.721	-.096
	AESS	.396			
	SSL2	.057			
Sum over the six seasons	PSL	.484	.753	1.064	.346
	SSL1	.294	.247	-.064	-.021

icients are negative, but genetic correlations between components are always inferior to phenotypic correlations. As a result the phenotypic variance of the resultant character is less affected by the relation between components than the additive variance (see equation 5 and 6).

Contribution coefficient estimates

At this level of subdivision, there is not an even contribution of the variation of the components to the variation of the resultant character, as shown in Table 5. PSL has a higher contribution coefficient than SSL1. The difference between coefficients between both components is increased from the phenotypic to the genetic level.

3.3. Third Level of Subdivision

At this level, a shoot corresponding to a given morphogenetic cycle is subdivided into the number of stem units

Table 6. — Genetic and phenotypic correlation coefficients between annual height increments.

Growing season	genetic correlation between PSL and SSL1	phenotypic correlation between PSL and SSL1
5 th	-.126 NS	-.061 NS
6 th	-.105 *	-.071 *
7 th	-.250 NS	-.002 NS
8 th	-.121 *	-.226 **
9 th	-.770 **	-.157 **
10 th	-.800 **	-.521 **
Sum over 6 seasons	-.646 **	-.244 **

** Significant at the 1 % level

* " " " 5 % level

NS not significant at the 5 % level

Table 7. — Heritability and contribution coefficients of morphogenetic components of different shoot cycles.

growing season and cycle	morphogenetic component a)	heritability	$C_{P_i,P}$	$C_{A_i,A}$	$C_{A_i,P}$
9 th growing season	NSU	.095	1.010	.773	.119
First cycle	MSUL	.110	-.010	.227	.035
10 th growing season	NSU	.134	.782	.707	.213
First cycle	MSUL	.072	.217	.293	.088
Sum of the 9 th and 10 th growing season	NSU	.207	.809	.775	.265
First cycle	MSUL	.132	.191	.224	.077
10 th growing season	NSU	.027	.613	.769	.009
Second cycle	MSUL	.017	.405	.231	.002

a) both components are expressed in logarithmic values

(NSU) and mean stem unit length (MSUL). It must be emphasized that the shoot length concerns only the part of the shoot that comprises needle fascicles, it does not include the "sterile" zone, as is mentioned in the "Methods" section. Therefore it is not strictly equivalent to PSL. However in the case of the second cycle it includes the sterile zone.

Heritability estimates (Table 7)

Two main results appear on Table 7.

- * Heritability of NSU is in general superior to heritability of MSUL. Differences are substantial.
- * Heritabilities of both components of PSL are higher than heritability of components of SSL2.

In contrast to the two first levels of subdivision phenotypic correlations between components are not consistently different from genetic correlations. As a result, it is not generally possible to predict the heritability value of the resultant character (PSL or SSL2) from the heritability of the components. However correlation coefficients are generally negative at the phenotypic and the genetic level.

Contribution coefficients (Table 7)

There is a general trend towards a superior contribution of NSU. Genetic contribution coefficients are constant from one cycle to another (.75 for NSU; .25 for MSUL). This difference is even greater at the phenotypic level.

4. Discussion

Results of this study are summarized in Figure 2. Several important points regarding breeding and biology deserve particular attention.

4.1. Breeding and Genetics

Genetic and phenotypic correlations between components

The most striking characteristic of the correlation matrices shown in Tables 3, 6 and 8 is the differences between genetic and phenotypic correlation. These differences explain the change (increase or decrease) of the heritability values from a component to a composite character (BURDON, 1982).

- * Genetic correlations between successive AHI are always significant and higher than the corresponding phenotypic correlations (Table 3). This result suggests that there is low genotype \times year interaction while there is phenotype

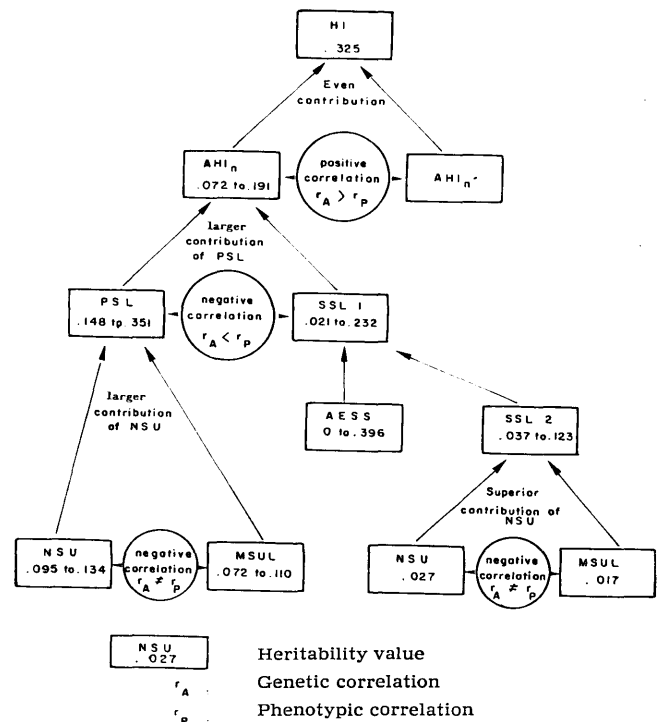


Figure 2. — Schematic diagram of the results.

\times year interaction for successive height increments. Such conclusions lead to an increase of the heritability values of HI compared to AHI as more and more AHI are added. Similar results were obtained in other progeny tests with different mating designs in maritime pine (KREMER, 1982). In this last study, the phenotypic coefficient of variation decreases when successive AHI are summed, while the genetic coefficient of variation remains constant.

- * Within a given AHI genetic and phenotypic correlations between PSL and SSL1 are always negative but genetic correlations are systematically inferior (Table 6). There seems also to be a constant decrease in these correlations as older AHI are considered. The main consequences of these results are the systematic decrease of heritability of AHI compared to PSL. Results are similar to those ob-

Table 8. — Genetic and phenotypic correlation coefficients between shoot components.

Growing season and cycle	Genetic correlation between NSU and MSUL	Phenotypic correlation between NSU and MSUL
9 th growing season	-.654 **	-.677 **
First cycle		
10 th growing season	+.187 NS	-.543 **
First cycle		
9 th and 10 th growing season	-.211 NS	-.570 **
First Cycle		
10 th growing season	-.547 **	.024 NS
Second cycle		

** significant at the 1% level
 * " " 5% level
 NS not significant at the 5% level

Table 9. — CGP (Coefficient of genetic prediction) Matrix between different height growth components and height increment over six successive years.

	HI	PSL ^a	SSL1 ^a	NSU ^b	MSUL ^b
HI	.325				
PSL ^a	.323	.484			
SSL1 ^a	-.026	-.244	.294		
NSU ^b	.172	.260	-.141	.207	
MSUL ^b	.068	.091	-.039	-.027	.132

a) summed over six successive height increments

b) summed over the ninth and the tenth growing season on the primary shoot length only

tained in an other progeny test of maritime pine, where the same measurements were made over successive AHI from age 5 to age 18 (BOISSIERAS, 1984).

* Within a given cycle, genetic and phenotypic correlations between NSU and MSUL are generally negative (Table 8). But, in this case, genetic and phenotypic correlation vary irrespective of each other. No conclusion can be drawn on how these correlations affect the heritability of PSL or SSL as compared to NSU or MSUL.

In contrast to the results obtained on measurement of total height (LAMBETH, 1980) this study points out the difference between phenotypic and genetic correlations when height increment components are considered.

Prediction purposes

Component analysis can be used for the search of optimal selection criteria. From the results shown on Table 2 and in Figure 2, there is no optimal growing season between age 5 and 10, when measurements should be made for selection purposes: each AHI has almost an equal contribution to HI. However PSL and NSU are components that contribute for the most part to their corresponding resultant character (Table 5 and 7).

Previous results on the same topic showed that the superior contribution coefficients of PSL and NSU as compared to SSL1 and MSUL are due to both a superiority of their path and correlation coefficients (KREMER, 1984). Results in this article are based on several progeny and provenance trials from which similar conclusions were drawn. They can therefore be held as general in maritime pine.

In order to verify that PSL or NSU could be used as indirect selection of HI, CGP (coefficient of genetic prediction, BARADAT, 1976) are computed between different components and HI (Table 9). This table shows that HI can be predicted as well by PSL as by itself. In early selection procedures, it would therefore be interesting to see if height increment of the first shoot would not be a better selection criterion for total height than AHI during the juvenile period.

4.2. Biology

Compensation between components

Negative phenotypic and genetic correlation between PSL and SSL1 on the one hand, and NSU and MSUL on the other hand can be interpreted in terms of compensation between components (KREMER and LARSON, 1983; KREMER, 1984). A similar situation exists in yield components of annuals plants (ADAMS, 1967). If this hypothesis holds then

compensation between components should increase in stress conditions and when both components occur simultaneously. The second situation is rare: PSL and SSL or NSU and MSUL are usually sequential characters, although there is an overlapping of both initiation and elongation of stem units especially in the juvenile stage. However various stress conditions during different growing seasons may explain the variation of the correlation coefficients between NSU and MSUL (Table 8). An attempt was made to quantify the compensation (LASCoux, 1984; KREMER, 1984) and to relate the degree of compensation between components of a genetic unit to its sensitivity to genotype × year interaction. However results were not conclusive. It has not yet been established if there is genetic variation in the degree of compensation.

Age trends of variation

Mean values of AHI do not vary significantly from age 5 to age 10 (Table 4). However SSL1 and AESS decrease consistently during this period and there is a major change from age 7 to 8.

Several other parameters had a similar pattern of variation including the change between age 7 to 8:

- heritability values of PSL, SSL1 and AESS increase consistently (Table 5).

- genetic and phenotypic correlations between PSL and SSL1 consistently decrease (Table 6).

Several biological events that occurred during this period can be responsible for this trend of variation.

- phase change. First flowering in maritime pine occurs as early as age 5 in some trees. Age 7 is generally be thought to be the age of the first flowering. Phase change is also associated with the change of the height growth pattern. In the adult stage the second cycle is entirely predetermined in the bud, while in the juvenile stage the second cycle is due to free growth or lammas shoot.

- Stand development. Stand closure is reached between age 7 and 10 years. Increase of heritability of total height during the period of crown closure was observed in loblolly pine and Douglas fir (FRANKLIN, 1979). It is interpreted as the phase during which differences between slow growing and fast growing trees reach a maximum.

Literature Cited

- ADAMS, M. W.: Basis of yield component compensation in crop plants with special reference to the field bean, *Phaseolus vulgaris*. *Crop Sci.* 7: 505–510, (1967). — BARADAT, PH.: Use of juvenile - mature relationships and informations from relatives in combined multitrait selection. In: Proceedings of the I.U.F.R.O. Joint meeting of genetic working parties on advanced generation breeding. p 121–138. INRA Pierroton, (1976). — BOISSIERAS, A.: Recherche de prédicteurs juvéniles de l'aptitude génétique à la croissance en volume du pin maritime. Détermination de l'âge optimum pour la sélection. Mémoire de stage B.T.S., Option Forêt, Ecole forestière de Meymac, 58 pp., (1984). — BURDON, R. D.: Breeding for productivity. Jackpot or Will-O-The Wisp? In: Proceedings of the seventh north american forest biology workshop. (B. A. THIELGES, editor). p 35–51. University of Kentucky, Lexington, (1982). — CANNELL, M. G. R.: Components of conifer shoot growth. In: Proceedings of the fifth north american forest biology workshop. (C. A. HOLLIS and A. E. SQUILLACE, eds). p 313–318. University of Florida, Gainesville, (1978). — DEBAZAC, E. F.: Morphologie et sexualité chez les pins. *Rev. For. Fr.* 114: 173–179, (1963). — DOAK, C. C.: Evolution of foliar types, dwarf shoots, and cone scales of *Pinus*. *Illinois Biol. Monogr.* 13: 1–106, (1935). — FALCONER, D. S.: Introduction à la génétique quantitative. Masson, 284 p., (1974). — FRANKLIN, E. C.: Model relating levels of genetic variance to stand development of four north american conifers. *Silvae Genet.* 28: 207–212, (1979). — GALLAIS, A.: Sélection pour plusieurs caractères. Synthèse critique et généralisation. *Ann. Amélior. Plantes* 26: 1–14, (1973). — GIANOLA, D.: Héritabilité of a polychotomous

character. *Genetics* 93: 1051–1055, (1979). — KREMER, A.: Déterminisme génétique de la croissance en hauteur du pin maritime (*Pinus pinaster* AIT.). 1. Rôle du polycyclisme. *Ann. Sci. Forest.* 38: 191–222, (1981). — KREMER, A.: Déterminisme génétique de la croissance en hauteur du Pin maritime (*Pinus pinaster* AIT.). 3. Evolution des composantes de la variance phénotypique et génétique. *Ann. Sci. Forest.* 38: 355–375, (1982). — KREMER, A., and LARSON, P. R.: Genetic control of height growth components in Jack pine seedlings. *Forest Sci.* 29: 451–464, (1983). — KREMER, A.: Component analysis of height growth, compensation between components and seasonal stability of shoot elongation in maritime pine (*Pinus pinaster* AIT.). In: "Crop physiology of forest trees". (P. M. A. TIGERSTEDT, P. PUTTONEN, V. KOSKI Eds). Helsinki University Press, p 203–217, (1984). — LAMBETH, C. C.: Juvenile-mature correlations in *Pinaceae* and their implications for early selection. *Forest Sci.* 26: 571–580, (1980). — LANNER, R. M.: The pine shoot primary growth system. Ph. D. Thesis, University of Minnesota, St. Paul. 136 pp., (1968). — LASCoux, D. M.: Décomposition de la croissance en hauteur du Pin maritime. Aspects morphogénétiques et génétiques. Mémoire de fin d'études à l'E.N.I.T.E.F., 80 pp., (1984). — MOLL, R. H., KAMPRATH, E. J. and JACKSON, W. A.: Analysis and interpretation of factors which contribute to efficiency of nitrogen utilization. *Agron. J.* 74: 562–564, (1982). — SEARLE, S. R.: Linear models. John Wiley and sons, (1971). — SQUILLACE, A. E. and GANSEL, C. R.: Juvenile mature correlations in slash pine. *Forest Sci.* 20: 225–229, (1974). — VAN VLECK, L. D.: Estimation of heritability of threshold characters. *Journal of dairy science* 55: 218–225, (1971). — WRIGHT, S.: Evolution and the genetics of populations. Vol. 1 Genetic and biometric foundations. Univ. Chicago Press. 469 pp., (1968).

Cyclophysis and Topophysis in Coast Redwood Stecklings

I. Rooting and Nursery Performance

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Summary

Two studies were conducted with vegetative propagules of *Sequoia sempervirens* to improve our understanding of the effects of branch order (topophysis) on the rooting of cuttings and growth performance of the resulting stecklings.

In the first study, cuttings of three branch orders were collected from hedged trees. Hedges were used since these could provide the different branch orders without confounding effects of cyclophysis. In the second study cuttings of the same three branch orders were collected from young seedlings and from two branch orders from the same hedges used above. The second study was expected to shed some light on the possible interaction between topophysis and cyclophysis, since hedges would be in a more advanced maturation stage than seedlings.

The results indicate that both maturation stage and branch order have significant effects on the rooting of cuttings and on the growth characteristics of the resulting stecklings. The results also support the concept of interaction between cyclophysis and topophysis.

Key words: Cyclophysis, Maturation, Plagiotropism, Propagation, Rooted Cuttings, Topophysis, Vegetative Propagation.

Zusammenfassung

Zwei Studien mit vegetativ vermehrten *Sequoia sempervirens* wurden zur Verbesserung unseres Verständnisses der Auswirkungen der Topophysis auf die Bewurzelung von Stecklingen und das Wachstum der daraus resultierenden Pflanzen durchgeführt.

In der ersten Studie wurden Stecklinge von heckenartig beschnittenen Bäumen von Ästen erster bis dritter Ordnung gesammelt. Hecken werden benutzt, da diese Äste verschiedener Ordnung liefern können, ohne daß der Cyclophysis-Effekt zerstört wird. In der zweiten Studie werden Äste gleicher Ordnung von jungen Sämlingen und Äste zweier verschiedener Ordnungen der oben erwähnten Hecke verwendet. Bei der zweiten Studie wurde erwartet, daß die mögliche Interaktion zwischen Topophysis und Cyclophysis zum Teil aufgeklärt werden könnte, da Hecken sich in einem fortgeschrittenen Reifezustand befinden als Sämlinge.

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Die Ergebnisse zeigen, daß sowohl Reifestadium als auch Astordnung signifikante Auswirkungen auf die Bewurzelung von Stecklingen und die Wachstumsmerkmale der daraus resultierenden Pflanzen haben. Die Resultate stützen auch das Konzept einer Interaktion zwischen Cyclophysis und Topophysis.

Introduction

Rooting techniques for a variety of forest trees are now fairly well developed (ARMSON and BIDWELL, 1971; ARMSON *et al.*, 1980; DEUBER, 1940; DORAN, 1954, 1957; FARRAR and GRACE, 1942; GIROUARD, 1970 a, b, 1971, 1972, 1974, 1975; HILL and LIBBY, 1969; LARSEN, 1955; LEPISTÖ, 1974, 1977; RAUTER, 1971; THIMANN and DELISLE, 1942; WERNER, 1979), but some problems still remain. A common problem in vegetatively propagating conifers is topophysis, in which stecklings (established rooted cuttings) maintain a growth habit similar to that of the donor shoots. Cuttings from branches often persist in growing plagiotropically for months, or even years, after grafting or rooting (DORMLING, 1980; FORTANIER and JONKERS, 1976; OLESEN, 1973, 1978; ROULUND, 1973, 1974, 1975, 1977, 1978, 1979 a, b, 1981; SCHAFFALITZKY DE MUCKADELL, 1959).

Several studies have attempted to quantify effects of topophysis on the rooting of cuttings, and the subsequent stem form of the resulting stecklings (TUFOUR, 1973; ROULUND, 1975, 1979 b). However, cuttings have generally been selected from different heights within the tree and with no attention being given to rank order of the cutting shoot on the parent branch. As OLESEN (1978) pointed out, results from these studies are unable to prove topophytic effects, since they are confounded by gradients of maturation (cyclophysis) within the crown.

During a decade's observations with various kinds of coast redwood (*Sequoia sempervirens* D. DON (ENDL)) propagules, we have noted that recently rooted young stecklings exhibit a wide spectrum of stem angles; some vertical, but most non-vertical to varying degrees. It was clear that the persistence of plagiotropic growth of stecklings was longer for cuttings taken from older plants, or for cuttings from higher in the crown of a tree. ROULUND (1975, 1979 b), and