Growth and yield of maritime pine (Pinus pinaster Ait): the average dominant tree of the stand

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(Received 31 August 1990; accepted 24 June 1991)

Summary — A stand growth model was developed using 2 attributes, height and basal area of the average dominant tree. The model is based on temporary plots corresponding to different silvicultural treatments, thinning and fertilization experiments.

- Regarding the first attribute, dominant height growth: a model using 2 uncorrelated parameters was developed. It was derived from a previous principal component analysis based on data issued from stem analysis. The first parameter is an index of general vigor, which is well correlated with the dominant height \( h_0 (40) \) at the reference age of 40 years. The second parameter refers to variations in the shape of the curve, particularly for initial growth. The growth curves of the various temporary plots could be accurately described with this model. Phosphorus fertilization at the time the stand was established improved both dominant height \( h_0 (40) \) and initial growth.

- Regarding the second attribute, basal area growth: the basal area increment was described using 4 independent variables: height increment, dominant height \( h_0 (40) \), age and competition. This model includes the effect of stand density. It was validated considering the error term and its first derivative according to age. The model may therefore be used as a growth function. Nevertheless, residual variance was rather high and could be subdivided into a random component (75% of the residual variance) and a slight autocorrelation term, i.e. a correlation between successive deviations due to unknown factors. The relationship between basal area growth and age was assumed to be the result of both increased leaf biomass and dry matter partitioning. The relationship to height increment may result from leaf biomass and morphogenetical components, both number of needles on the leader and the other foliated shoots.

变压pine / stand / growth model / competition / fertilization

Résumé — Croissance et production du pin maritime (Pinus pinaster Ait). L'arbre dominant moyen du peuplement. On a construit deux modèles de croissance concernant deux caractéristiques du peuplement dominant: sa hauteur et sa surface terrière. On a utilisé les données d'analyses de tiges, de placettes temporaires mesurées plusieurs fois, ainsi que d'expérimentations sur la fertilisation minérale, les densités de plantation et les éclaircies. 1) Croissance en hauteur. Un modèle à deux paramètres non corrélés entre eux a été mis en œuvre. Il est issu d'une analyse en composantes principales de données d'analyses de tiges. Le premier paramètre exprime une vigueur générale tout au long de la croissance du peuplement et est bien corrélé avec la hauteur dominante \( h_0 (40) \) à l'âge de référence de 40 ans. Le second paramètres exprime la croissance initiale jusqu'à 10 ans et caractérise ainsi la forme de la courbe de croissance. Le modèle s'adapte bien aux données de placettes temporaires de divers âges. La fertilisation phosphorée améliore la hauteur dominante \( h_0 (40) \) ainsi que la croissance initiale. 2) Croissance en surface terrière. L'accroissement en surface
The objective of the study was to determine the functions that describe growth of the average dominant tree in maritime pine stands. Two important attributes of a tree are considered: height and basal area. Competition effects are also taken into account. The study refers to the entire Landes forest in southwestern France and includes fertilized stands. Mauge (1975) worked on the same species in the same region. He considered height and girth of the average tree of the entire stand and obtained 3 growth submodels: height, girth in open growth conditions and girth with competition effects.

The construction of a growth model should be seen within the framework of an evolving silviculture: intensive cultivation and dynamic stand management. Growth and production of younger stands are thus notably higher than that of older stands. For these reasons the constructed model takes these modalities into account. However, the model needs to be verified in the future.

The dominant height

The biological variation in height increment curves for maritime pine stands originating from natural regeneration has been previously studied by a factorial analysis based on stem analysis (Lemoine, 1981). The study showed that at least two parameters (principal components) were necessary to adequately describe the variation. Lappi and Bailey (1988) reached the same conclusion for loblolly pine (Pinus taeda L.). The site index alone, or the height at a specific age, was therefore not sufficient. Several authors have reported similar conclusions. Monserud (1985) noticed that the shape of the growth curves in Douglas fir varied significantly between 3 major habitats of the natural range of the species. He concluded that the geographic variation of environmental or genetic factors may lead to these results. Milner (1988) used a method to characterize the shape of growth curves for Douglas fir. Garcia (1983) obtained a multiparametric growth function that could be applied to plots measured 3 to 4 times.

Based on the results of earlier studies (Lemoine, 1981) the present analysis attempts to develop a growth model using more than 1 parameter. In fact, the principal component analysis mentioned above demonstrates the existence of more than 1 single cause for growth variation. The model will then be applied to both traditional and modern silvicultural stands.
The dominant basal area

Purpose of the study

Diameter growth of the average dominant tree of the stand has rarely been studied per se. In most cases it constitutes only an output of the model used to develop yield tables (Bartet, 1976). It is important to underline that: i), it is possible to determine for this average tree a biological interpretable relationship between basal area and height growth; ii), in maritime pine stands, the volume of the 100 largest trees per hectare represents ≈ 50% of the final harvest (250 stems per ha).

Effect of competition

In this study the effect of competition on the dominant tree will be studied at 3 levels.

Dendrometrical level

The "crown competition factor" or CCF (Arney, 1985) is often used in models of individual tree growth. It leads to the concept of "growing space" or GS, which is the area a single tree needs for maximal growth. GS is a function of the surface of the crown in completely open growth conditions and can be estimated by the diameter at breast height. In this paper the effect of competition is studied by considering tree size.

Social level

Competition between trees in a stand can be either 1- or 2-sided.
- 1-sided competition refers to competition of a dominant tree towards its neighbors, which in turn do not compete with it;
- 2-sided competition refers to reciprocal competition between neighboring trees.

Studies of individual trees are obviously the best adapted to the identification of the competition type. For instance, in young stands of Pinus contorta and Picea sitchensis, competition is 1-sided (Cannel et al., 1984).

One objective of this study was also to identify the competition type of the dominant average tree: does the density of the surrounding non-dominant stand have a negative influence on growth of the average dominant tree?

Ecophysiological level

Theoretical aspects of this topic and experimental results have been given in an earlier publication (Lemoine, 1975).

Mitscherlich (in Kira et al., 1953) considered that the available space for plant growth was a proportion (z) of the factor used for the growth increment y, where the total quantity available within a given area was Z. If N is the stand density, then each tree benefits by a quantity z = Z/N. The reaction equation of the plant to the density is:

\[ y = M \cdot (1-e^{-c \cdot z/N}) \]  

where \( M \) and \( c \) are 2 parameters dependent on species, age and site.

This equation takes into account a law used in agronomy, "the law of diminishing returns" (in Prodan, 1968). The first derivative of \( z \) of the previous function is:

\[ \frac{dy}{dz} = M \cdot c \cdot e^{-c \cdot z} \]  

This shows that the efficiency of an additional quantity (dz) decreases with the quantity z already offered by this factor.

Based on Mitscherlich's theory, we have shown (Lemoine, 1975) that: i), competi-
tion acts not only for energy, but also for water and alternates according to seasonal and climatic fluctuations; ii), competition for energy and water decreases when temperature and rainfall increase.

An alternative way of varying the energy and water factor for one tree is to increase available space, *ie*, by increasing the intensity of thinnings. As a result, the difference between the efficiency of heavy and average thinnings for diameter growth should be less than the difference between the efficiency of average and low thinnings.

From this brief review of the effects of competition, it becomes obvious that conclusions obtained in previous growth studies on maritime pine should be included in the development of growth models. This study attempts to include these aspects in the model itself.

**MATERIAL AND METHODS**

**Variables assessed**

The following variables were assessed in experimental plots:

- the age *A* of the stand (years);
- the number of trees per ha (*N*);
- the dominant basal area *g₀* (cm²), *ie*, the average tree basal area of the 100 thickest trees per ha.*g₀* was considered to represent the basal area of the average dominant tree.
- the dominant height *h₀* (m), *ie*, the height of the tree with a basal area *g₀*. *h₀* is obtained on the basis of the "height curve" constructed for the plot sample using the relationship between height and diameter on an individual tree basis. *h₀* was considered to represent the height of the average dominant tree.
- dominant height *h₀* (40) at the reference age of 40 years, *ie* close to final harvest.
- the annual mean increments *Ig₀* (cm².year⁻¹) and *Ih₀* (m.year⁻¹) of the 2 attributes *g₀* and *h₀*.

**Material (table I)**

Data for the analysis came from 6 different sources:

- stem analysis in traditional silvicultural stands;
- experimental plots set up in stands of various ages. Data were collected every 3-5 years. It is important to underline that these samples include stands established between 1916 and 1973 which have been subjected to different silvicultural practices;
- a fertilization experiment with 5 blocks and 7 treatments: T (unfertilized control), P (phosphorus), N (nitrogen), K (potassium), NP, PK and NPK. Since only phosphorus treatments had a significant effect (Gelpe and Lefrou, 1986), only data from the control T and P treatment were analyzed at 8, 12, 16, 21 and 26 years of age;
- a first thinning experiment (THIN1) with 5 blocks and 5 treatments: sanitary thinning, low, average, heavy and extremely heavy thinning (Lemoine and Sartolou, 1976). The experiment was conducted between 19-38 years of age with 4 thinnings;
- a spacing trial (SPACING) which also focused on studying genotype and ground clearance factors. Only results for 2 densities from this experiment (2 x 2 m and 4 x 4 m spacings) are used here;
- a second thinning experiment (THIN2) was carried out over 0-40 years and including 6 blocks. The procedure involved 2 treatment periods: i), from 0 to 25 years of age, with 2 types of thinning, low or heavy; ii), from 25-40 years of age, with 4 types of thinning: initially low (up to 25 years of age) and remaining low, initially low becoming heavy, initially heavy remaining heavy, initially heavy becoming low. The fertilization factor (phosphorus supply at 25 years of age) was also studied through 2 treatments, either with or without fertilization.

All data were processed with the statistical software designed by Baradat (1980).
Methods

Growth of dominant height

The analysis involves 2 steps: construction of the growth model and its application.

Construction of the growth model

The data from the stem analysis (SA experiment; see table I) are interpreted in terms of autocorrelation. Successive stages of the same variable $h_0$ are considered as separate variables. They are more or less correlated between one another depending on the lag time separating them. Principal component analysis (PCA)
can then be used to identify genetic, physiological or environmental effects (Baker, 1954). However, to our knowledge this method has not yet been used for prediction purposes.

The method for obtaining the growth curve of each specific individual (a stand) is as follows:
- $\beta_0 (A)$ is the mean height growth curve (i.e., the mean of the observed values of $h_0$ at successive ages $A$);
- PCA supplies $p$ principal factors $\beta_1 (A), \beta_2 (A), \ldots, \beta_p (A)$ which are independent;
- for a specific individual the variable $h_0 (A)$ is a linear combination of $\beta_0 (A), \beta_1 (A), \beta_2 (A), \ldots, \beta_p (A)$:

$$h_0 (A) = \beta_0 (A) + \beta_1 (A)Y_1 + \beta_2 (A)Y_2 + \ldots + \beta_p (A)Y_p \quad (3)$$

where $Y_1, Y_2, \ldots, Y_p$ are the factorial coordinates of the individual curve.

Equation (3) can be written as a growth function:

$$h_0 (A) = f(A, Y_1, Y_2, \ldots, Y_p) \quad (4)$$

in which $Y_1, Y_2, \ldots, Y_p$ may be assimilated to the parameters of the specific individual.

Another method (Houllier, 1987) consists of fitting a non-linear model with several parameters to each individual observed curve. Then the variability of the parameters is studied with multivariate techniques (analysis of variance and PCA).

**Application to the experimental plots**

The objectives are 2-fold: i), to realize an initial verification of the model within the framework of current or recent silvicultural techniques; ii), to consider the growth tendencies induced by these techniques. In both cases, a comparison with traditional silvicultural stands is performed.

Compared to stem analysis, only a few successive measurements were available in the experimental plots. These data could be analyzed using the following model with only 2 parameters (see Construction of the growth model):

$$h_0 (A) - \beta_0 (A) = \beta_1 (A)Y_1 + \beta_2 (A)Y_2 \quad (5)$$

For each height–age couple, the values of $h_0 (A), \beta_0 (A), \beta_1 (A), \beta_2 (A)$ are known. $Y_1$ and $Y_2$ are the coefficients of a multiple regression passing through the origin. They are estimated for each stand.

These coefficients are the curve parameters calculated for each experiment plot. The accuracy of each calculated curve is evaluated and compared to the parts of curves obtained by measurements. General evolution of $Y_1, Y_2$ parameter couples from the oldest to the youngest stands makes it possible to characterize the overall impact of modern silvicultural techniques on growth.

**Growth of the dominant basal area**

**General methodology**

In most cases the relationship between dendrometrical variables $Y$ and $X$ ($Y = f(X)$) or between their increments $\Delta Y$ and $\Delta X$ ($\Delta Y = f(\Delta X)$) are estimated on the basis of a single measurement made at the same time or growth period in different plots of various ages. From these data a growth function can be obtained that is applicable to each stand. The hypothesis is then usually made that stands of various ages but of similar vigor can be regarded as consecutive stages of the same stand. However, the differences between measurements of these plots could be due not only to the effect of age but also to growth conditions, i.e., genetic and environmental factors.

This methodology is also used in this study. However, because of the above-mentioned reasons, the validation of this approach is evaluated. The model used for prediction of the basal area increment is:

$$\log B = f(lh_0, A, h_0 (40), COMP) \quad (6)$$

where $COMP$ is a competition factor.

The choice of an equation type for model (6) is based on the following considerations:
- Mitscherlich's law of growth factor effects (in Prodan, 1968) suggests the use of a multiplicative model including variables of model (6).
- Arney (1985) found an appropriate multiplicative model for individual tree diameter increment ($\Delta DBH$) as a function of diameter ($DBH$), top height ($TOP$) and its increment ($\Delta TOP$) and crown competition factor ($CCF$).
\[ \frac{\Delta \text{DBH}}{\Delta \text{TOP}} = B_1 \cdot \left(\frac{\text{CCF} \cdot 100}{\text{DBH}}\right)^{B_2} \left(1 - e^{B_3 \cdot \left(\frac{\text{DBH}}{\text{TOP}}\right)}\right)^{B_4} \]

He evaluated the intensity of the CCF effect by calculating the \( B_2 \) regression coefficient. Here, for maritime pine, the experimental plots (SPACING, THIN1 and THIN2) made it possible to directly define and validate a competition function.

The following type of equation is used for temporary plots:

\[ \ln(y_{01}/y_{00} \cdot \text{COMP}) = b_0 + b_1 \cdot h_0 + b_2 \cdot h_0 + b_3 \cdot A + b_4 \cdot \text{COMP} \]

(7)

where:
- the independent variables \( h_0 \) and \( A \) are introduced as growth factors;
- the independent variable \( h_0 \) is introduced to point out a possible lack of proportion between \( y_{00} \) and \( y_{01} \);  
- the independent variable \( \text{COMP} \) is introduced to verify the proportionality of \( y_{00} \) and \( \text{COMP} \) by confirming that \( b_4 \) is not significant.

Coefficients are estimated by multiple regression.

Predictors of model (7) are obtained as follows:
- \( h_0 \) and \( h_0 \) are obtained by model (5) applied to each plot (S1 to S4 in table I). The height increment of the smoothed curve is a better predictor of girth increment than the height increment itself because the latter is affected by measurement errors (Lemoine, 1982).
- Calculation of \( \text{COMP} \) (competition factor) is described in detail in Effect of competition (model (9)).
- \( A \) (age) is the mean value of age during the growth period.

The validation of the model does not consider the deviations of the dependent variable \( \ln(y_{01}/y_{00} \cdot \text{COMP}) \) from model (7), but refers to the \( \epsilon \) deviations of the initial variable, \( y_{00} \):

\[ \epsilon = y_{00} - (h_0, \text{COMP}) \cdot (b_0 + b_1 \cdot h_0 + b_2 \cdot h_0 + b_3 \cdot A + b_4 \cdot \text{COMP}) \]

Three characteristics of \( \epsilon \) are analyzed:
- its variation according to the independent variables of equation (7), mainly age \( A \) to evaluate the precision and the accuracy of long-term-prediction made by the model and competition \( \text{COMP} \) to evaluate the value of the model as a mean of optimizing successive thinnings.
- the value of the first derivative to the model:

\[ e = \frac{df}{dA} \]

if \( y_{01} \) and \( y_{02} \) are 2 successive measurements of \( y_{00} \) and \( A_1 \) and \( A_2 \) are the mean ages for the 2 successive growth periods, then an approximate value of \( e \) can be obtained by:

\[ e = \frac{y_{02} - y_{01}}{A_2 - A_1} - \frac{\hat{y}_{02} - \hat{y}_{01}}{A_2 - A_1} \]

(8)

where \( \hat{y}_{01} \) and \( \hat{y}_{02} \) are the estimates of \( y_{01} \) and \( y_{02} \) obtained from model (7). If \( e \) is a random variable with a mean zero, the growth model remains valid for all the studied stands.

- The nature of the correlation between 2 successive \( \epsilon (\epsilon_1 \) and \( \epsilon_2 \) ie, the autocorrelation (Björnsson, 1978). Generally the correlation between successive deviations decreases when the lag time increases. If there is a significant autocorrelation, then model (7) excludes at least 1 growth factor which classical dendrometrical methods have not identified.

This basal area growth model, like the height growth model, should continue to be verified as the young stands grow.

Effect of competition

The effect of competition on the dominant tree is studied in the thinning experiment (THIN1 experiment in table I). The data corresponding to 4 successive measurements between 19 and 38 years of age are fitted to Mitscherlich's law (model (1)). For the basal area increment (\( y_0 \)) the law can be written as follows:

\[ y_0 = y_{0M}(1-e^{-cs}) \]

(9)

where:
- \( y_{0M} \) is the asymptotic value, corresponding to open growth;
- \( s \) is the space available for a tree \( s = 10000/ \) N, where \( N \) is the number of trees per ha;
- \( c \) is a coefficient that can be interpreted as the variation of \( y_0 \) related to deviation from the open growth conditions;
\((1-e^{-c\cdot t})\) represents COMP, the competition factor in models (6) and (7).

The THIN2 experiment makes it possible to validate this law of competition. The COMP variable is used to establish the general growth model (6) and (7) from the data obtained from all experimental plots \((S_1 \text{ to } S_4 \text{ in table I})\). An additional validation of this law can thus be performed.

*Estimation procedure*

Experimental plots \(S_1 \text{ to } S_4 \) (see table I) are subdivided into 2 sets: ECH1 and ECH2. The subdivision is made according to the distribution of the plots on the graph \((A, h_0)\). 46 couples of similar plots for \(h_0\) and \(A\) values are chosen. Plots within a couple are randomly assigned to ECH1 and ECH2. Two successive measurements of \(Ig_0\) are available for each plot.

The first measurements in the ECH1 sample are used to fit model (7) to the data. The second measurements of \(Ig_0\) in ECH1 and both measurements in ECH2 are used to verify model (7).

**RESULTS**

*Growth of dominant height*

*Construction of the model*

Stem analysis carried out within each of the 25 stands yielded successive dominant heights from age 5 to 50 every 5 years. The data are arranged in a 2-way table (age, stand) with 10 columns and 25 lines.

The correlation coefficient matrix between dominant heights at different ages is calculated and interpreted using principal component analysis. Eigen values of the principal components in percent of total variation are respectively: 88.8, 9.2, 1.2, 0.6 ... Vectors corresponding to the 10 original variables, ie, dominant heights at different ages, are represented on the graph with the first 2 principal components as axes (fig 1).

The mathematical structure of the data is similar to that described in other biological fields. As stated by Buis (1974) and using his terminology, the data refer to a "growth geometry", ie, the vectors corresponding to the original variables in figure 1 follow each other in chronological order. This "growth geometry" illustrates the fact that correlation between dominant height at a given age \((h_0(A))\) and the first dominant height \((h_0(5))\) decreases with increasing age. For example, the correlation coefficient between \(h_0(10)\) and \(h_0(5)\) is 0.90, while the correlation coefficient between \(h_0(40)\) and \(h_0(5)\) is only 0.52.

These results have practical consequences: any model using \(h_0(5)\) or \(h_0(10)\) as independent variables will have poor predictive value.

![Fig 1. Growth of dominant height. Principal component analysis. Graph with the 2 principal components \(Y_1\) and \(Y_2\) as axes. Vector projections of the 10 initial \(h_0(A)\) variables. Nos 1–10 = successive heights from age 5 to age 50 years.](image)
Principal components based on stem analysis can now be used as parameters for a dominant height growth model. Only the 2 first components (Y₁ and Y₂) are included in the model, since the eigen values of the remaining components are very low.

Dominant height (h₀ (A)) at a given age A is expressed as follows:

\[ h₀ (5) = β₀ (5) + β₁ (5).Y₁ + β₂ (5).Y₂ \]
\[ h₀ (10) = β₀ (10) + β₁ (10).Y₁ + β₂ (10).Y₂ \]
... \[ h₀ (A) = β₀ (A) + β₁ (A).Y₁ + β₂ (A).Y₂ \]

Table II shows the values of the different coefficients β₀ (A), β₁ (A) and β₂ (A) at the different ages. They are assumed to be constant throughout the Landes area. The first coefficient β₀ (A) follows Mitscherlich's growth function (in Prodan, 1968) with age:

\[ β₀ (A) = 29.93.(1−e^{−0.036.A})^{1.501} \]

Data are adjusted to model (10) using the transformed bilogarithmic equation; the value of the c coefficient is the one leading to the lowest residual variance; the intercept is the logarithm of the asymptote; the exponent is the regression coefficient.

Since β₀ (A), β₁ (A) and β₂ (A) are only known for A = 5, 10, ..., 50, it is necessary to estimate intermediate values. The first coefficient β₀ (A) follows model (10). For β₁ (A) and β₂ (A) linear and quadratic interpolations are used.

As indicated by the correlations between the original variables of the stem analysis and the principal components, the first component (Y₁) can be interpreted as an index of general vigor from 15 to 50 years of age. Therefore it is well correlated with the dominant height h₀ (40) at the reference age of 40 years. The second component (Y₂) is related to the initial heights at 5 and 10 years of age and to the shape of the growth curve. As shown in figure 1, the lower the Y₂ component, the higher the initial growth.

**Table II. Dominant height.**

<table>
<thead>
<tr>
<th>A</th>
<th>βₐ,0</th>
<th>βₐ,1</th>
<th>βₐ,2</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>2.03</td>
<td>0.071</td>
<td>-0.123</td>
</tr>
<tr>
<td>10</td>
<td>4.84</td>
<td>0.207</td>
<td>-0.303</td>
</tr>
<tr>
<td>15</td>
<td>8.00</td>
<td>0.344</td>
<td>-0.220</td>
</tr>
<tr>
<td>20</td>
<td>11.06</td>
<td>0.46</td>
<td>-0.063</td>
</tr>
<tr>
<td>25</td>
<td>13.84</td>
<td>0.531</td>
<td>0.102</td>
</tr>
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</tr>
<tr>
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<td>18.31</td>
<td>0.61</td>
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</tr>
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<tr>
<td>50</td>
<td>22.63</td>
<td>0.666</td>
<td>0.489</td>
</tr>
</tbody>
</table>

Coefficients of the growth function (model (3)):
\[ h₀(A) = β₀(A) + β₁(A).Y₁ + β₂(A).Y₂ \]
Successive values according to age A.
4 times according to the method explained in *Application to the experimental plots*.

**Accuracy of the model**

The $Y_1$ and $Y_2$ parameters of equation (5) are calculated using the least-square method for each plot independently: then the specific curve of each plot is obtained.

Eight temporary plots with typical growth are chosen to illustrate the application of the model (5) (fig 2). The model is quite flexible since different shapes of

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*Fig 2. Growth of dominant height. Eight growth curves estimated by model [5]. P205 and control = mean values of the fertilization experiment. $S_1$ = stands established between 1916 and 1936. $S_4$ = stands established between 1968 and 1973.*
growth curves can be represented without experimental errors.

In order to check the quality of the model, the plots which had been measured more than four times were grouped by age classes. For each age class and each successive measurement the average of the deviations from the model was computed. Figure 3 shows that there is no particular trend and that deviations may be considered as randomly distributed. The deviation corresponding to the fourth measurement in young stands is important and negative. One explanation is the reaction of the trees to the extremely and unusually low temperatures that occurred in January 1985.

Variation of the experimental plots

Mean values \((Y_1, Y_2)\) of the parameters of each set of experimental plots except the THIN1, THIN2 and SPACING experiments (table I) are represented in figure 4. The origins of the axes correspond to the stem analysis experiment (SA). In addition, the ellipse including all the individual plot values of the SA experiment is also represented. The striking features of figure 4 are the location of all the points in the fourth quarter of the graph and the distribution of the points along a chronological slope. \(Y_1\) increases and \(Y_2\) decreases from older to more recent stands. In other words, when dominant height \(h_0\) (40) increases, the shape of the growth curve is also modified by increasing the initial height.

**Dominant height growth in fertilization treatments**

Compared to the control, phosphorus treatment (P205 in figs 2 and 4) shows a higher value of parameter \(Y_1\) and a lower value of parameter \(Y_2\). Because of the significance of the 2 parameters, phosphorus fertilization therefore has an effect on the dominant height \(h_0\) (40) at the reference age of 40 years (increase of 2.5 m) and on the shape of the growth curve by increasing initial growth.

**Dominant basal area growth**

As mentioned in the Method section, the effect of competition on basal area is first studied before the growth model is con-

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**Fig 3.** Growth of dominant height. Deviations from model [5] for each plot measured at least 4 times. Mean values for 10 samples of 4–6 same age plots. \(- - - \bullet \bullet \bullet\) = measurements corresponding to frost effect in January 1985 (data not used in model [5]).
structed in order to identify the competition parameter that had to be introduced into the model as an independent variable.

**Effect of competition**

**Verification of Mitscherlich's law**

Data from the THIN1 thinning experiment are used. Variations in $Ig_0$ according to average space $s$ are shown for 4 successive ages (fig 5). Data are adjusted to model (9) using a regression passing through the origin. The value of the $c$ coefficient considered for each age is the one leading to the lowest residual variance. $Ig_{0M}$ is the regression coefficient obtained. Figure 5 shows that in each case the curve obtained follows closely Mitscherlich's law.

**Variation from Mitscherlich's law**

The results obtained above show that the value of parameter $c$ decreases when basal area $g_0$ increases (fig 6). Data from the SPACING experiment provide information lacking at a younger age (very low basal area $g_0$). As only 2 couples of data are available, $Ig_{016}$ for $s = 16$ m$^2$ and $Ig_{04}$ for $s = 4$ m$^2$, the $c$ value is obtained by solving the following equation:

**Fig 4.** Growth of dominant height. Mean values of $Y_1$ and $Y_2$ parameters for each set of experimental plots. Origin of the graph = means of stem analysis experiment SA. Ellipse = distribution of SA data (25 plots). PSSA = average plot simulation with the 3 first data ($h_0(5)$, $h_0(10)$ and $h_0(15)$) of SA. $S_1$ to $S_5$ = sample of the stands established from 1916 to 1973. P205 and control = fertilization experiment.

**Fig 5.** Growth of dominant basal area. Thinning experiment (THIN1). Mitscherlich's law applied to competition (model [9]). Four growth periods: 1) and $\bullet$ = 19–23 years of age; 2) and $\bigcirc$ = 23–27 years of age; 3) and $\triangle$ = 27–32 years of age; 4) and $\blacktriangle$ = 32–38 years of age. Curves of model [9].
where \( c = 0.350 \) and \( I_{0M} = 40.37 \text{ cm}^2 \) for \( g_0 = 108 \text{ cm}^2 \). The variation law for \( c \) as a function of \( g_0 \) is obtained by the least-square method:

Validation of model (12)

The THIN2 experiment is used to verify model (12). The \( c \) values are obtained by the method described above in the verification of Mitscherlish's law. Nine additional points are obtained and only one is notably off the curve calculated by model (12) (fig 6). It should also be noted that the competition law remains the same whether fertilization is applied or not.

Construction of the model

Figure 7 represents the variation of \( I_{0} \) as a function of \( l_{0} \). When considering the whole sample of points, there is no relationship between both variables. However, when the sample is stratified according to age and \( h_0 (40) \) classes, there is a significant relationship within each age class and a less obvious relationship within each \( h_0 (40) \) class.

The relationship \( I_{0}/l_{0} \) also varies according to age \( A \).

The following regression equation can be found for model (7):

\[
I_{0}(l_{0} \cdot COMP) = 14.69 - 90.74 \cdot l_{0} + 3.40 \cdot h_{0} (40) + 1.57 \cdot A \quad (13)
\]

Model (13) has the following properties:

i), the \( COMP \) independent variable in the second part of the equation is not significant (probability of Student's test = 0.60) and can thus be maintained as \( COMP^1 \) in the first part; ii), all the other independent variables are significant (probability of Student's test = \( \leq 0.005 \)); iii), the multiple regression coefficient is \( R = 0.9179 \) and the residual standard deviation (\( = 12.56 \)) represents 17% of the average dependent variable.

Validation of the model

Model (13) is then applied successively to the different ECH1 (second measurement) and ECH2 (first and second measurements) samples. Deviations (see General methodology) between \( I_{0} \) observed values and \( I_{0} \) estimated values by model (13) are compared with the predictive variables \( l_{0} \), \( h_0 (40) \), \( A \) and \( COMP \) in figures 8a, b, c and d. The deviations obtained are never dependent on the values of these variables. However, the average deviation obtained for all the 186 data points is sig-

\[
\frac{I_{016}}{I_{04}} = 40.23/30.37 = (1-e^{-c.16})/(1-e^{-c.4}) \quad (11)
\]

where \( c = 0.350 \) and \( I_{0M} = 40.37 \text{ cm}^2 \) for \( g_0 = 108 \text{ cm}^2 \). The variation law for \( c \) as a function of \( g_0 \) is obtained by the least-square method:

\[
c = 115.854/(g_0 + 215) \quad (12)
\]
significantly different from zero (probability of Student's test = 0.025). Nevertheless, this bias for Ig0 (+ 0.952 cm².year⁻¹) has a relative low value.

Use of the model as a growth function

The mean value of the first derivative of the deviations to model (13) is close to zero ($e = 0.164$ cm².year⁻²) and not significant (probability of Student's test = 0.20). The studied variable $e$ follows a parabolic law according to the age of the plots (global correlation = 0.378). This fact means mainly that $e$ has a negative value in very young stands ($e = -1.01$ cm².year⁻²). Some drift could occur in this specific case. Model (13) can therefore be considered to be a growth function for plots of any age.

Autocorrelation

Successive deviations from model (13) ($\epsilon_1$ and $\epsilon_2$) are correlated, which indicates a slight autocorrelation:

![Graph showing growth of dominant basal area.](image-url)
Fig 8. Growth of dominant basal area (N) deviations from model [13] for temporary plots (S_i to S_j in table). Relationships with variables: A: with AGE; B: with COMP; C: with h; D: with h_i. 1: ECH1 1st measurement; 2: ECH2 1st measurement; 3: ECH1 2nd measurement; 4: ECH2 2nd measurement.
The value of the regression coefficient obtained, which is significantly different from 1.00 (probability of Student’s test < 0.001 ***) shows that there is a regressive autocorrelation. The stand thus contained growth factors whose activity is limited over time and which is not taken into account by the model used.

DISCUSSION

Dominant height

Dominant height growth can be described by a model including 2 parameters that have dendrometric significance: dominant height $h_0$ (40) at the reference age of 40 years and shape of the growth curve.

When considering all the experimental plots throughout the Landes area, a variation trend of the 2 parameters over time is shown (fig 4). It corresponds to the evolution of silvicultural practices since the beginning of the 20th century. They have been improved constantly from natural regeneration to sowing using ploughing and fertilization. According to this study (fig 4), they have resulted in an increase in the initial growth and dominant height $h_0$ (40).

Similar conclusions have been already obtained in the same fertilization experiment (Gelpe and Lefrou, 1986). The results showed that initial phosphorus fertilization led to an improvement in the annual height increment up to age 16 yr. The initial gain in total height was maintained after age 16 yr and led to an increase in dominant height $h_0$ (40).

It has yet to be proven whether genetic selection of maritime pine will improve height growth in the same manner. There is some evidence that it will as selection criteria for production are based on height growth performance up to age 12 years (Baradat, 1976).

Basal area increment

Three main conclusions can be drawn from the model of basal area growth of the dominant tree.

- Height increment is a significant predictive variable only if age, dominant height $h_0$ (40) and competition are introduced into the model as independent variables.
- The model has an average predictive value. However, the error term can still be subdivided into a systematic component (autocorrelation) representing 25% of its variation and a residual random component. As suggested by equation (14), successive deviations are correlated which indicates the existence of growth factors whose action on the stand is constantly reduced over time (for example, climatic fluctuations).
- The first derivative of the error term has a mean value close to zero except for very young stands or for stands in their initial stage of growth. There is practically no drift in the model and it can therefore be considered to be a growth function.

The model has been constructed for management and silvicultural purposes. It is basically a statistical model and no functional or biological interpretations can be made except concerning dominant height $h_0$ (40) and competition.
Cambial growth is dependent on the development of the crown and leaf surface of the tree (Kozlowsky, 1971). Experimental data have often shown significant correlations between leaf biomass or crown size and basal area increments (Kittredge, 1944; Lemoine et al., 1986). These relationships were used to build single tree growth models (Mitchell et al., 1982). From these observations one may interpret the relationship between basal area increment and age. Increase of leaf biomass with age induces an increase in the basal area increment. However, "dry matter partitioning" (Cannel, 1985; Ford, 1985) may vary with age and as a result modify allocation to the basal part of the stem.

The relationship between height increment and basal area increment is questionable. Is it only statistical or could it also be biological? It can be interpreted as resulting from the control of cambial growth by leaf biomass. Two morphogenetical components of height growth have been identified in maritime pine (Kremer and Roussel, 1982): the number of stem units (NSU), and mean stem unit length (MSUL). According to Doak (1935) a stem unit is "an internode, together with the node and nodal appendages at its extremity". In various experimental trials, it has been shown that NSU is better correlated to height increment than MSUL (Kremer, 1985). NSU gives a good estimate of the number of needle fascicles on a shoot (Kremer and Roussel, 1982). There is also a significant correlation of NSU between the leader and the branches (Lascoux, 1984). One can therefore consider it as an important component of leaf biomass of a tree.

From all these observations the correlation between height increment and basal area increment can be interpreted as resulting from the morphogenetical component of the leaf biomass.

General considerations

This growth model of dominant stand, when associated with submodels (passage from basal area of the dominant stand to that of the whole stand, technical effect of thinning, stand volume table, etc) is currently a useful management tool. Collaboration with public forestry management officials (Lemoine and Champagne, 1990) has made it possible, first, to evaluate the aptitude of a model to optimize stand management, and, second, to use experimental techniques to verify this growth model in the future.

ACKNOWLEDGMENTS

The authors is grateful to J Bouchon and P Duplat for helpful discussions. Special thanks are due to A Kremer for translation of the manuscript, A Sartolou for the measurements of the plots and J Darnaudery for execution of the graphics.

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