Ann Sci For (1991) 48, 593-611

Original article

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% ot the residual variance) and a slight autocorrelation term, *ie* 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.

maritime 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* *terrière est décrit par une régression multiple dont les variables explicatives sont: l'accroissement en hauteur, l'âge, la hauteur h_0 (40) et la concurrence. On a vérifié que le modèle est bien une relation de croissance en étudiant la dérivée du résidu selon l'âge: sa moyenne générale est voisine de 0 ce qui reste vrai pour presque toutes les classes d'âge. Cependant la variance résiduelle de l'accroissement est plutôt forte mais elle peut être subdivisée en une composante aléatoire (les trois quarts de la variance résiduelle) et une légère autocorrélation due à des facteurs inconnus. La relation avec l'âge pourrait être due au développement de la masse foliaire et à des modifications de l'allocation des ressources dans l'arbre. La relation avec l'accroissement en hauteur prendrait son origine dans les composantes communes à la masse foliaire et à la morphogénèse, aussi bien en ce qui concerne le nombre d'aiguilles sur les pousses latérales que sur la pousse terminale.*

pin maritime / peuplement / modèle de croissance / concurrence / fertilisation

INTRODUCTION

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:

$$y = M.\,(1 - e^{-c.Z/N}) \qquad (1)$$

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 to *z* of the previous function is:

$$\frac{dy}{dz} = M.c.e^{-c.z} \qquad (2)$$

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

Based on Mitscherlich's theory, we have shown (Lemoine, 1975) that: i), competition 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 g_0 (cm^2), *ie*, the average tree basal area of the 100 thickest trees per ha.g_0 was considered to represent the basal area of the average dominant tree.

– the dominant height h_0 (m), *ie*, the height of the tree with a basal area g_0. h_0 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. h_0 was considered to represent the height of the average dominant tree.

– dominant height h_0 (40) at the reference age of 40 years, *ie* close to final harvest.

– the annual mean increments Ig_0 (cm^2.year^{-1}) and Ih_0 (m.year^{-1}) of the 2 attributes g_0 and h_0.

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 sylvicultural 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).

Table I. Material.

Experimental design and code	*No of plots*	*Date of establishment of the stand*	*P205*	*Age at the first and last measurement*		*Plot area (ares)*	*No of trees per ha at the 1st measurement*
				First	*Last*		
Stem analysis							
S_A	25	1897–1929	No	5	50		
Temporary plots							
S_1	30	1916–1936	No	30–50	38–62	15–50	232–568
Temporary plots							
S_2	43	1937–1950	No	14–35	27–42	9–36	301–2444
Temporary plots							
S_3	19	1952–1964	No	8–19	16–27	8–27	648–2765
Temporary plots							
S_4	43	1968–1973	Yes	4–9	11–16	9–19	1 189–3 060
Fertilization experiment							
P205	5	1957	Yes	8	26	16	1 298
Control	5	1957	No	8	26	16	1 427
Thinning experiment							
THIN1	25	1947	No	19	38	10–15	391–1210
Thinning experiment							
THIN2	24	1947	No	13	41	20–32	1 643–2 070
THIN2	24	1947	Yes	13	41	20–32	1 576–1 953
Spacing experiment							
SPACING	16	1979	Yes	6	10	13–15	625–2 500

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:

– β_0 *(A)* is the mean height growth curve (*ie* the mean of the observed values of h_0 at successive ages *A*);

– PCA supplies *p* principal factors β_1 *(A)*, β_2 *(A)*, ..., β_p *(A)* which are independent;

– for a specific individual the variable h_0 *(A)* is a linear combination of β_0 *(A)*, β_1 *(A)*, β_2 *(A)*, ..., β_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, ..., 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, ..., 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)*, β_0 *(A)*, β_1 *(A)*, β_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 *IY* and *IX* ($IY = f(IX)$) 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, *ie,* 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:

$$Ig_0 = f(Ih_0, A, h_0 (40), COMP) \quad (6)$$

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 (*ΔDBH*) as a function of diameter (*DBH*), top height (*TOP*) and its increment (*ΔTOP*) and crown competition factor (*CCF*).

$\Delta DBH/\Delta TOP = B_1.(CCF/100)^{B_2}.(1-e^{B_3}.(DBH/TOP))^{B_4}$

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:

$$lg_0/(lh_0.COMP) = b_0 + b_1.lh_0 + b_2.h_0\,(40) + b_3.A + b_4.COMP \qquad (7)$$

where:

– the independent variables h_0 (40) and age A are introduced as growth factors;

– the independent variable lh_0 is introduced to point out a possible lack of proportion between lg_0 and lh_0;

– the independent variable *COMP* is introduced to verify the proportionality of lg_0 and *COMP* by confirming that b_4 is not significant.

Coefficients are estimated by multiple regression.

Predictors of model (7) are obtained as follows:

– lh_0 and h_0 (40) are obtained by model (5) applied to each plot (S_1 to S_4 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 *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 $lg_0/(lh_0.COMP)$ from model (7), but refers to the ε deviations of the initial variable, lg_0:

$$\varepsilon = lg_0 - (lh_0.COMP).(b_0 + b_1.lh_0 + b_2.h_0\,(40) + b_3.A + b_4.COMP)$$

Three characteristics of ε 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 *COMP* to evaluate the value of the model as a mean of optimizing successive thinnings.

– the value of the first derivative to the model:

$$e = \frac{d\varepsilon}{dA}$$

if lg_{01} and lg_{02} are 2 successive measurements of lg_0 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:

$$e = \frac{lg_{02} - lg_{01}}{A_2 - A_1} - \frac{\widehat{lg_{02}} - \widehat{lg_{01}}}{A_2 - A_1} \qquad (8)$$

where $\widehat{lg_{01}}$ and $\widehat{lg_{02}}$ are the estimates of lg_{01} and lg_{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 ε(ε_1 and ε_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 (lg_0) the law can be written as follows:

$$lg_0 = lg_{0M}.(1-e^{-c.s}) \qquad (9)$$

where:

– lg_{0M} is the asymptotic value, corresponding to open growth;

– s is the space available for a tree (s = 10 000/N, where N is the number of trees per ha);

– c is a coefficient that can be interpreted as the variation of lg_0 related to deviation from the open growth conditions;

– $(1-e^{-c.s})$ represents *COMP*, the competition factor in models (6) and (7).

The THIN2 experiment makes it posible 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 to S_4 in table I). An additional validation of this law can thus be performed.

Estimation procedure

Experimental plots S_1 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 lg_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 lg_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.

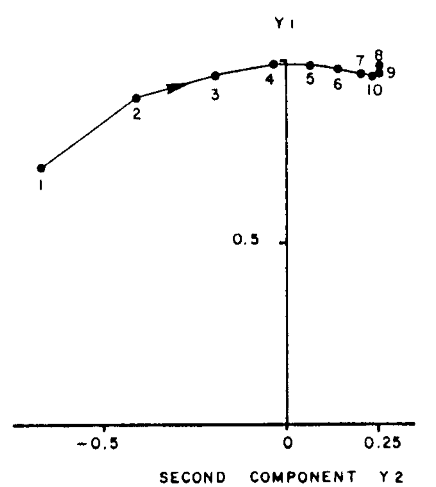

Fig 1. Growth of dominant height. Principal component analysis. Graph with the 2 principal components Y_1 and Y_1 as axes. Vector projections of the 10 initial $h_0(A)$ variables. Nos 1–10 = successive heights from age 5 to age 50 years.

Principal components based on stem analysis can now be used as parameters for a dominant height growth model. Only the 2 first components (Y_1 and Y_2) are included in the model, since the eigen values of the remaining components are very low.

Dominant height ($h_0(A)$) at a given age A is expressed as follows:

$$h_0(5) = \beta_0(5) + \beta_1(5).Y_1 + \beta_2(5).Y_2$$
$$h_0(10) = \beta_0(10) + \beta_1(10).Y_1 + \beta_2(10).Y_2$$
$$\ldots$$
$$h_0(A) = \beta_0(A) + \beta_1(A).Y_1 + \beta_2(A).Y_2$$

Table II shows the values of the different coefficients β_0 (A), β_1 (A) and β_2 (A) at the different ages. They are assumed to be constant throughout the Landes area. The first coefficient β_0 (A) follows Mitscherlich's growth function (in Prodan, 1968) with age:

$$\beta_0(A) = 29.93.(1-e^{-0.036.A})^{1.501} \qquad (10)$$

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 β_0 (A), β_1 (A) and β_2 (A) are only known for A = 5, 10, ..., 50, it is necessary to estimate intermediate values. The first coefficient β_0 (A) follows model (10). For β_1 (A) and β_2 (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 (Y_1) 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 h_0 (40) at the reference age of 40 years. The second component (Y_2) 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 Y_2 component, the higher the initial growth.

Application

Model (5) is then applied to the different experimental plots measured at least 3 or

Table II. Dominant height.

A	$\beta_{A,0}$	$\beta_{A,1}$	$\beta_{A,2}$
5	2.03	0.071	–0.123
10	4.84	0.207	–0.303
15	8.00	0.344	–0.220
20	11.06	0.46	–0.063
25	13.84	0.531	0.102
30	16.24	0.572	0.251
35	18.31	0.61	0.394
40	20.04	0.646	0.521
45	21.44	0.654	0.522
50	22.63	0.666	0.489

Coefficients of the growth function (model (3)):
$h_0(A) = \beta_0(A) + \beta_1(A) . Y_1 + \beta_2(A) . Y_2$
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

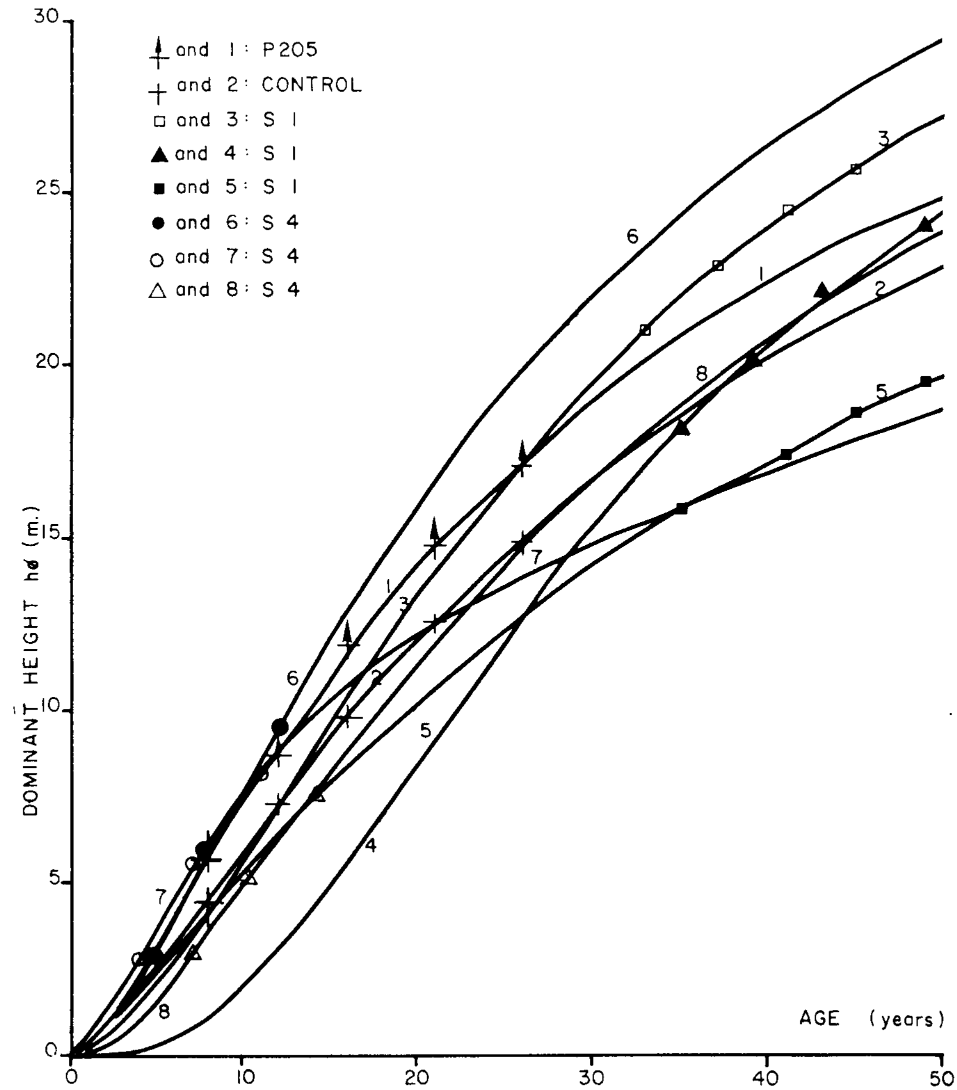

Fig 2. Growth of dominant height. Eight growth curves estimated by model [5]. P2O5 and control = mean values of the fertilization experiment. S_1 = stands established between 1916 and 1936. S_4 = stands established between 1968 and 1973.

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-

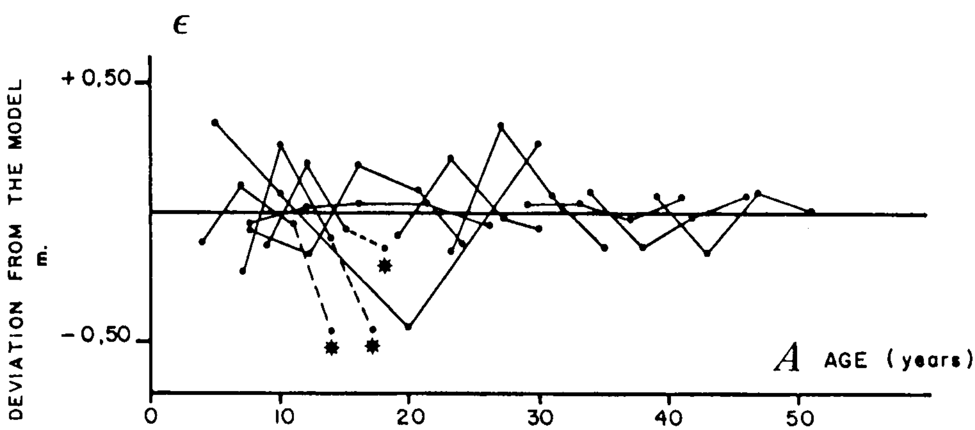

Fig 3. Growth of dominant height. Deviations from model [5] for each plot measured at least 4 times. Mean values for 10 samples of 4–6 same age plots. – – – • ✱ = measurements corresponding to frost effect in January 1985 (data not used in model [5]).

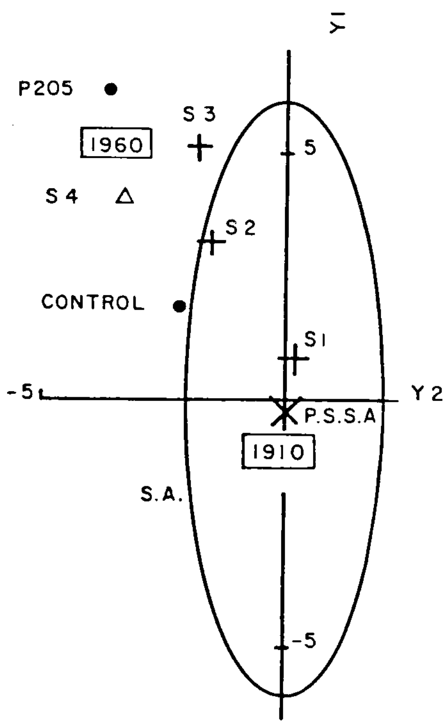

Fig 4. Growth of dominant height. Mean values of Y_1 and Y_2 parameters for each set of experimental plots. Origin of the graph = means of stem analysis experiment SA. Ellipse = distribution of SA data (25 plots). PSSA = average plot simulation with the 3 first data ($h_0(5)$, $h_0(10)$ and $h_0(15)$) of SA. S_1 to S_4 = sample of the stands established from 1916 to 1973. P2O5 and control = fertilization experiment.

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 Mitscherlish's law

Data from the THIN1 thinning experiment are used. Variations in lg_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. lg_{0M} is the regression coefficient obtained. Figure 5 shows that in each case the curve obtained follows closely Mitscherlish'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, lg_{016} for s = 16 m^2 and lg_{04} for s = 4 m^2, the c value is obtained by solving the following equation:

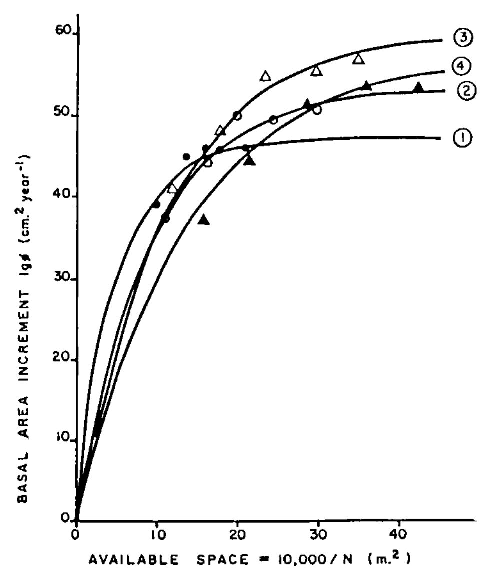

Fig 5. Growth of dominant basal area. Thinning experiment (THIN1). Mitscherlich's law applied to competition (model [9]). Four growth periods: 1) and ● = 19–23 years of age; 2) and ○ = 23–27 years of age; 3) and Δ = 27–32 years of age; 4) and ▲ = 32–38 years of age. Curves of model [9].

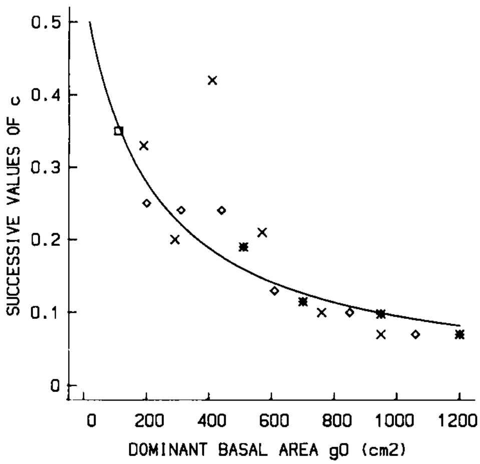

Fig 6. Growth of dominant basal area. Variations in *c* parameter of model [9] according to basal area g_0 variations with age. ✱ : THIN1 experiment;□, spacing experiment; X, THIN2 experiment without phosphorus;◇, THIN2 experiment with phosphorus. Curve: model [12] fitted to THIN1 and SPACING data.

$$lg_{016} / lg_{04} = 40.23/30.37 = (1-e^{-c.16})/(1-e^{-c.4}) \quad (11)$$

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

$$c = 115.854/(g_0 + 215) \quad (12)$$

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 lg_0 as a function of lh_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 lg_0/lh_0 also varies according to age *A*.

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

$$lg_0/(lh_0.COMP) = 14.69 - 90.74.lh_0 + 3.40.h_0\,(40) + 1.57.A \quad (13)$$

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 = ≤ 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 lg_0 observed values and lg_0 estimated values by model (13) are compared with the predictive variables lh_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-

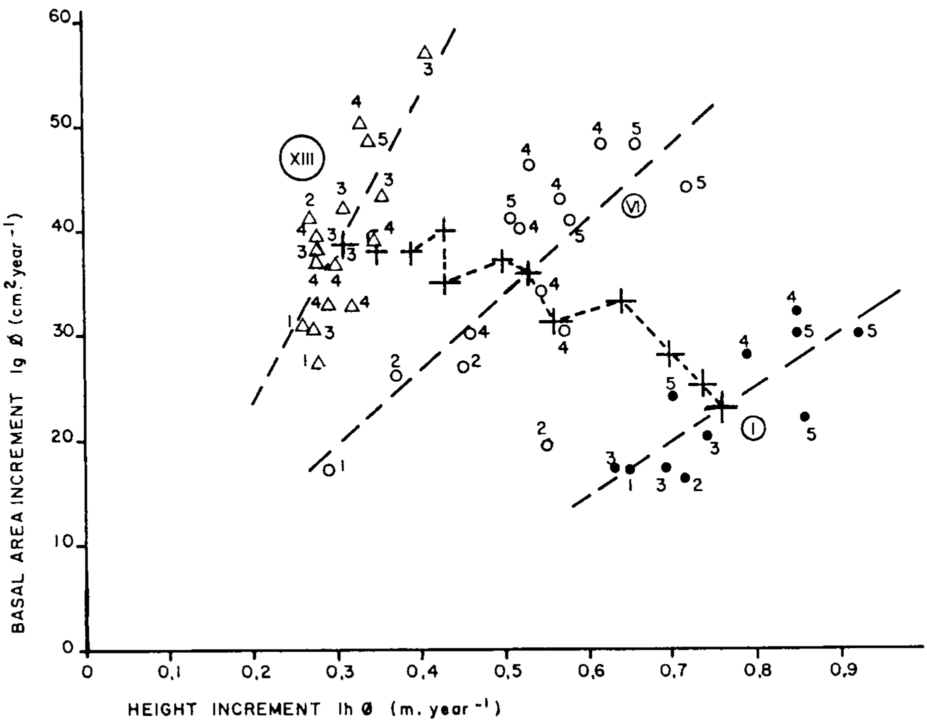

Fig 7. Growth of dominant basal area. Relationship between basal area increment (lg_0) and dominant height increment (lh_0). + = means of 13 age classes: I $\bar{A}$ = 7.3; $\bar{N}$ = 1651. VI $\bar{A}$ = 21.5; $\bar{N}$ = 757. XIII $\bar{A}$ = 41.8; $\bar{N}$ = 309. ●, ○, Δ = individual plot data for these 3 age classes. Nos 1–5 = classes of dominant height $h_0(40)$: No 1 = 15 m... No 5 = 25 m. Broken lines = overall relationship for the 3 age classes.

nificantly different from zero (probability of Student's test = 0.025). Nevertheless, this bias for lg_0 (+ 0.952 $cm^2.year^{-1}$) 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 $cm^2.year^{-2}$) 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 $cm^2.year^{-2}$). 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) (ε_1 and ε_2) are correlated, which indicates a slight autocorrelation:

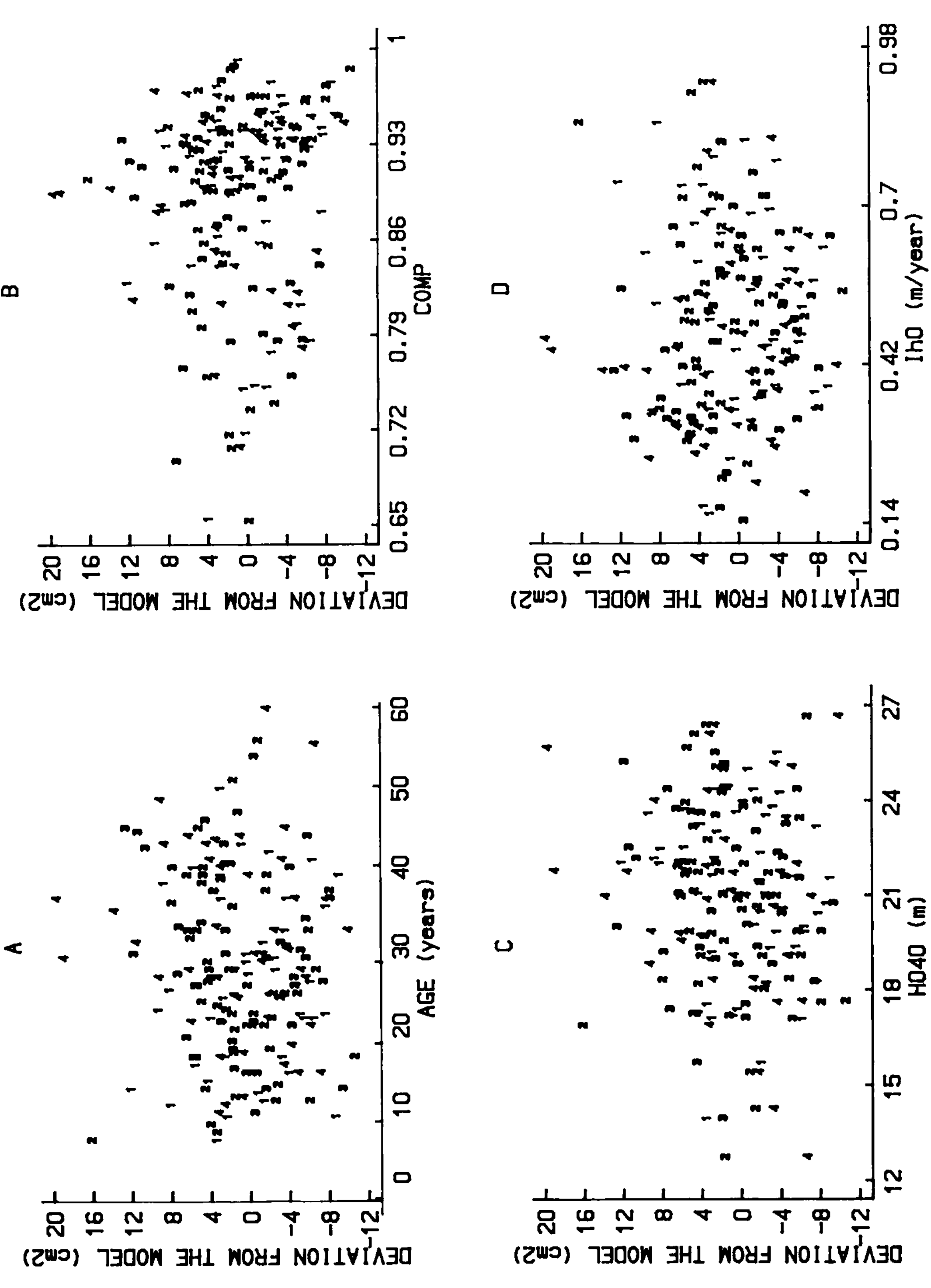

Fig 8. Growth of dominant basal area. *Ig0* deviations from model [13] for temporary plots (S_1 to S_4 in table I). Relationships with variables : *A*: with AGE; *B*: with *COMP*; *C*: with h_{040}; *D*: with Ih_0. 1: ECH1 1st measurement; 2: ECH2 1st measurement; 3: ECH1 1st measurement; 4: ECH2 2nd measurement.

$$\varepsilon_2 = 0.60.\varepsilon_1 \quad (r = 0.48) \qquad (14)$$

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 praticaly 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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