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**Original article**

# A model of even-aged beech stands productivity with process-based interpretations

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**Summary** — In order to describe the productivity of pure even-aged stands of common beech, a system of three differential equations is proposed for dominant height, basal area and total volume growth. The model was derived and fitted to 317 observation periods in 29 long-term experimental plots ranging from northwest to northeast France. It involves parameters at the forest and stand levels. Site index is the asymptote of the height-age curve. Model structure is such that, for any given height, some differences in total volume yield exist between stands of different productivities. This result is in contradiction with Eichhorn's rule. However, in our model, no parameter other than site index is necessary to characterize stand productivity. The possibility to generalize the model to a larger range of ecological conditions is discussed by a process-based interpretation. The site dependence of the parameters can be understood by reference to carbon-balance models. A linear relationship between basal area and height-growth rates is investigated by a separate model of sapwood geometry and dynamics.

***Fagus sylvatica*** **L / stand productivity / Eichhorn's rule / growth and yield models / carbon-balance models / sapwood**

**Résumé — Un modèle de productivité des hêtraies régulières avec des interprétations écophysiologiques.** *Afin de décrire la productivité de peuplements purs et réguliers de hêtre, on propose un système de trois équations différentielles pour la hauteur dominante, la surface terrière et le volume. Le modèle a été construit et ajusté à partir de 317 périodes d'observations dans 29 anciennes placettes expérimentales réparties entre le nord-ouest et le nord-est de la France. Il comprend des paramètres aux niveaux de la forêt et du peuplement. L'indice de fertilité est l'asymptote des courbes hauteur– âge. La structure du modèle est telle que, pour une hauteur dominante donnée, la production totale en volume diffère entre peuplements de fertilités différentes. Ce résultat est en contradiction avec la loi d'Eichhorn. Pourtant, dans notre modèle, seul l'indice de fertilité est nécessaire pour caractériser la production d'un peuplement. À partir d'une interprétation écophysiologique, on discute la possibilité de généraliser ce modèle à une large gamme de conditions écologiques. La dépendance des paramètres par rapport au milieu peut être justifiée par référence aux modèles de bilan de carbone. La relation linéaire entre croissances en hauteur et en surface terrière est explorée grâce à un modèle de la géométrie et de la dynamique de l'aubier.*

**Fagus sylvatica** ***L / productivité des peuplements / loi d'Eichhorn / modèles de croissance / modèles de bilan de carbone / aubier***

## INTRODUCTION

The problem of productivity assessment is a crucial one in the field of growth and yield of forest stands. Four related issues can be distinguished: *i)* How can we define productivity of a stand? *ii)* How can we measure it? *iii)* How can we model the components of productivity? *iv)* What are the relationships between the measured productivity and variables describing site (qualitative, eg, species association, and/or quantitative, eg, soil depth, etc). This paper deals with the first three questions, on the basis of a set of long-term experimental plots of even-aged common beech.

### *Definition of total yield*

As stressed by Assmann (1970, pp 158-163), the practical definitions, methods of measurement and analysis are quite different in the cases of annual plant crops or forest stands. Yield of annuals is harvested at the end of a season, so that long series of data are available. The methods are quite sure and the external factors such as soil characteristics or climate may be used for yield prediction. As in the case of forest stands, only part of the global yield is actually of agricultural interest (aerial or underground, fruits, etc), which leads to additional variables such as the harvest index (ratio between harvestable part and total biomass; see Cannell, 1989).

The very long time spread of forest development, from installation to final harvest, is a first, obvious difficulty. Many natural or man-induced processes contribute to the particular level of standing biomass which can be measured in a stand: natural mortality, removals by thinnings, age and so on. The structure of the standing crop may also be very diverse: mixed-species stands with species composition changing through time, uneven-aged stands where even the notions of age or final harvest cannot be defined.

In almost pure even-aged stands, which this paper deals with, the present state of the art is based upon the notion of total yield, sensu Assmann (1970, p 160): total yield is the sum of the standing crop and all past removals from the date of stand creation (natural mortality and thinnings). The decision to include mortality is important, since the silvicultural treatment (initial spacing, thinning weight) directly influences the rate of mortality and hence the apparent growth of living basal area or volume.

### *Practical and methodological problems related to total yield*

The unit of measurement is usually volume over bark to a specified end diameter. There is a considerable variation in the procedures for defining the volume of interest (stem only or total tree volume, under or over bark, different end diameters). This makes it difficult to compare different data sets, not only in the absolute amounts, but also in the shape of curves with respect to age. Total yield in basal area is also considered (Duplat, 1993).

A second problem lies in the fact that volume of trees or stands is not measured, but estimated from volume tables. The accuracy of volume tables may seriously limit what can be deduced even from the best series of data. This is especially the case when computing volumes for permanent plots on the basis of "local" volume equations, that is, independent equations derived from independent data samples at different dates of measurement: the estimation of volume generally implies sampling errors (selection of a population of trees to build the equation), measurement errors (of diameters, heights and volumes) and modeling errors. Christie (1988) and Assmann (1970, p 152) emphasize that part of the variability in volume increments is due to such artifacts of calculation.

Total yield in volume or basal area may also be defined as the integral of gross growth rate, which is the apparent growth of living stand plus mortality. From this point of view, growth and yield are mathematically equivalent. The integration of growth rate to compute yield produces an integration constant, which can reasonably be set to zero if integration starts at a relatively early age. In many permanent plots, however, the age at beginning of observations is such that a significant part of yield is unknown (Christie, 1988). This leads to problems if one wants to compare stands in various conditions of site and/or silviculture: apparent differences in yield between stands may be due partly or completely to different amounts of the "missing yield".

The major argument against using total yield versus age as a index of stand productivity is that it includes and mixes instantaneous increments, which may have been achieved under very different conditions: for example, silviculture is rarely applied in a uniform way on the whole period of observation; this is the case in our data set, where thinning weight was very irregular. If, for example, stand density affects stand increment, it may lead to differences in total yield due to silviculture only and reflecting no differences in site potential. Other possible silvicultural sources for differences in total yield are the growing conditions at the very young stages (plantation densities, length of the regeneration period).

### *"Eichhorn's rule"*

At least in the European literature, "Eichhorn's rule" has a major importance for the issue of productivity assessment and the design of yield tables (Assmann, 1970). Since this concept will be discussed in light of the model presented in this paper, a brief presentation is given here. For a comprehensive analysis of the relevant literature, see reviews by Houllier (1990), Hautot and Dhôte (1994).

Eichhorn's rule may be termed with the two basic relationships ("Grundbeziehungen") of Assmann (1955): for pure, even-aged and closed stands of a particular species, in a given region, total volume yield is a function of dominant height only, whatever the age and site index of the stand; hence, we have

$$H_0 = \mathrm{F}_1\,(A,\mu_s) \qquad [1]$$

and

$$VT = \mathrm{F}_2\,(H_0,v) \qquad [2]$$

where $A$ is age, $H_0$ is dominant height, $VT$ is total volume yield, $\mu_s$ is a vector of parameters depending on site (local parameters) and $v$ is a vector of parameters independent on site (global parameters).

Generally, only one parameter is necessary to characterize the site dependence of $\mu_s$, the site index. Because $v$ is independent on site, the problems of estimating total volume yield or mean height are completely equivalent (Assmann, 1970, p 159). All the variability of yield between sites is deduced from the variability of dominant height. Thus, low productivity sites follow the same curve as highly productive sites in the ($H_0$, $VT$) plane, although the latter follow it more rapidly.

Another important point to stress in this conception of stand productivity is that silviculture is not explicitly considered. The area of validity of Eichhorn's rule is restricted to closed stands, but no explicit model describes how silviculture would influence yield. In some papers on yield tables design (see, eg, Bartet and Pleines, 1972), it is assumed that "total yield is independent on stand density, in a large range of stand densities". This additional assumption allows the use of equations [1] and [2] for a larger range of situations than the original "normal stands" of Eichhorn (1904).

An intensive critique of Eichhorn's rule was undertaken by German scientists in the 1950s. They progressively identified some consistent differences in total yield for a given dominant height. These results led to the notion of yield level ("Ertragsniveau"), which is indeed a measure of deviation from Eichhorn's rule (Hautot and Dhôte, 1994).

### *Objectives of this study*

This study on productivity is part of a larger project aimed at modeling growth of pure even-aged stands of common beech, on the basis of a network of permanent plots observed since the turn of the century (Dhôte, 1991). For the purpose of modeling stand productivity, the data base for this project was not optimal. Although the climatic conditions represented by the permanent plots spread from a mild atlantic to a semicontinental climate, the ecologic amplitude within each region is limited: plots are located in one or two forests, average soil conditions are favorable.

Furthermore, series of data for volume or basal area yield often started at late ages, resulting in large amounts of the "missing yield" described in previous sections. This prevented us from a direct analysis of total yield versus height, for example. The analysis focused on modeling increments rather than total yield. A preliminary glance at the yield table for beech, northern Germany (Schober, 1972) and at the data discussed by Kennel (1973) revealed that none of these 2 sources verified Eichhorn's rule (Dhôte, 1992). So this rule was not imposed as a constraint for data analysis: our position was to test a posteriori whether the model verified Eichhorn's rule.

We decided to build a model of the components of stand productivity: dominant height, basal area and volume. The objective was a system of differential equations, describing the interactions between the growth rates of the three components. The main factors affecting growth were the stage of development (stand age or height) and site factors assumed to vary at two different scales: climatic factors (differences of growth between climatic regions) and site index (differences of growth within each region).

The last step of the research was to propose a process-based interpretation of the model. The interpretation was expected to give us indications on how the model would behave outside the range of the observed situations. This, we believed, was a means to overcome the limitations of the data base (narrow range of site conditions).

## MATERIALS AND METHODS

### *Definitions and notations*

The following variables and notations will be used: quadratic mean diameter is $D_g$; stand basal area, $G$; stand volume over bark of whole tree (stem and branches) to a final diameter of 7 cm, $V$; dominant height, $H_0$, which is the average height of the 100 largest trees per ha (see practical estimation later). Basal area and volume figures refer to the whole stand, ie, trees belonging to the main vegetation story and the understory. As a result from an analysis of individual tree growth (Dhôte, 1991), the increments of understory trees in beech are very close to zero in the range of observed treatments: their contribution to production might be neglected in situations where only the upper story has been recorded.

We will also consider total yield in basal area ($GT$), which is the sum of standing basal area and basal area of all trees removed in thinnings or dead since installation of the plot; the same definition holds for total volume yield ($VT$). These quantities are different from the "true" total yields sensu Assmann (1970), mentioned earlier. His starting point is the creation of stand, ours is the date of plot installation; therefore, our values will be different from the "true" ones by an unknown constant, whereas the increments are known exactly, except for measurement or estimation errors. This will not be a major drawback, since most of the analysis will focus on modeling increments.

Growth rates of basal area (resp volume) are noted either as discrete increments $\Delta G/\Delta t$ (resp $\Delta V/\Delta t$) or as differentials $dG/dt$ (resp $dV/dt$). These figures stand for gross increments, *ie* including mortality.

## *Material: a set of permanent plots*

The French network of permanent plots in common beech was installed between 1883 and 1924. Plots are located in four state forests ranging from Normandy (atlantic climate) to Lorraine (semicontinental climate); an intermediate is the north of the Bassin Parisien, whose climate is characterized by lower rainfalls than the two other areas, but high average atmospheric humidity. These conditions are very favorable for beech vegetation. Partial summaries of these plots (site conditions, treatments, results) have been issued by Arbonnier (1958), Pardé (1962, 1981) and Oswald and Divoux (1981).

The experimenters wanted to gain some series of data on the production of beech stands at various stages of development. Ultimately, this would lead to the construction of yield tables. A special interest was devoted to the phase of natural regeneration (how heavy should the shelterwood cuttings be in order to allow a successful regeneration?) and to the tending of pole-stage stands (what is the effect of different thinning regimes on yield and quality of the remaining stems?).

The design of the whole network does not correspond to the statistical conception of forest growth and yield experiments: no repetitions, very few control plots, variability of site conditions not clearly identified as an external factor to take into account. There are several major reasons for this: *i)* No statistical background of the analysis of variability was available at that time; *ii)* few broadleaved forests had been treated in regular high forest, so that the existing material imposed severe constraints; *iii)* apart from the scientific objective, the experimenters also wanted to implement some "models of treatment" that could be directly applied by foresters.

The design of the plots was the following: In each forest, several stands of different ages were selected according to the criteria of complete and homogeneous canopy, homogeneous site conditions, origin from seed (natural regeneration) and dominance of beech. Stands where beech represented less than 80% in basal area for part of the observation period were rejected from this study. These stands will be considered as approximately pure, complete and even-aged. The composition and density of the understory are variable between stands, but in all cases its growth rate is very low and we have considered that these stands "work" as single-storied.

In younger stands (aged 30 to 60 years), several plots were installed to test different thinning regimes. Only treatment is different between these plots, site conditions and initial state being identical. In stands older than 60 years, a single "production plot" was installed and received an ordinary treatment (selective, not too heavy thinnings of a mixed nature, ie, both in dominant and suppressed trees). In the oldest stands, 1 plot was defined as "production plot during the regeneration phase" and was subject to shelterwood cuttings. Site conditions may be slightly different between stands.

The definition of treatments to be practiced in the "thinning plots" was rather loose. In the oldest experiment of Haye, a comparison of low *versus* crown thinnings was the objective. In all plots installed in the 1920s, the main objective was to test different combinations of thinning weight and cutting cycles.

In order to quantify thinning weight, a relative density index (RDI) was hand-fitted after the idea of Reineke (1933): it reads as $\mathrm{RDI} = N * D_g^{1.5} / 119866$ ($N$ in $\mathrm{ha}^{-1}$, quadratic mean diameter $D_g$ in cm). As indicated in figure 1, stand densities have remained between 0.4 and 1, except in the regeneration phase (shelterwood cuttings are the reason why stands older than 160 years have RDI values lower than 0.4; see fig 1). This interval indicates a rather conservative silviculture; previous work has shown that, for a given age, stand basal area or dominant height growth rates are almost independent on density, in this range of densities (Dhôte, 1991).

## *Data*

All plots were measured at intervals of 3 to 10 years (6 to 19 measurements per plot; see table

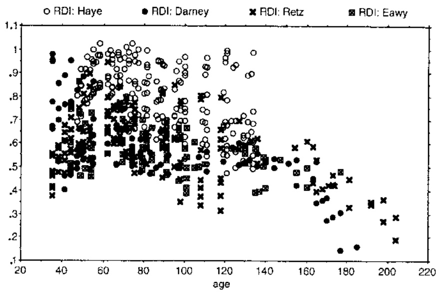

**Fig 1.** Stand density measured by Reineke's relative density index (RDI), as a function of age for the 346 dates of measurement. Forests are distinguished. All values (before and after thinning) are plotted.

I). In young stands, diameter was measured with a caliper (2 cm precision) on all live trees and the data are a collection of histograms for each species. As soon as stand density allowed it, trees were numbered physically; then girth was measured at the nearest 1 cm and the data structure became a tree list (see table I for dates).

The estimation of mortality is easy in the case of tree lists. For the early recordings of histograms, mortality trees per diameter class and species were estimated by comparing successive histograms. This procedure relies on the fact that growth rate in the lower diameter classes is almost zero in these stands and hence deficits of trees may be interpreted as mortality (Dhôte, 1990).

**Table I.** Summary of the characteristics for the permanent plots used in this study.

| *Stand* | *Nb of plots* | *Plot area (ha)* | *Initial age* | *Date of creation* | *Tree lists since* | *Last measure* | *Nb of measures* | *Nb of h(d) samples* |
|---|---|---|---|---|---|---|---|---|
| Eawy (Normandy) | | | | | | | | |
| Camp Cusson | 3 | 1.00 | 44 | 1924 | 1931 | 1981 | 11 | 10 |
| Côte aux Hêtreaux | 1 | 1.00 | 100 | 1924 | 1927 | 1971 | 8 | 3 |
| Camp Souverain | 1 | 1.00 | 130 | 1924 | 1927 | 1971 | 7 | 3 |
| Retz (Bassin Parisien) | | | | | | | | |
| Faîte | 4 | 0.20 | 35 | 1922 | 1922 | 1978 | 12 | 10 |
| Chrétiennette | 4 | 0.25 | 62 | 1922 | 1922 | 1978 | 10 | 5 |
| Pré des Seigneurs | 1 | 1.00 | 127 | 1922 | 1922 | 1968 | 9 | 3 |
| Mortefert | 1 | 1.00 | 165 | 1922 | 1922 | 1968 | 8 | 3 |
| Haye (Lorraine) | | | | | | | | |
| Chavigny | 2 | 0.20 | 26 | 1883 | 1904 | 1989 | 17 | 9 |
| Charlemagne | 3 | 0.25 | 28 | 1883 | 1904 | 1989 | 17 | 8 |
| Epicéas | 2 | 0.25 | 27 | 1883 | 1904 | 1989 | 19 | 9 |
| Grand Pierrier | 1 | 0.25 | 28 | 1883 | 1904 | 1989 | 15 | 6 |
| Darney (Lorraine) | | | | | | | | |
| Sainte-Marie | 3 | 1.00 | 35 | 1923 | 1958 | 1966 | 10–12 | 10 |
| Beaulieu | 1 | 1.00 | 80 | 1923 | 1923 | 1962 | 8 | 4 |
| Fontaine aux Ordons | 1 | 1.00 | 124 | 1923 | 1923 | 1962 | 9 | 4 |
| Verbamont | 1 | 1.00 | 165 | 1923 | 1923 | 1943 | 6 | 3 |

For each forest (region indicated) are given the different even-aged stands and, by stand, number of plots, plot area, age at plot installation, date of installation, date when trees were numbered (so that tree lists are available later on), date of last available measurement, number of measurement and number of height-diameter samples.

In addition, a sample of trees were measured for total height and volume at repeated dates. Until the 1940s, only felled trees were measured. From the 1950s on, a composite sample of felled and standing trees was defined, the latter being measured with optical devices (see Pardé and Bouchon, 1988). Successive samples were independent. Height and volume measurements were not performed at each date of inventory (see number of measurements in table I).

A total of 15 stands, 29 plots, 346 dates of measurement and 317 observed growth periods were available. Plot area ranged from 0.20 to 1 ha.

### *Estimation procedure for dominant height*

The figures for dominant height used in this study were estimated by means of sets of height-girth curves (details on the model properties can be found in Dhôte and de Hercé, 1994). On every sample of height-girth measurements, we used nonlinear least squares to fit an equation of the following form:

$$h = \frac{\alpha - \sqrt{\alpha^2 - 4\,\mu_2\mu_3\,(\mu_1 - 1.3)\,c}}{2\,\mu_3} + 1.3 \qquad [3]$$

where $\alpha = \mu_1 - 1.3 + \mu_2\,c$ and $c$ is girth (cm), $h$ is total tree height (m), $\mu_i$ $(1 \leq i \leq 3)$ is a vector of parameters. Parameter $\mu_3$ must remain in the interval [0,1].

This model is a hyperbola with an upper horizontal asymptote at $\mu_1$, $\mu_2$ being the derivative in 0 and $\mu_3$ an index of shape: $\mu_3 = 0$ is for the rectangular hyperbola, increasing values of $\mu_3$ indicate increasing curvature for medium values of girth. The curve is constrained to pass through 1.30 m for $c = 0$.

The estimation procedure is a modification of that used by Dhôte and de Hercé (1994). In order to accomodate for poorly conditioned samples, parameters $\mu_2$ and $\mu_3$ were fixed as functions of stand age:

$$\mu_2 = \frac{30}{30 + Age} + 0.2 \text{ and } \mu_3 = \text{TanH}\left(\frac{4\,Age}{100 + Age}\right) \qquad [4]$$

These two functions are common to all plots and forests. Only parameter $\mu_1$ is estimated for each data set. The fitting procedure provides an estimate of $\mu_1$ as well as an estimate of its precision (standard deviation). The series of successive estimates of $\mu_1$ through time were controlled, for every plot. In order to prevent erratic estimates of dominant height, we corrected some of the estimates of $\mu_1$ by adding or substracting a maximum of 1 standard deviation. For dates of measurement when no sample of heights was available, $\mu_1$ was estimated by linear interpolation.

A first graphical examination of the data revealed that the data clouds for different plots were almost identical. Hence, for fitting the model, all plots within a stand were pooled together. In some dubious cases, separate fittings were performed; no differences in the estimates of $\mu_1$ were found significant.

If $C_g$ is quadratic mean girth and $C_0$ is dominant girth (quadratic mean of the 100 largest trees per ha), the application of equation [3] at each date for $c = C_g$ and $c = C_0$ provides estimates of the mean height $H_g$ and the dominant height $H_0$.

This is a classical procedure for permanent plot data computation (see, eg, Kennel, 1972), but one has to stress some weaknesses of the method:

– Not all tree heights are measured; instead of computing a standard "mean" of actual measurements, three steps are involved: sampling trees, measuring heights, fitting a model to relate height and diameter. Thus, three sources of error are introduced in the estimation of dominant height by this procedure.

– In our case, the successive samples are independent. Every point estimate of dominant height may be biased and successive biases may be in opposite directions, resulting in a large imprecision of height increments.

– On the long term, however, the general curve dominant height versus age is probably a good approximation of the actual one. This indicates that smoothing this curve may be a good solution in order to analyze height increments.

### *Estimation of volumes*

Volume was estimated by means of a general volume table computed by Bouchon (1981). This equation provides an estimate of volume as a function of diameter and total height. It was fitted to data for 1 066 beech trees coming from ten forests covering the whole distribution of the species in France. The volume data from the permanent plots we use here were the main part of this material. No attempt was made to fit "local" volume tables for every plot or forest.

For application, we used the measured value of girth and the estimated value of height according to that used earlier.

## RESULTS

### *Dominant height growth*

On the whole data set, dominant height at a base age of 100 (a kind of site index) ranges from 25 to 35 m, but most of the values lie between 30 and 35 m (fig 2). In addition, the classification of stands according to site index is strictly valid within one particular climatic region. Only the two forests in Lorraine (Haye and Darney) exhibit some differences in height at a particular age. The differences between stands within the forests of Retz and Eawy are very small. This is a confirmation that site conditions are very homogeneous within each forest.

As a consequence, this data set is not adequate for a complete modeling of dominant height growth, including the separation of curves according to the site index. Our choice was to describe height increment with a simple, provisional model:

$$\frac{dH_0}{dt} = r_f(K_s - H_0) \qquad [5]$$

where $r_f$ is a parameter characterizing the forest and $K_s$ is a parameter characterizing the stand ($K_s$ is the asymptote and $r_f\,K_s$ is the growth rate when height is zero).

This is the monomolecular model, which has the following property: since the derivative decreases for all positive values of height, this model cannot feature an inflexion point. If such an inflexion point exists in our stands, it occurs at a very early point in stand life and in all cases before the plots were installed (extrapolate from fig 2). For the observed part of curves, equation [5] provides an efficient summary of data and requires only two parameters.

Although this model can be integrated easily, we chose to fit it in the differential form, ie, by modeling the increments. The statistical model for fitting was:

$$\left.\frac{\Delta H_0}{\Delta t}\right|_{f,s,i} = r_f(K_s - H_{0_{mean,f,s,i}}) + \varepsilon_{f,s,i} \qquad [6]$$

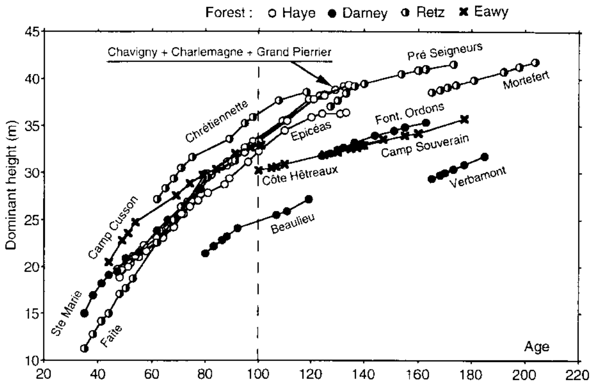

**Fig 2.** Overview of dominant height growth for the 15 stands in the data set. Forests are distinguished by different symbols. Stands are indicated (see table I for complete names). Three stands in Forêt de Haye are indicated together.

**Table II.** Statistics of fit for model [6]. One parameter $K_s$ is estimated for each stand.

| | *Eawy* | *Retz* | *Haye* | *Darney* |
|---|---|---|---|---|
| Nb of observations | 43 | 95 | 130 | 49 |
| SD of residuals (m/yr) | 0.0508 | 0.0866 | 0.0841 | 0.1154 |
| Coefficient of determination | 0.86 | 0.65 | 0.28 | 0.50 |
| Parameter $r_f * 10^2$ | 3.118 | 1.387 | 0.9026 | 2.232 |
| (SD $* 10^2$) in $\text{yr}^{-1}$ | (0.247) | (0.194) | (0.124) | (0.595) |
| Parameters $K_s$ (SD) in m | Camp Cusson<br>35.76 (0.685) | Faîte<br>48.25 (4.03) | Chavigny<br>56.24 (3.94) | Ste Marie<br>36.39 (4.16) |
| | Côte Hêtreaux<br>33.87 (0.642) | Chrétiennette<br>51.82 (2.84) | Charlemagne<br>56.04 (3.95) | Beaulieu<br>31.83 (2.86) |
| | Cp Souverain<br>35.61 (0.687) | Pré Seigneurs<br>49.19 (2.58) | Gd Pierrier<br>54.96 (4.35) | Font Ordons<br>37.97 (2.19) |
| | | Mortefert<br>45.85 (2.50) | Epicéas<br>52.79 (3.68) | Verbamont<br>36.42 (2.83) |
| Largest correlation between $r_f$ and the $K_s$ | –0.900 | –0.972 | –0.940 | –0.973 |

SD: standard deviation.

where subscripts *f, s, i* refer to the forest, the stand and the time period, respectively; $\left.\frac{\Delta H_0}{\Delta t}\right|_{f,s,i}$ is the observed height increment for forest *f*, stand *s* between dates $t_i$ and $t_{i+1}$; $H_{0_{mean,f,s,i}}$ is the mean of height values at dates $t_i$ and $t_{i+1}$; $\varepsilon_{f,s,i}$ is a normally distributed error of mean 0 and constant variance.

Since no parameters were common to all forests, the model was fitted separately to each forest.

The results are given in table II. The proportion of variance explained by the model is variable. The quality of the fitting can be considered satisfactory in Eawy and Retz. In Haye, the early growth (at the pole stage) was rather slow, so that the data cloud has a low slope (parameter $r_f$) and the model is poorly determined. In Darney, the amount of noise around the increments is important, due to the short periods between two successive measurements (height sampling every 3 years).

High coefficients of correlation between parameter $r_f$ and the different $K_s$ are noted. The highest values are observed for the youngest stands: this is logical since these stands have the largest variance in the dependant variable and determine the slope of the whole data cloud.

Within each forest, stands were grouped according to the grading of the observed heights (fig 2) and the values of the estimated $K_s$, taking into account their precision. A second fitting was performed, with one $K_s$ for each group (see table III). These parameter values will be used in the following sections.

**Table III.** Statistics of fit of model [6]. Parameters $K_s$ are estimated for groups of stands.

| | *Eawy* | *Retz* | *Haye* | *Darney* |
|---|---|---|---|---|
| Nb of observations | 43 | 95 | 130 | 49 |
| SD of residuals (m/yr) | 0.0502 | 0.0875 | 0.0835 | 0.1152 |
| Coefficient of determination | 0.87 | 0.64 | 0.29 | 0.50 |
| Parameter $r_f$ * $10^2$ | 3.140 | 1.211 | 0.9005 | 1.910 |
| (SD * $10^2$) in $yr^{-1}$ | (0.210) | (0.108) | (0.122) | (0.305) |
| Parameters $K_s$ (SD) in m | Camp Cusson,<br>Cp Souverain<br>35.68 (0.527) | Faîte,<br>Chrétiennette,<br>Pré Seigneurs<br>53.09 (2.43) | Chavigny,<br>Charlemagne,<br>Gd Perrier<br>56.01 (3.74) | Ste-Marie,<br>Font Ordons<br>38.90 (2.60) |
| | Côte Hêtreaux<br>33.85 (0.623) | Mortefert<br>46.72 (2.79) | Épicéas<br>52.84 (3.66) | Beaulieu,<br>Verbamont<br>34.94 (2.19) |
| Largest correlation between $r_f$ and the $K_s$ | −0.863 | −0.948 | −0.967 | −0.924 |

SD: standard deviation.

There is a decrease of parameter $r_f$ along the gradient west (Eawy) to east (Haye). The very high value obtained in Darney, which is located in Lorraine as the Forêt de Haye, must be taken with caution because it is very imprecise. Anyway, our data set is clearly not adequate for testing any geographic trend of this parameter. This work is a preliminary analysis and must be completed by use of other data sets (series of plots located in different climatic regions and/or stem analyses).

### Basal area growth

The basis of the modeling was to try to relate basal area and dominant height growth rates. A preliminary analysis of the yield table for common beech in northern Germany by Schober (1972) had revealed that the basal area growth rate $\Delta G/\Delta t$ was linearly related to dominant height growth rate $\Delta H_0/\Delta t$ and that this relation was identical for all four productivity classes (Dhôte, 1992).

A direct fit of basal area increments on the "observed" values of height increments proved to be difficult, because of the important noise around the latter variable. So we computed the "predicted dominant height increments", defined as follows:

$$\left.\frac{\Delta H_0}{\Delta t}\right|_{pred,f,s,i} = r_f\left(K_s - H_{0_{mean,f,s,i}}\right) \qquad [7]$$

where $H_{0_{mean,f,s,i}}$ is the mean of observed height values at dates $t_i$ and $t_{i+1}$; $r_f$ and $K_s$ are parameters computed in the previous section.

We fitted the following model:

$$\left.\frac{\Delta G}{\Delta t}\right|_{f,s,i} = \alpha + \beta \left.\frac{\Delta H_0}{\Delta t}\right|_{pred,f,s,i} + \varepsilon_{f,s,i} \qquad [8]$$

**Table IV.** Statistics for linear regression of observed basal area increment on predicted dominant height increment (see equations [7] and [8]).

| *Regression summary* | |
|---|---|
| Nb of observ | 317 |
| Adjusted $r^2$ | 0.717 |
| RMS residual | 0.135 ($m^2$/ha/yr) |

| *ANOVA table* | *DF* | *Sum of squares* | *Mean square* | F *value* | P *value* |
|---|---|---|---|---|---|
| Regression | 1 | 14.598 | 14.598 | 800.898 | < 0.0001 |
| Residual | 315 | 5.742 | 0.018 | | |
| Total | 316 | 20.340 | | | |

| *Parameters* | *Coefficient* | *Std error* | *Std coeff* | t *value* | P *value* |
|---|---|---|---|---|---|
| $\alpha$ ($m^2$/ha/yr) | 0.150 | 0.020 | 0.150 | 7.580 | < 0.0001 |
| $\beta$ (m/ha) | 2.056 | 0.073 | 0.847 | 28.300 | < 0.0001 |

where $\alpha$ and $\beta$ are regression parameters and $\varepsilon_{f,s,i}$ is a normally distributed error of mean 0 and constant variance.

Since there were no parameters specific to subunits (plots or forests), all data were pooled together for fitting this model. Table IV and figure 3 give a summary of the results. The overall quality of the linear regression is apparent. No attempt was made to test for the significance of a quadratic term, in order to keep the model as simple as possible (as shown by the graph, the residual variance is slightly higher at high values of the independent variable). Neither did we test for different regression lines for the four forests: the distributions of data for predicted height increment have different amplitudes, so that we could hardly conclude concerning the practical meaning of different regression lines (statistical artifact or true difference in behavior).

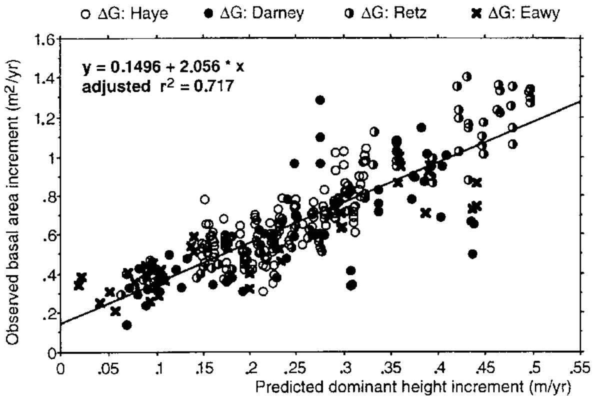

**Fig 3.** Regression plot of observed basal area increment on predicted dominant height increment. The four forests are distinguished by different symbols.

In order to test for the effect of silviculture, we performed an analysis of the residuals against various measures of stand density (number of stems, basal area, relative density index): no trend was detected. Possible reasons for this: stand densities in our data set are very often more than half the maximum; even low densities were achieved progressively, by maintaining a reasonable degree of ground cover; common beech productivity is not very sensitive to density in a large range of silvicultures (Assmann, 1970; Dhôte, 1991); even if a slight trend existed in that range (monotonic or other types of response curves), it might not be detected because the major source of noise is periodic (for a given stand and observation period, all plots are either above or below the regression line). This "periodic effect" is due to climate and/or measurement biases and was not modeled.

Since the amplitude in both the dependent and independent variables is fairly large, we can be confident in the application of this result, at least within the ecological range of our plots. The intercept of the regression is highly significant, which means that basal area growth rate should remain approximately constant as height growth approaches zero.

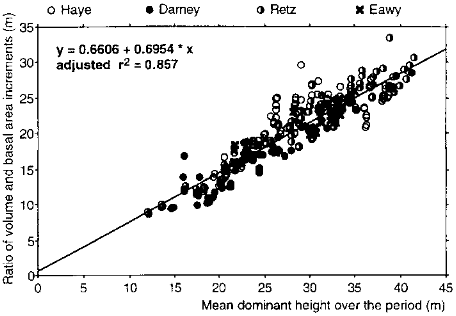

**Fig 4.** Regression plot of the ratio volume increment/basal area increment on the current mean dominant height (see equation [9]). The four forests are distinguished by different symbols.

### *Volume growth*

Volume growth results from area increments laid over the actual cambial surface of stems and branches. This introduces a relationship between volume growth on the one hand, basal area growth and height on the other hand. In this regard, it is usual to take into account the current taper of stems (see, eg, Assmann, 1970, p 151). Another method to relate basal area and volume growth originates from Pressler's law (used by Mitchell, 1975), which states that area increment at any point of the stem is proportional to the amount of foliage located above that point (butt swell is ignored). Testing whether this result actually holds for beech is beyond the scope of this study. If it holds at the stand level and for stems and branches as well, then we would expect that total stand volume increment be proportional to the product of basal area increment and height (no taper is to be considered).

To test this expectation, we considered the following model:

$$\left.\frac{\Delta V}{\Delta G}\right|_{f,s,i} = \gamma + \delta H_{0_{mean,f,s,i}} + \varepsilon_{f,s,i} \qquad [9]$$

where $\left.\frac{\Delta V}{\Delta G}\right|_{f,s,i}$ is the ratio between volume and basal area increments between dates $t_i$ and $t_{i+1}$; $H_{0_{mean,f,s,i}}$ is the mean of height values at dates $t_i$ and $t_{i+1}$; $\gamma$ and $\delta$ are regression parameters and $\varepsilon_{f,s,i}$ is a normally distributed error of mean 0 and constant variance.

Once again, equation [9] was fitted to all data pooled together (fig 4). The quality of the regression is very high, but one has to remember that modeling the ratio between volume and basal area increments eliminates much of the variability: basal area and volume are computed from the same data, climatic or experimental noise influences the figures in the same way. Furthermore, it

**Table V.** Statistics for the no intercept-linear regression of the ratio volume increment/basal area increment on the current mean dominant height.

| *Regression summary* | |
|---|---|
| Nb of observ | 317 |
| Adjusted r$^2$ | 0.991 |
| RMS residual | 1.974 |

| *ANOVA table* | *DF* | *Sum of squares* | *Mean square* | F *value* | P *value* |
|---|---|---|---|---|---|
| Regression | 1 | 136667.54 | 136667.54 | 35061.29 | < 0.0001 |
| Residual | 316 | 1231.76 | 3.898 | | |
| Total | 317 | 137899.30 | | | |

| *Parameters* | *Coefficient* | *Std Error* | *Std Coeff* | t *value* | P *value* |
|---|---|---|---|---|---|
| d | 0.7176 | 0.0038 | 0.9556 | 187.2466 | < 0.0001 |

is logical that height appears highly correlated to this ratio.

The most important result is that the intercept term is not significant. Table V gives the statistics for the no intercept regression (ie, $\gamma$ fixed to zero).

## Synthesis: a possible generalization of Eichhorn's rule

The data analysis of the 3 previous sections provides a model for the 3 components of productivity in even-aged beech stands:

$$\frac{dH_0}{dt} = r_f (K_s - H_0) \quad [10]$$

$$\frac{dG}{dt} = \alpha + \beta \frac{dH_0}{dt} \quad [11]$$

$$\frac{dV}{dt} = \delta H_0 \frac{dG}{dt} \quad [12]$$

where $\alpha$, $\beta$, $\delta$ are global parameters (common for the whole area); $r_f$ is characteristic of the forest and $K_s$ is characteristic of the stand.

These equations may be combined and integrated to provide an expression of the relationship between dominant height and volume yield. The integration is analytically tractable because we have chosen simple differential equations. We obtain:

$$\frac{dV}{dt} = \delta H_0 (\alpha + \beta \frac{dH_0}{dt})$$

$$= \delta \alpha (K_s - \frac{1}{r_f} \frac{dH_0}{dt}) + \delta \beta H_0 \frac{dH_0}{dt} \quad [13]$$

hence $VT = \gamma + \delta \alpha K_s Age$

$$- \frac{\delta \alpha}{r_f} H_0 + \frac{\delta \beta}{2} H_0^2 \quad [14]$$

where $\gamma$ is an integration constant.

Equation [14] defines volume yield as a second-order polynomial function of dominant height, with an intercept term depend-

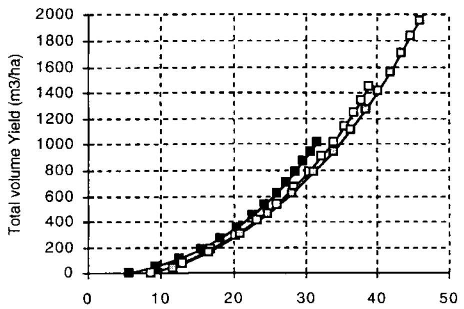

**Fig 5.** Simulation of total volume yield as a function of dominant height (m) for three stands of different site indices: (■) low site index, (□) medium site index; (■) high site index. The parameters for this simulation were the following (parameter $r_f$ of Retz, initial values for basal area and volume taken from the yield table of Schober, 1972):

| *Variable* | *Low site index* | *Medium site index* | *High site index* |
|---|---|---|---|
| Asymptote $K_s$ (m) | 38.5 | 47 | 55 |
| Dominant height at age 100 (m) | 24 | 30 | 36 |
| Initial age | 30 | 30 | 30 |
| Initial dominant height (m) | 6 | 9 | 12 |
| Initial basal area ( $m^2$/ha) | 12 | 13.6 | 15.4 |
| Initial volume ($m^3$/ha) | 0 | 0 | 48 |

ing on stand *Age*. Because of parameter $r_f$, different forests will have different curves. $r_f$ traduces the general shape of height growth: if we assume that this shape varies according to climate (eg, Décourt, 1964; Le Goff, 1981), then we would expect from equation [14] that the volume-height curve varies on a large scale (ie, the scale of climatic regions).

Parameter $K_s$ has an effect on the time dependence of the equation. This means that, in a given forest, stands with different site indices will follow different volume-height curves. While $H_0$ approaches its asymptote $K_s$ (the term

$$-\frac{\delta\alpha}{r_f}H_0+\frac{\delta\beta}{2}H_0^2$$

then remains approximately constant), volume continues to increase as the term $\gamma + \delta\ \alpha\ K_s\ Age$. See simulations in figure 5.

Although there is no single total volume yield-height relationship for all the forests (see Assmann, 1955) and although total yield may vary at a given height when site index varies (coherent with Kennel, 1973), only one local parameter is necessary to describe stand productivity (the asymptote $K_s$).

Thus, equation [14] does not comply with Eichhorn's rule (equation [2]), but it may be considered as a kind of generalization of the productivity assessment method based on Eichhorn's rule. Provided that equation [14] holds and that sets of height-age curves are available, any couple of height-age data for a stand allows the estimation of the asymptote $K_s$ and hence of the corresponding total volume yield.

These conclusions are valid only if parameter $r_f$ is actually constant in a given climatic region, which cannot be assured from our material. The differences in yield level between different site indices predicted by our model (see fig 5) are in good agreement with the yield table by Schober (1972), but less important than those reported by Kennel (1973).

The second problem of practical importance is how to estimate, from simple stand measurements (one single measure of age and dominant height), the asymptote $K_s$, if this proves to be an appropriate index of stand productivity. A series of stem analyses could bring some insights to these questions.

The stability of equations [11] and [12] is also very important. By this we mean that our results are valid only if these two equations are indeed constant over large regions (at least within a given climatic region). If this is not the case, local parameters other than $K_s$ may have an influence. The only way to know is to gain information from other data sets. In the following sections, we try to derive a functional explanation of these relationships, in order to increase the confidence in the model and to guide future research.

## A FUNCTIONAL INTERPRETATION OF THE STAND GROWTH MODEL

### *Volume growth equation and carbon-balance models*

Equations [10] and [12] may be assembled in the following way:

$$\frac{dV}{dt} = \delta H_0 \frac{dG}{dt} = \delta H_0 (\alpha + \beta \frac{dH_0}{dt})$$

$$= H_0 (\alpha + \beta r_f (K_s - H_0)) \qquad [15]$$

hence $$\frac{dV}{dt} = \delta (\alpha + \beta r_f K_s) H_0 - \delta \beta r_f H_0^2$$

This expression is a conventional balance between a positive term, which is proportional to dominant height, and a negative term proportional to the square power of height. This looks very much like the carbon-balance models, where the positive term represents the allocation of photosynthates to stem and branch growth and the negative term the losses of carbon due to mortality and maintenance respiration (Linder *et al*, 1985; Valentine, 1985; Mäkelä, 1986). Here, we consider gross volume yield, including tree mortality; hence, loss of matter comprises only maintenance respiration and mortality of tissues (leaves, twigs, branches). We may consider that growth respiration is implicitly included if it is assumed proportional to growth rate.

If the forest-level parameters $r_f$ are assumed to reflect average climatic conditions and the stand-level parameters $K_s$ the stand productivity, then equation [15] can be interpreted as follows: there is an influence of regional climate on both terms of the balance (assimilation and maintenance respiration); the length of the vegetation period and the course of daily temperatures can influence both processes in annual terms (on the influence of temperature on maintenance respiration, see Kira, 1975, cited by Cannell, 1989; Yokoi *et al*, 1978; Frossard and Lacointe, 1991). The index for stand productivity $K_s$ appears only in the positive term, which could be interpreted as the effect of primary production factors (water and nutrients) on net photosynthesis and/or on the allocation of photosynthates to above-ground parts. Possible processes here are a reduction of the assimilation rate due to water shortage (stomatal closure) and a larger share of photosynthates to fine roots turnover on sites with poor water or nutrient supply (Reynolds and Thornley, 1982; Linder *et al*, 1985; Cannell, 1989). The site-dependence of the model is therefore coherent with some current results or theories in ecophysiology.

A more unexpected feature of this model is the height-dependence of both terms of equation [15]. It seems logical that the negative term is related to height: the loss of carbon through maintenance respiration is proportional to the amount of living biomass. If this living biomass is roughly equivalent to stem and branch sapwood (Mäkelä, 1986; Sievänen, 1993) and if there is a regulation between foliar area and sapwood area (see, eg, Grier and Waring, 1974; Rogers and Hinckley, 1979; Granier, 1981), then we would expect that respiration losses depend on height. The fact that this term depends on the square power of height is further investigated in the next section.

Concerning the positive term, it is reasonable to assume that net photosynthesis is approximately constant as soon as the stand has achieved a stable foliar area, although some authors argue that the water constraint increases with height development (Møller *et al*, 1954). If net assimilation then remains constant, it could be assumed that the proportion of assimilates allocated to above-ground wood depends on height. Because living tissues in stems are an increasing proportion of total biomass, it is possible that there is an increasing demand for assimilates in stems and branches as height increases, in order to maintain other regulations (eg, sapwood-foliar areas). A theoretical derivation of a height-dependence for allocation to wood can be found in Mäkelä (1986). But a review by Cannell (1989) indicates that partitioning to wood remains fairly constant after canopy closure.

### *Height-basal area relationships and dynamics of sapwood*

To complete the previous interpretation, we propose here a separate model for sapwood geometry and dynamics. This model will possess 2 properties coherent with our empirical findings: there is a site-independent linear relationship between basal area and height growth and, in addition, the negative term of the volume growth equation is proportional to a square power of height.

We consider a stand of $N$ identical trees of height $h(t)$ at date $t$.

**A1.** We assume that total stand sapwood (including stems and branches) has the geometry of a paraboloïd, that is, sapwood area $sa(z,t)$ at any level $z$ above ground and at any date $t$ is:

$sa(z,t) = \varphi\,(h(t) - z)$ with $\varphi$ a parameter.

**A2.** We assume that sapwood area at the level of crown base $h(t) - cl(t)$ (where $cl(t)$ is crown length) is proportional to stand foliar biomass $fm(t)$:

$$sa(h(t) - cl(t),t) = \chi\, fm(t) \qquad [16]$$

with $\chi$ a parameter.

$$\text{Hence} \quad sa(z,t) = = \frac{\chi\, fm(t)}{cl(t)}(h(t) - z) \qquad [17]$$

The evolution with time of sapwood area is featured by the following partial derivative:

$$\frac{\partial sa}{\partial t}(z,t) = \chi \frac{d}{dt}\left(\frac{fm}{cl}\right)(h(t) - z) + \frac{\chi\, fm(t)}{cl(t)}\frac{dh}{dt} \qquad [18]$$

If we introduce the rate of creation of new (external) sapwood $(\partial s / \partial t)$ $(z,t)$ (which is equivalent to the annual increment in discrete terms) and the rate of conversion of sapwood to heartwood $\delta(z,t)$, then we may write:

$$\frac{\partial s}{\partial t}(z,t) = \delta\,(z,t) + \chi \frac{d}{dt}\left(\frac{fm}{cl}\right)(h(t) - z) + \frac{\chi\, fm(t)}{cl(t)}\frac{dh}{dt} \qquad [19]$$

**A3.** We assume that the density of foliar weight per m of crown length is constant with time, *ie*

$$\frac{fm(t)}{cl(t)} = \phi$$

**A4.** We assume that the rate of conversion of sapwood to heartwood is constant with respect to date $t$ and vertical level $z$, *ie* $\delta(z,t) = \omega$.

Provided that assumptions A3 and A4 hold, we can write:

$$\frac{\partial s}{\partial t}(z,t) = \omega + \chi\,\phi\,\frac{dh}{dt} \qquad [20]$$

Sapwood volume *sv(t)* may be computed by integration of equation [17]:

$$sv(t) = \frac{\chi\, fm(t)}{cl(t)}\,\frac{h(t)^2}{2} = \chi\,\phi\,\frac{h(t)^2}{2} \qquad [21]$$

As a first consequence of equation [20], the area of the external ring does not depend on the vertical position. This result is coherent with "Pressler's law", which postulates that area increment at any point along the stem is proportional to the amount of foliar biomass located above that point (see Mitchell, 1975; Ottorini, 1991 for applications to growth modeling). So a parabolic geometry of sapwood may be compatible with Pressler's law, under some additional hypotheses. This result is important, since Pressler's law is often considered more or less equivalent with the pipe model of Shinozaki *et al* (1964). Here we demonstrate that a constant area of increments along the stem is compatible with a tapered sapwood, whereas derivations based on the pipe model generally consider that sapwood area is constant along the stem.

Equation [20] is equivalent to our empirical relationship between basal area and dominant height growth. If parameters $\omega$, $\chi$ and $\phi$ are independent on site, then we would expect a single general relation, as stated experimentally. In addition, volume of sapwood is a square power function of stand height, which is coherent with equation [15] for volume increment and the argument that maintenance respiration rate is proportional to sapwood volume (or biomass).

A discrepancy between observations and the predictions provided by this model is that volume increment should be the exact product of basal area increment and dominant height (because area increment is uniform along the stems, eg, [20]). We found that these values are indeed proportional, but with a proportionality constant of 0.7, which was statistically different from 1. Reasons for this might be that our model of sapwood distribution is overly simple and neglects the presence of butt swell and the effect of branching. In addition, dominant height is probably a biased estimator of the height of the dominant story (mean height has some other drawbacks, especially when computed from all trees including the understory).

### *Discussion of the model for sapwood*

The cost for obtaining an appropriate relationship between area and height increments was rather high: we had to make four successive assumptions, which are discussed here. To begin with, it is important to emphasize that our model is at the stand level, whereas most of the work cited later is at the individual level (eg, sapwood).

Assumption A1 is a schematical representation of sapwood distribution: we simplified the actual geometry and neglected the problems associated with branching patterns and butt swell in order to make the problem analytically tractable. More realistic simulations based on a three-dimensional featuring of trees could help in a sensitivity analysis. Such models exist only for some particular situations (Mitchell, 1975). The parabolic nature of sapwood distribution is coherent with experimental findings of Granier (1981), Waring *et al* (1982), Hatsch (1993) on different conifer or broad-leaved species.

Concerning A2, many authors claim that the proportional (or linear) relationship between sapwood area and leaf area (or biomass) is better determined when sapwood area is taken at crown base (Granier, 1981; Dean and Long, 1986; Maguire and Hann, 1986), because sapwood taper introduces a source of noise. Unpublished work by Karimi and Keller (personal communication) indicates that the distinction of heartwood and sapwood in common beech is very difficult, by any of the usual methods (anatomy, water content, coloration, *etc*): this would be in favor of an approximately parabolic taper of sapwood (sapwood is roughly equivalent to total wood, and hence both have the same geometry, which is close to a paraboloïd). Parameter $\chi$ is implied by the proportional relationship between sapwood area and foliar biomass (or area). Some results indicate that this parameter may be altered, at least temporarily, by thinning or fertilization (Brix and Mitchell, 1983; Aussenac and Granier, 1988). Nevertheless, the first two assumptions are strengthened by a series of experimental results.

The status of assumptions A3 and A4 is quite different: they are a speculation which makes it possible to solve the problem, but their validity is questionable. The fact that the rate of conversion of sapwood to heartwood is constant with respect to spatial location (site conditions), vertical position (along the stems and branches) and time (age of stand) seems very hard to support. Experimenting on dynamics of sapwood is probably a difficult issue. We would expect that this rate of conversion be different according to site conditions (water regime). In this case, parameter $\omega$ in equation [20] could vary with site, resulting in different linear equations for different sites.

Finally, the density of leaf biomass per m of crown length $fm(t) / cl(t) = \phi$ must be constant with stand age and site. This fact does not seem very intuitive: total stand leaf area (or biomass) remains approximately constant after canopy closure and crown length increases slowly on the long term as a result of self thinning or silviculture. So we would expect this ratio to decrease. Maybe the leaf biomass and crown length to be considered in equation [17] are not the actual, measurable ones, but those figures concerning the most efficient part of crowns (topmost parts).

## DISCUSSION AND CONCLUSION

A modeling of the three components of stand productivity (growth rates of dominant height, basal area and total volume) in 29 plots of common beech located in four forests of northern France led to a set of three simple differential equations. Local parameters had to be considered for modeling dominant height growth. They characterize two levels of structure in our data set: the forest and the stand. Basal area and volume growth could be described with global parameters (common for the whole studied area). This system of equations provides at least an adequate summary of the data; however, the method based on modeling increments could be applied as well in other situations, since this provides a framework for analyzing the joint effect of site and silvicultural treatment.

The variability of the local parameters needs further investigation. Two issues are to be distinguished. i) Is the stand-level parameter an appropriate measure of site productivity, how is it related to traditional measures like site index and how to estimate it from simple stand measurements? ii) Is the forest-level parameter stable inside 1 climatic region? An experiment to address these problems could be a series of stem analyses in even-aged stands at two levels: large variations in climatic conditions (fortunately, common beech is present from the British Islands to central Europe) and a large range of site conditions inside each region.

It is not yet clear whether the set of equations applies as well for a large range of site conditions and, if not, whether the form of equations and/or parameterization should change with site. The solution would be to reanalyze some series of long-term experimental plots on a variety of sites (such plots exist in other European countries). However, existing data do not cover all possible climate-site situations and we think that having a process-based interpretation of models will help to generalize them.

Under the assumption that this model holds as well for different site conditions, simulations revealed that there is no single relationship between dominant height and total volume yield, even within a particular climatic region. This is a contradiction with Eichhorn's rule (Assmann, 1955). But if there is no other effect of site than the local parameter in height growth (site index), the yield level may be estimated from site index. Finally, the differences in yield level predicted by this model are not very important (less than those reported by Kennel [1973] for the same species).

In an attempt to justify the set of equations from physiological considerations, 2 major questions have been underlined. i) The carbon-balance framework can provide some structures of equations coherent with the practical experience of growth and yield specialists; in this regard, the problem of assimilate allocation to different plant parts (variations with site and stand development) is central (Mäkelä, 1990). ii) In order to derive the attributes of stand and tree geometry (heights, diameters) from the biomass compartments of carbon-balance models (Sievänen, 1993), a promising solution is to incorporate the water regime and some associated questions (sapwood geometry, sapwood dynamics, relationships between sapwood and leaf area). Our process-based interpretation of the productivity model has some weaknesses, but it indicated that, at least, the linear relation between height and basal area growth may vary with site.

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