

Growth and development of individual Douglas-fir in stands for applications to simulation in silviculture

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Summary — Growth and development of individual Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco) were studied on the basis of a sample of 44 trees felled in the north east of France, taking into consideration various stand conditions. This work was conducted with a view to future use of the information in a simulation system, to predict the effects of silvicultural treatments on Douglas fir stands. Stem and branches were analysed in all trees, and relationships combining branch growth with growth and development of crown and stem were obtained. These relationships give insight into interactions between tree growth and stand dynamics. Among the prediction equations obtained, a major one was tested on a further 12 newly felled trees, analysed for past bole increments and crown development reconstruction. This suggested the use of a scaling factor to correct a possible underestimation.

Douglas-fir = *Pseudotsuga menziesii* / crown / stem / growth and development / silviculture

Résumé — **Croissance et développement individuels du douglas en peuplement. Applications à la simulation en sylviculture.** La croissance et le développement individuels du douglas (*Pseudotsuga menziesii* (Mirb) Franco) ont été étudiés à partir d'un échantillon de 44 arbres abattus dans le Nord-Est de la France, en tenant compte de différentes conditions de peuplement. Ce travail a été effectué dans le cadre d'une exploitation ultérieure des résultats par un système de stimulation, de façon à prédire les effets de traitements sylvicoles sur les peuplements de douglas. La tige et les branches de tous les arbres ont été analysées, et des relations liant la croissance des branches à la croissance et au développement du houppier et de la tige ont été obtenues. Ces relations renseignent sur les interactions entre la croissance individuelle des arbres, et la dynamique du peuplement. Parmi les équations de prédiction obtenues, l'une d'entre elles, particulièrement importante, a été testée sur un nouvel échantillon de 12 arbres abattus, analysés pour obtenir les accroissements de la tige au cours du temps, et reconstituer le développement du houppier. Ce contrôle a fait apparaître une possible sous-estimation, pouvant être corrigée par un facteur multiplicatif.

douglas = *Pseudotsuga menziesii* / croissance et développement / tige / houppier / sylviculture

INTRODUCTION

Silvicultural studies rely on long-term records from permanent spacing and thinning trials. Unavoidably, these reflect opinions or concerns for socioeconomic values that applied 20–30 years ago (or more), although they may include treatments judged extreme at that time. In this domain, setting up a new trial implies decades of observations before it can be useful. To predict the effects of recently speculated treatments, it is necessary to widen the basis of the data provided by existing permanent stands. This can be done, for instance, with “temporary” or “semi-temporary” sample plots, measured once, or over a period of a few years. Generally, it is hard to find contrasting stands in this case, because the management practices tend to standardize the treatments. Moreover, temporary stands of quite different developments in fact provide unrelated data (Johnson, 1986).

Whatever the data sources used, to optimise the information they provide, it is necessary to set up a more or less conceptual framework of inter-related components which can be mapped to a real stand, and make use of the various measurements through this framework, usually called a model. A model is a simpler representation of a more complex reality, which allows the extension of the validity of the available data, based on some hypothesis.

At first, the basic model components simply consisted of stand characteristics. Versions of this method were proposed, among others, by Decourt (1972), Hamilton and Christie (1974), Curtis *et al* (1981), Ottorini (1981). In the early models (called yield tables), stand composition was not considered. So, there was no clear basis to extrapolate the predictions to growth conditions fundamentally differing from those observed, and intended to give com-

pletely new stand structures and evolution. The stand composition was needed for a better understanding of growth phenomena, and also as an important output for treatment evaluations and decision-making. Originally, diameter distributions were incorporated into models at a descriptive level. For example, in Hyink and Moser (1983), the parameters of such distributions were derived from stand characteristics, and in Ek (1974) a non-parametric principle was used. Diameter distributions have also arisen from a more basic approach, considering stand development through individual tree growth, as discussed in this study.

To anticipate the responses of a wide variety of treatments that have never been put into practice, there has been an increasing concern to rely on basic information of general applicability and immediate availability. This kind of information is best found at the level of individual tree growth. An advantage of this approach is that large stand data are not necessarily needed for the model construction, and it is easier to find trees, rather than stands, in practically all possible growing conditions.

Staebler (1951) was the first to attempt to relate individual tree growth to local stand conditions. Numerous works followed to express for a given tree the distance and relative size of the surrounding trees with a single value in a “competition index”, sometimes used in a computer program to simulate the development of a whole stand, based on the growth of individual trees (Newnham, 1964; Bella, 1970, 1971; Hegyi, 1974; Lin, 1974; Daniels and Burkhart, 1975). But these indices (a recent comprehensive review of which is given by Tomé and Burkhart, 1989) always appear to be highly correlated with tree size, reducing their potential to improve the prediction of tree growth. A parallel less detailed approach is possible, by not con-

sidering the positions of the trees; in this case, for each tree in a stand local conditions are only accounted for statistically, by comparison between the tree and the stand characteristics (Goulding, 1972; Alder, 1979; Arney, 1985).

It becomes more apparent that the studies of stand dynamics that allow the most diverse explorations of treatments are based on individual tree growth, including information on crown development, and its connections with stem growth and development. This was done to some extent by Mitchell (1969) and Arney (1972). The exemplary work of Mitchell (1975a) showed the full potential of this procedure. Relying on stem on branch analysis, his methods resulted in relationships expressing laws of individual tree growth in general stand conditions. Similar works were later presented by Inose (1982, 1985). The work presented here is also related to this approach.

The importance of Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco) is growing in France, where the total area occupied by this species is estimated to be 300 000 ha, with a steady rate of 10 000 ha increase each year (Bouchon, 1984). It is widely accepted by foresters that larger initial spacings and heavier, less numerous thinnings should be used now, in order to reduce management costs. Long-term data are lacking to rationalize these opinions, and quantify the effects of the different possible treatments. A basic approach is therefore required to help managers and decision-makers with these questions. A research program was set up to contribute to the study of the silviculture of Douglas fir in France, in consideration of the local needs and conditions. The present paper reports this work, that has been concentrated on the main growth and development features of Douglas fir at the tree level. Preliminary results of the work reported here have been published earlier (Mitchell *et al*, 1983).

SAMPLING AND MEASUREMENTS

Sample trees were selected in various stands of the northeast of France, in the Nancy region (48.41° N lat), at elevations not exceeding 200 m. Mean annual temperature is 9.1 °C (max Jul 17.6 °C, min Jan 1.3 °C), and mean annual rainfall is 697.4 mm, about evenly distributed. In all the sampling locations, edaphic conditions were constituted by leached brown forest soils of good quality, with acid mull, occasionally not well drained, where Douglas fir productivity could be rated as Decourt's site class 2 (Decourt, 1967), or King's upper site class 3 (King, 1966). We selected and felled 44 trees (table I) for the measurements. As far as possible, the trees were chosen with an approximately circular crown projection, that is, the same height of lower live branches in every direction. Tree age extended from 10 to 45 years, and the greatest range of local stand conditions were sought, though not all conditions could be represented for each age class, as this would have been ideally desirable.

For each felled tree 3 branches were measured at each whorl, for the length (B), and the spread (BL) (cf fig 1), that is, the distance of the branch extremity to the stem axis (while the portion of stem bearing the branch was held vertically). Distinction was made between free-growing branches above the zone of crown contact, rubbed or broken branches at this level, and dying branches below. The distance (L) of each node to the stem apex was measured, and discs were cut at about equal spacings. An average of 10 discs per tree was collected; the biggest trees were over-sampled toward the butt, while it seemed unnecessary to take more than 8 discs on the smallest. The last 5 annual cross-sectional area increments along the stem were calculated from the measure-

Table I. List of tree characteristics of the main sample: age, diameter at breast height, height, and competitive status (measured by a "competition ratio" defined later).

Tree	Age	Dbh	Height	Status
1	20	0.22	10.85	0.59
2	20	0.17	9.45	0.50
3	20	0.14	9.25	0.56
4	20	0.23	13.10	0.52
5	27	0.27	20.20	0.17
6	27	0.23	19.75	0.12
7	27	0.12	15.80	0.05
8	27	0.20	18.25	0.13
9	27	0.18	18.80	0.08
10	27	0.22	19.50	0.13
11	27	0.27	21.20	0.12
12	27	0.19	18.05	0.12
13	18	0.20	12.10	0.34
14	18	0.13	12.01	0.06
15	18	0.06	6.93	0.19
16	18	0.16	13.35	0.25
17	18	0.09	9.92	0.13
18	18	0.23	13.12	0.62
19	18	0.11	12.33	0.08
20	18	0.13	10.00	0.14
21	45	0.47	28.55	0.34
22	46	0.49	25.60	0.39
23	45	0.47	27.70	0.37
24	46	0.41	28.75	0.34
25	16	0.11	8.20	0.70
26	16	0.11	7.28	0.58
27	16	0.10	6.90	0.55
28	27	0.14	16.15	0.06
29	27	0.09	13.25	0.04
30	27	0.11	15.37	0.01
31	27	0.07	13.75	0.02
32	27	0.09	12.65	0.03
33	27	0.09	13.45	0.02
34	27	0.30	21.60	0.14
35	25	0.15	14.96	0.04
36	25	0.18	16.15	0.09
37	25	0.18	16.60	0.06
38	25	0.14	15.35	0.04
39	25	0.16	16.60	0.06
40	25	0.28	20.00	0.26
41	10	0.06	3.97	0.90
42	10	0.06	3.70	1.00
43	9	0.06	4.27	0.90
44	10	0.05	3.83	0.87

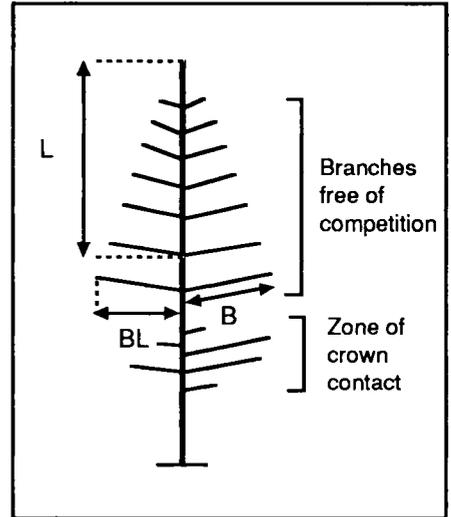


Fig 1. Details of the branch measurements. B is the length of a branch, and BL its spread. L is the distance of the base of a branch to the terminal bud of the tree.

ments of each disc in 8 directions forming equal angles.

Afterwards, 12 other sample trees were used to evaluate the prediction potential of an equation obtained from the analysis of the main sample. These trees, in similar sites, were felled and measured following a procedure simplified in some instances. This procedure, suggested by the results obtained from the main sample, is described later.

RESULTS

Crown shape and size relationships

Crown shape and size result from the relationship between branch growth and height

growth. The following equation, relating distance L of branch base from the leader, to branch length B (cf fig 1), is compatible with a decreasing branch growth rate when the distance L is increasing (Mitchell, 1975a):

$$B = b \ln [(L / c) + 1] \quad (1)$$

where b and c are scale and shape parameters. This equation proved quite adequate, with the tree sample, to describe a component of the crown morphology. Though the coefficients b and c could have been individually estimated for each tree, after a visual inspection of the data, it was judged acceptable to fit a single equation for all trees. Three trees, though, were discarded from this collective representation, because a probable loss of apical dominance gave them longer branches than expected, at a given distance L from the apex. The following values of the coefficients were obtained with a non-linear least square fitting procedure, based on a

subsample of 17 representative trees, and 426 free-growing branches (fig 2):

$$B = 11.59 \ln [(L / 20.10) + 1] \text{ metres} \quad (2)$$

(sd = 0.29)

The residual values (observed-fitted) were then examined against age, height, and competitive status (measured by a "competition ratio", defined later). No relationship with these variables was found, discarding, thus, a possible dependance upon these characteristics of the coefficients b and c .

Moreover, branch spread BL is proportional to branch length B (fig 1), as suggested by the least squares regression line through the origin fitted to the data (fig 3):

$$BL = d B \quad (3)$$

The following value, based on a subsample of 24 trees covering the range of branch spreads, and 407 free-growing branches, was obtained for d :

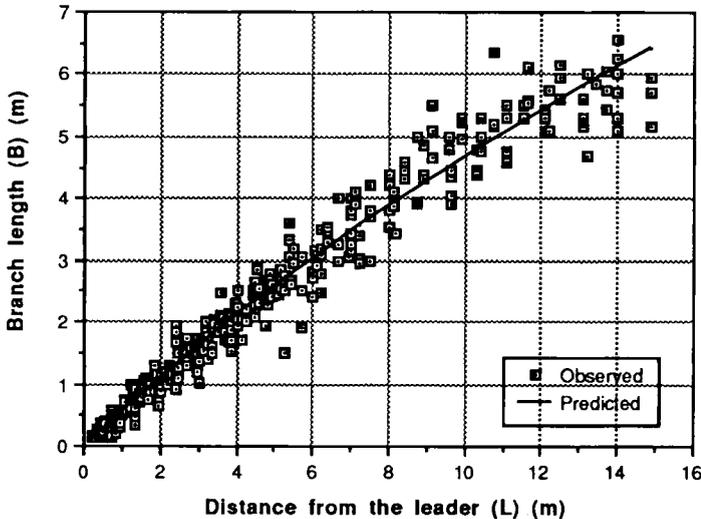


Fig 2. Relationship between branch length B and distance L of branch base from the leader.

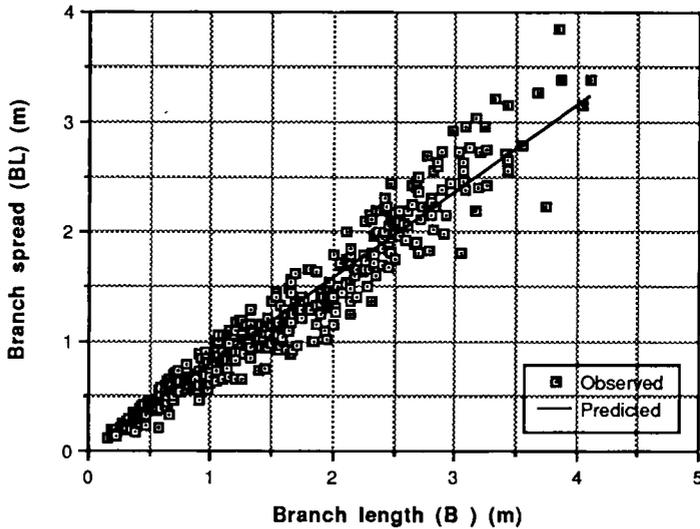


Fig 3. Relationship between branch spread *BL* and branch length *B*.

$$BL = 0.79 B \text{ metres} \quad (4)$$

(sd = 0.19)

From a static point of view, equations (1) and (3) are an expression of crown shape and size. As for a given branch *L* varies with tree height in association with height growth, these equations reflect the process of radial expansion of the parts of a crown free from competition from surrounding trees. Putting together equations (1) and (3) gives the following equation:

$$BL = b d \ln [(L / c) + 1] \quad (5)$$

Growth and development relationships between stem and crown

Stem increment

We observed that, for any tree, the dimensions and state of the live crown control

the volume increment of the stem and its distribution. More precisely, stem (or bole) volume increment (*BI*) is related to foliage quantity of the live crown; in consequence, this quantity has to be estimated, to predict *BI* from crown dimensions. The distal parts of a branch that have developed free from competition may be considered as distributed on a surface of revolution that delimits the crown (fig 4a). This "crown surface" is generated by the curve delimiting a half crown profile that Equation (5) defines. It results that the volume (*FV*) between the crown surface of a year and that of the preceding one is the volume of the needle layer developed in one growth season. For each tree we can compute a "foliar volume" (*FV*) (Mitchell, 1975a), as a weighted sum of the volumes *FV_i* of needle layers developed in the last 5 years:

$$FV = \sum_{i=1}^5 w_i FV_i \quad (6)$$

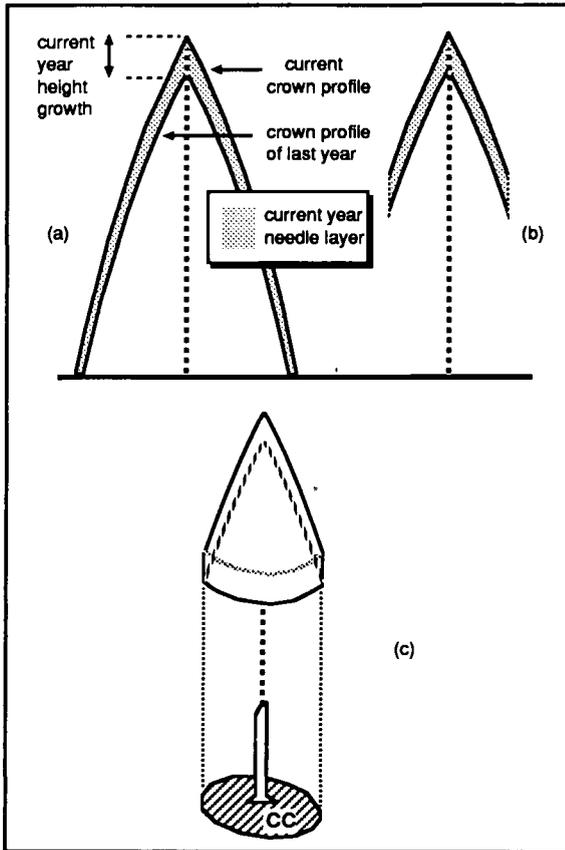


Fig 4. Stylised typical crown shapes: (a) for an open-grown tree extending ideally to the ground, (b) and (c) for a stand tree with approximately cylindrical shape at zone of crown contact.

where, for year i , coefficients w_i combine a leaf retention ratio (*ret*) and a photosynthetic efficiency ratio (*phot*).

Silver (1962) established that the last 5 years of needle contribute to 90% of the total needle count; considering the shading conditions of the older needles, the 5 youngest needle layers should contribute to most of the photosynthetic production of a tree. A leaf retention ratio was obtained from Silver's data expressing numbers of

needles per inch of shoot. For the photosynthetic efficiency ratios, as such a detailed study as Clark's (1961) on White spruce (*Picea glauca*) was not known, for Douglas fir, to the author, a photosynthetic efficiency ratio was derived from this work, based on the evolution of apparent photosynthesis along the growth season. The area under the curve of a given year was divided by the corresponding value for the current year curve to obtain this ratio. The

weights were finally obtained as shown in table II.

For an open grown tree with crown extending (hypothetically) to the ground, volumes FV_i can be computed by calculus on the basis of Equation (5). Observations of crown profiles (fig 5) indicate that the lower part of the crown of a stand tree subject to competition from the surrounding crowns is almost cylindrical in shape (fig 4b and c); from a geometrical argument (Mitchell, 1975a) it follows that the volume FV_i is the product of crown projection area (CC) (fig 4c) by height growth in year i .

In the study of relationships between stem volume increment BI and foliar volume FV , the best results were obtained by using the increment preceding the year of the tree felling (and not the last one, or the trend of the last increments). Figure 6a shows a linear relationship between Napierian logarithms of these values for the tree sample. To assess the effect of crown state on stem volume increment, the potential maximum foliar volume (FV_{max}), the tree would have in open grown conditions (with crown extending to the ground), was computed. The ratio FV/FV_{max} can be taken as a measure of competition effects, or, in other words, an expression of the competitive status. A least square linear regression line was fitted to the data, and

Table II. Combined weights obtained to compute foliar volume FV .

Photosynthetic efficiency (phot)	Needle retention (ret)	Combined weight ($w = phot \times ret$)
0.90	1.00	w1 = 0.90
1.00	0.90	w2 = 0.90
0.87	0.80	w3 = 0.70
0.78	0.70	w4 = 0.55
0.65	0.60	w5 = 0.39

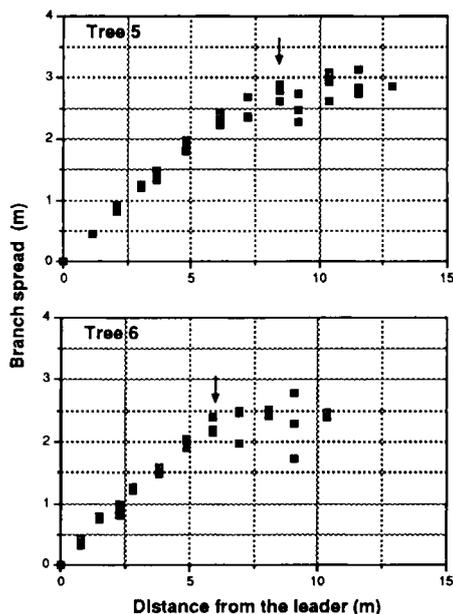


Fig 5. Observed branch spreads of 2 sample trees, to illustrate typical (half) crown profiles of stand trees, as stylised in figure 4. Graphs include the branches at the zone of crown contact, which upper limit is shown by the arrow.

the residuals were examined against $\ln(1 - \ln(FV/FV_{max}))$, showing again a linear relationship that appears in figure 6b). This analysis establishes the possibility of a linear fit to express $\ln(BI)$ as a function of $\ln(FV)$ and $\ln(1 - \ln(FV/FV_{max}))$. The method of least-squares gave the following equation fitted on the 44 sample trees:

$$\ln(BI) = -10.10 + 1.53 \ln(FV) + 0.45 \ln[1 - \ln(FV/FV_{max})] \quad (7)$$

$$(r^2 = 0.93)$$

The corresponding analysis of variance table for the multiple regression (table III) confirms a significant effect (observed in figure 6b)) of the competitive status in this

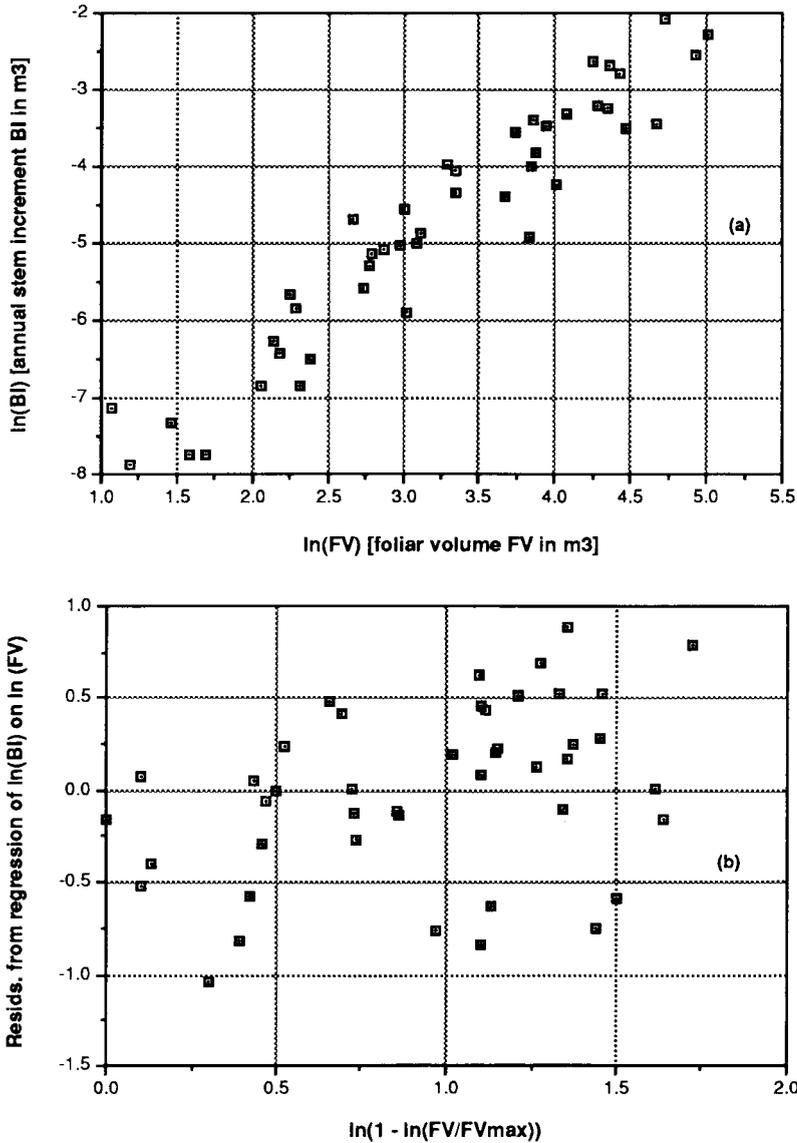


Fig 6. Relationship between stem increment BI and foliar volume FV (a), and FV/FV_{max} measuring the competitive status (b).

fit. To obtain an unbiased estimate of BI , the exponential of the right side member of Equation (7) must be multiplied by exp

$(s^2/2)$ for bias correction, where s^2 is the mean square error of the fit given in table II (Flewellling and Pienaar, 1981):

Table III. Analysis of variance table for relation [7].

Source	Degrees of freedom	Residual sum of squares	Mean square	F ratio
Regression on $\ln(FV)$	42	9.659 2	0.229 98	
Reg model of Eq [7]	41	8.049 9	0.196 33	8.196 8

As $F = 8.1968$, and because the probability for an $F(1, 41)$ variable to be > 8 is $< 1\%$, it is not likely that the term $\ln(1 - \ln(FV/FV_{\max}))$ in Eq [7] could be omitted.

$$BI = 0.000\ 045FV^{1.53} [1 - \ln(FV/FV_{\max})]^{0.45} \text{ m}^3 \quad (8)$$

Pressler law (Larson, 1963), was observed on the whole tree sample, with more or less typical features. It is illustrated by 3 sample trees of various development stages, and competitive status, in figure 7. These trees show the typical variation scheme of the stem cross sectional area of the annual increment, along the stem. This area increases linearly from the base of the stem annual shoot; then it stays equal to the value reached at the base of the live crown, and increases again toward the tree foot to contribute to the butt swell. The successive additions of stem annual increments following this scheme, in varying stand conditions, result ultimately in the bole size and shape.

Stem height growth

Individual height growth is reduced when competition is severe. This effect is noticeably visible on height growth curves of intermediate or suppressed trees, when height growth is steadily decreasing, to eventually reach a virtually null value. Potential height growth rate ($Hg0$) is the height growth rate in absence of competition. It could be estimated on the height

growth curves of the sample trees by the slope of the curves, prior to the competition effects. Potential height growth rate is possibly equal to the observed growth rate (Hg), when competition by the surrounding trees is low. Figure 8 shows the variation of the ratio $Hg/Hg0$ with the competition ratio FV/FV_{\max} . As no single functional expression was available to represent the observed response, a piecewise function was constructed. It needed to be continuous and smooth, and to eventually be constant with the value 1, to be consistent with the well-known effect of no height growth rate reduction for the dominant trees, that appears in figure 8. The function was fitted using the non-linear least-squares procedure, that resulted in the following equation:

$$Hg/Hg0 = ([FV/FV_{\max})/0.39]^{0.6} - 1)^2, \quad \text{if } FV/FV_{\max} < 0.39 \quad (9)$$

$$Hg/Hg0 = 1, \quad \text{if } FV/FV_{\max} \geq 0.39 \quad (\text{sd} = 0.08)$$

Validation of the relationship between crown state and stem increment

To evaluate Equation (8) validity, a further 12 felled trees of ages ranging from 20 to

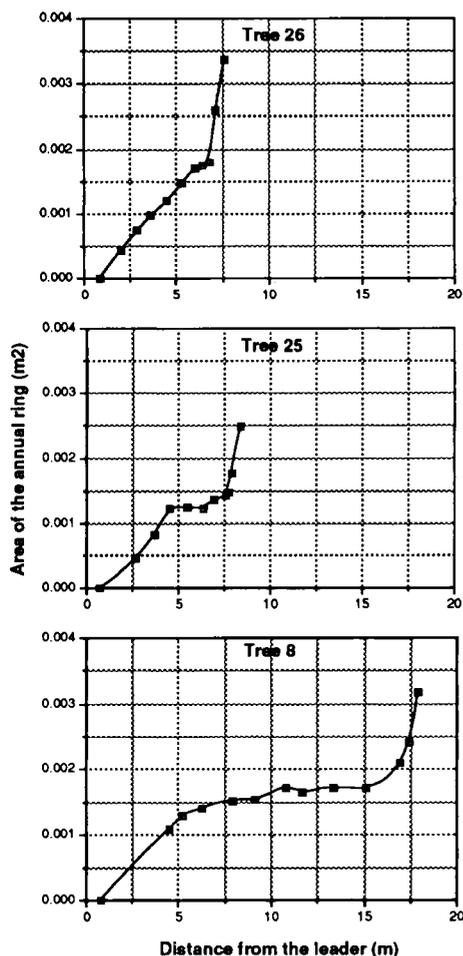


Fig 7. Distribution of the annual increment along the stem. Relationship between area of the annual ring and distance from the leader for trees of various development stages and competitive status: open-grown tree (no 26), and trees with crown base at mid-height (no 25), and at 2/3 of the height (no 8).

37 years were used. The new sample of trees, in site conditions similar to those of the first sample, included dominant, co-dominant, and intermediate trees, from stands of initial density ranging between

1 100 stem per ha and 4 400 stem per ha, with various thinning regimes. On each tree, a disc was cut at each internode, and 4 radii were measured in 2 perpendicular directions, to estimate the cross sectional area under bark of the stem for all successive years. From these measurements, stem increment of the tree at any age could be obtained. Moreover, graphic inspection of the variation of annual ring areas along the stem allowed, using Pressler law, to trace crown recession. Then, by application of Equations (2) and (4), the foliar volumes FV and FV_{max} , corresponding to each annual bole increment of a given tree, were obtained (beginning at 6 years of age, for compatibility with Equation (6)).

The results are presented in figure 9, where for each tree of this new sample the mean of observed stem increments is plotted against the mean of the stem increments predicted by Equation (8). The coordinates of the points are averaged from 15 to 32 years, depending on tree age. The position of all points, relative to the first quadrant bisector indicate some degree of under-estimation, though the overall order to magnitude, and the accordance of all but 2 points seem quite acceptable.

APPLICATIONS TO SIMULATION

Mitchell (1975a) gave a detailed diagram of the processes involved in the growth and development of a tree in a stand, and Inose (1982), a limited linear one. Our context being more similar to that of the former author, to obtain a simplified description of these processes, we have enriched Inose's diagram (fig 10). For each tree in a stand, crown expansion depends on height growth, through branch extension, following Equations (3) and (4), when it is not hampered by some obstacle, as a neighboring crown. Otherwise, the expansion is

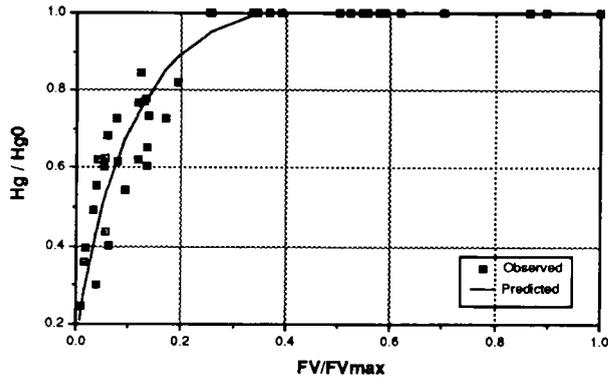


Fig 8. Variation of the ratio of observed height growth rate H_g to potential height growth rate H_{g0} , with the competitive status measured by FV/FV_{max} .

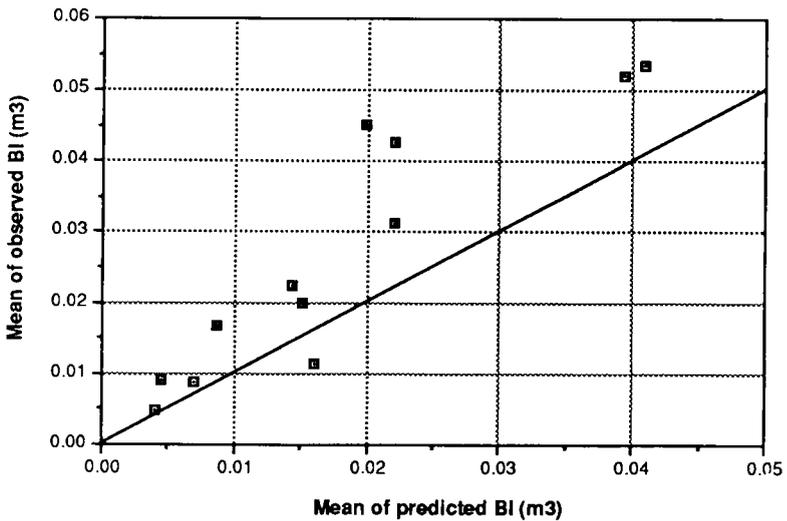


Fig 9. Mean (per tree) of observed *versus* mean of predicted stem annual increments for 12 trees. These were not included in the sample used to estimate the parameters of the prediction equation (Equation (8)). The coordinates of the points are based on 15 to 25 past years of annual increment, depending on the age of the tree.

stopped at the contact region. This growth and development scheme results in a crown state and a foliar volume, that deter-

mine a given bole increment volume, and possibly some height growth reduction, predicted by Equations (8) and (9).

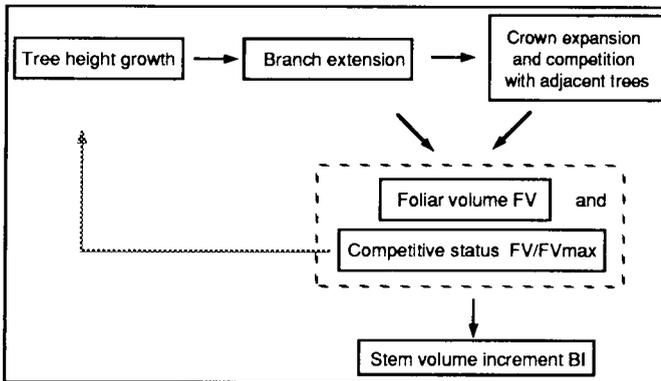


Fig 10. Diagrammatic view of individual growth and development of a tree in stand, including interactions with the surrounding trees.

As demonstrated by Mitchell (1971, 1975a, b), a computer can be used to simulate the whole growth and development process depicted here, for all the trees of a stand, allowing to study stand dynamics under various silviculture treatments. More precisely, at any development stage of the stand, the programmed computer (that becomes a simulation system) can store the state of all tree crowns by means of a stand map, and the various corresponding stem increments can be computed. Then stand state for the next stage is obtained when the state of each tree crown is established from the radial expansion following height growth, allowing for the obstruction from the surrounding crowns.

We are working on a similar computer program. Figure 11 shows the crown map of a portion (≈ 17 m on one side) of a larger stand in a simulation trial submitted to this simulation system, whose completion of a preliminary version is under way. In this map only the crown projections appear. But the elevation of crown exterior part, at the vertical of any point of the stand pertaining to a crown projection, is stored in the simulation system and used

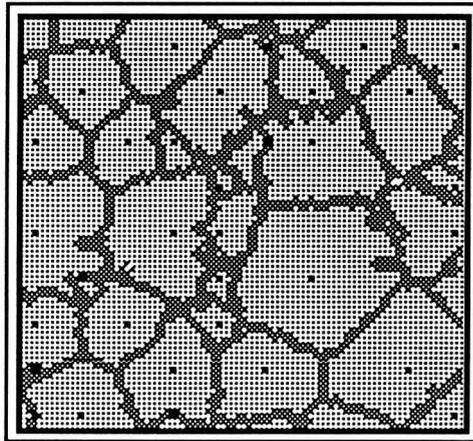


Fig 11. Map of crown projection resulting from simulated growth and development of a stand.

when needed by the simulation process. Further work is needed to derive tree characteristics for the crown dimensions, to process inputs for various thinning treatments, and to repeatedly submit simulations to the system.

DISCUSSION AND CONCLUSION

The methods described in this paper rely on a crown architecture structured by a main axis, with branches and shoots about evenly occupying space with circular symmetry at each whorl. As they also assume that stem extension growth controls branch growth (named apical control; after Wilson, 1984), they are specific to conifers.

It has to be stressed that the most important aspects of Douglas-fir individual growth, in various stand conditions, described by the relationships established by Mitchell (1975) have been confirmed. No formal comparison of both sets of relationships, for local conditions in British Columbia and in France, is feasible without the possibility of pooling the data. Nevertheless, it seems through a cursory comparison of the equations obtained that crown diameter at a given distance of the apex is smaller in the first case, while bole increment for given crown dimensions is greater. This could result partly from the combined effects of provenance and climate.

The foliar volume, derived from geometrical arguments, might be an estimate of the leaf area – or possibly a weighted sum version of this – commonly used by physiologists (for instance, Waring *et al*, 1980; Vose and Allen, 1988). Experimental work could establish a correspondance between these quantities to unify the results of both origins. Moreover, the estimation of weighting factors used to calculate the foliar volume could benefit from the methods where in “process-based” models (Grace, 1990), used canopy structure and light interception, are taken into account.

Equations (8) and (9), expressing the effect of crown absolute and relative dimensions upon stem volume increment on one hand, and upon height increment on the other hand, should be considered as

fundamental, because they give insight into the relationships between individual tree growth and the surrounding tree competition, which is of major concern in silviculture. Concerning Equation (8), it is probably unnecessary to use an expression combining the most recent increments to relate stem volume increment to crown dimensions, because height growth in the last 5 years, used to compute foliar volume, should account for climatic variations.

As already stated, the best results to fit Equation (8) were obtained with the increment of the year preceding the last one. This could be attributed to a large part of determinacy of the growth of the last year by the preceding one (Wilson, 1984), combined with a somehow intermediate position of this year, which would better reflect the state of the crown (whose foliar volume is based on the last 5 years). Equation (8) expresses that for a given foliar volume, the crowns with smaller competitive status FV/FV_{\max} are more productive considering stem increment. This could arise from smaller maintenance needs of these crowns, and was already noticed by Hamilton (1969).

Concerning the validation attempted for Equation (8), it should be noted that the correction for inverse transformation of Equation (7) was not the uniform multiplication by a factor applied above, but the full correction which depends on the values at which the prediction is to be made (see Flewelling and Pienaar, 1981; or the original paper by Bradu and Mundlack, 1970). The bias observed is possibly caused partly by the positioning of the middle part of the zone of crown contact, on the test trees, for the past years (we recall that this position was presumably set at the point of stabilization of the annual ring area of stem cross section, but not directly observed). This could be amplified be-

cause the successive annual increments concerning a given test tree are dependent on the peculiarities of this tree. Nevertheless, in figure 9, this bias appears as a linear deviation that could be corrected by a mere scaling factor.

This last question will be best approached in the application of this study to the stimulation of growth and development of trees in stands, by means of the stimulation system discussed in the preceding section, that should be soon operational. We plan to present the results of such simulations, compared to data of observed permanent stands, in a subsequent paper.

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