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Functional-Structural Tree Models

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Functional-Structural Tree Models

Papers selected from the Helsinki Workshop
on Functional-Structural Tree Models,
12–13 September, 1996

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Preface

Computer models that treat plants as consisting of elementary units have become increasingly popular. The core of such a model is the description of what happens in a single plant element. Models can use various elements, such as bud, leaf, internode, stem segment, etc. A computer program takes care of all the elements and integrates their activities to the functioning of the whole plant. Both the 3-D architecture and the metabolic processes can be treated in the same model at the same time in a natural way. Increasing speed of computers, developing programming tools and available mathematical techniques have made the construction of such models increasingly feasible.

Modelling plants using computer models where the plant consists of elementary units can be viewed as an extension of the classical method of differential calculus. Traditionally, the analysis of an entity proceeds in three steps: First, the elemental processes are analysed in a small (differential) volume and/or time element. Second, a differential equation is derived on the basis of this analysis, and third, this differential equation is solved with adequate boundary conditions and assuming adequate geometry (if spatial aspects are involved). In the computer models, the program acts both as the "differential equation" and as the "means of solution". The difference in comparison with analytical solutions of differential equations is the immensely greater capacity of the computer to deal with complex situations. There are no per se limitations to the 3-D architecture or interactions of elements which could be programmed into the code. These models can hence be viewed as an extension of the existing methods of describing plant growth and development.

The stimulus to organise the "Helsinki workshop on functional-structural tree models" grew from the persuasion that models dealing with the functioning and structure in terms of elementary units will constitute an important extension to the methods of plant modelling in the future, and that the construction of such models will be an intriguing challenge to scientists. We coined the name "functional-structural model" to emphasize that both functioning (processes producing material for growth) and structure (true 3-D structure) can be and are dealt with in the same model[1]. The present volume collects the articles of this workshop held 12–13 December 1996 in Helsinki. The aim was to deal with functional-structural tree models and important factors affecting these models. The program consisted of invited lectures and voluntary

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[1] Also other names have been used for this kind of models, e.g. virtual plant models or models of plant morphogenesis (Room, P., Hanan, J. and Prusinkiewicz, P. 1996. Virtual plants: new perspectives for ecologists, pathologists and agricultural scientists. Trends in Plant Science 1(1): 33–38).

papers. Speakers were asked to submit manuscripts expanding their presentations at the meeting for inclusion in a special issue of Silva Fennica, in which the normal reviewing procedure has been applied. Articles in this issue cover the major part of the presentations.

The articles fall in five categories: First, modelling the distribution of growth in a system consisting of many parts is focal in these models. The transport/conversion process framework developed by J.H.M Thornley is of key importance in this. It and distribution of growth in general is analysed in the articles by J.H.M. Thornley, and C. Deleuze and F. Houllier.

Second, there exist constraints to the structure of trees, among others the so-called pipe model theory. The article of H. Valentine considers the height growth of trees in the pipe model framework and A. Mäkelä et al. use the same concept to predict the branch distribution in a tree.

Third, mathematical description and measurement of 3-D tree structure is of key importance for functional-structural models. The article by C. Godin et al. presents a method for analysis and description of topology of plants and the article by H. Sinoquet et al. describes measuring 3-D structure of a tree. The article by T. Früh describes a method of solving water flow (in terms of a partial differential equation) in a complex tree architecture.

Fourth, L-systems offer an effective mathematical means for constructing models for detailed simulation of tree structure. The article by W. Kurth and B. Sloboda presents the possibilities of L-systems and explores possibilities to represent complex interactions in them.

Fifth, the articles by Ph. de Reffye et al., S. Le Dizés et al. and R. Sievänen et al. give examples of functional-structural models.

We hope that this collection of papers gives insights into the possibilities and problems in the field of functional-structural modelling of plants, as well as invites new scientists to construct new models and to solve research problems using them.

We gratefully acknowledge the support provided by the Academy of Finland, the Finnish Society of Forest Science and the Finnish Forest Research Institute for making the Helsinki workshop feasible. We would also like to thank the contributors to this special edition. The work provided by the reviewers of the manuscripts is highly appreciated.

Risto Sievänen	*Eeva Korpilahti*
Annikki Mäkelä	Editor
Eero Nikinmaa	
Workshop organisers	

A Transport Model for Tree Ring Width

Christine Deleuze and François Houllier

Deleuze, C. & Houllier, F. 1997. A transport model for tree ring width. Silva Fennica 31(3): 239–250.

Process-based tree growth models are recognized to be flexible tools which are valuable for investigating tree growth in relation to changing environment or silvicultural treatments. In the context of forestry, we address two key modelling problems: allocation of growth which determines total wood production, and distribution of wood along the stem which determines stem form and wood quality. Growth allocation and distribution are the outcome of carbon translocation, which may be described by the Münch theory. We propose a simpler gradient process to describe the carbon distribution in the phloem of conifers. This model is a re-formulation of a carbon diffusion-like process proposed by Thornley in 1972. By taking into account the continuity of the cambium along the stem, we obtain a one dimensional reaction-diffusion model which describes both growth allocation between foliage, stem and roots, and growth distribution along the stem. Distribution of wood along the stem is then regarded as an allocation process at a smaller scale. A preliminary sensitivity analysis is presented. The model predicts a strong relationship between morphology and foliage:root allocation. It also suggests how empirical data, such as stem analysis, could be used to calibrate and validate allocation rules in process-based growth models.

Keywords allocation, carbon, wood distribution, functional balance, Münch's theory, optimization, partitioning, process-model, reaction-diffusion, stem taper, Thornley's model

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1 Introduction

The ecological and social context of silviculture is changing. The environment is being modified by global climatic changes as well as by local air pollution, and the management of forest plantations is becoming more intensive with a growing concern for wood quality. This changing context results in changing silvicultural treatments and forest productivity, that requires new modelling approaches. Most traditional yield and growth models have been developed from a strong empirical basis (experiments, long-term permanent plots, regional forest surveys, destructive stem analysis). These models provide reliable predictions of forest growth and yield, as long as they are used for interpolation, i.e. for ecological and silvicultural conditions which fall within the range of conditions under which the model was built. However these models cannot be applied when conditions fall outside this range. This limitation is a major reason for the development of more flexible models, based on the description of tree and stand growth ecophysiological processes (Kimmins 1986, 1990, Nikinmaa 1992, Sievänen 1993).

Most process-based growth models predict biomass growth (Reynolds and Thornley 1982, MacMurtrie 1985, Mäkelä 1986) but foresters are also interested in a detailed description of the stem, as an indicator of timber quality (Väisänen et al. 1989, Lindström 1996). We have already proposed a process-based model which generates a vertical stem profile (Deleuze and Houllier 1995). In this paper we improve this description and propose a more detailed and flexible allocation submodel. We first briefly review existing approaches to modelling carbon allocation and the distribution of wood increment along the stem. We then outline the mechanistic Münch theory of carbon translocation and formulate a simpler mechanistic model of allocation in three stages: for a simple plant without stem, for a stem and for a complete tree with foliage and roots. We study the behaviour of the latter model and show how it can be interpreted in terms of reaction to a changing environment (water stress, fertilization).

2 Carbon Allocation and Wood Distribution

Carbon or growth allocation is the outcome of many different processes that are not yet well understood (Dewar 1993), including chemical transformations, phloem loading, mass flow, and phloem unloading. However, allocation is crucial in process models for forestry because the quantity of wood produced is highly sensitive to this aspect of the model. Even if photosynthetic production is known, wood production depends on the proportion of carbon allocated to the stem. Moreover, allocation is very sensitive to environmental conditions and describes the adaptative capacity of trees (Bossel 1987). For instance, fertilization often results in a decrease of root growth (in relative terms) and an increase of foliage and stem growth (in relative and absolute terms). Partitioning also depends on other ecological conditions, such as nutrient and water availability, temperature and light (McMurtrie and Wolf 1983, McMurtrie 1985, Bassow et al. 1990), and silvicultural treatments, such as thinning (Mäkelä and Hari 1986).

As well as predicting the total wood production, i.e. timber volume or biomass, it is also desirable to describe the distribution of wood along the stem because ring width variation and stem profiles are good predictors of wood quality and basic density for conifers (Larson 1969, Väisänen et al. 1989, Lindström 1996). Stem profile and ring width distribution are affected by ecological and silvicultural factors (Farrar 1961) such as social position (Sterba 1981, Gordon and Graham 1986), thinning (Reukema 1964, Meng 1981, Thomson and Barclay 1984, Valinger 1992, Thomas et al. 1995), fertilization (Mitchell and Kellog 1971, Miller and Cooper 1973, Snowdon et al. 1981, Thomson and Barclay 1984, Jack et al. 1988, Mead and Tamm 1988, Valinger 1992), water stress (Sterba 1981) and other environmental disturbances (Schmid-Haas et al. 1986).

3 Existing Approaches to Modelling Carbon Allocation and Wood Distribution

There are various extant approaches to modelling carbon allocation: (i) fixed partitioning coefficients (McMurtrie 1985) but the model is then very rigid; (ii) proportional partitioning according to Warren-Wilson's *principle* (Wyse 1986). This principle, based on empirical observations, assumes that carbon is partitioned according to the strength of each sink. It is observed in steady-state conditions and does not describe the dynamics in a variable environment; (iii) hierarchical partitioning assigning a priority to each sink. This hierarchy is subjective and changes with phenology and environmental conditions; (iv) partitioning coefficients constrained by internal allometries such as the functional balance or the pipe model (Valentine 1985, Mäkelä 1986, Sievänen 1993). These allometric relationships are assumed to be stable and their variability under environmental changes has rarely been analyzed; (v) adaptation of the partitioning coefficient in order to optimize growth given some external constraints. This is a teleological approach (Thornley 1991) which assumes that the tree adapts its partitioning to the combination of external conditions. The solution depends on how the optimization problem is formulated (choice of the growth variable, the time and spatial steps) and is thus subjective; (vi) mechanistic partitioning based on the physiological processes of translocation (Tyree et al. 1974, Bassow and Ford 1990). Because of the complexity of the processes and of problems of instability, these models are good research tools for understanding the physiology of translocation, but they are not yet practical tools; (vii) simpler mechanistic models based on a concentration gradient-dependent process such as diffusion (Thornley 1972, 1991). This model can give similar results to those obtained with the functional balance (Mäkelä and Sievänen 1987) or optimization approaches (Thornley 1995).

Modelling wood distribution in process-based models is still uncommon but there are three main approaches: (i) the distribution is constrained by an internal allometry as in the pipe model (Nikinmaa 1992, Mäkelä et al. 1996); (ii) an uniform distribution according to Pressler's rule that "the area increment on any part of the stem is proportional to the foliage capacity in the upper part of the tree" (Assmann 1970, Mitchell 1975); (iii) growth is distributed in order to achieve constant mechanical stress along the stem (Mattheck 1990).

Methods (iv) for partitioning and (ii) for wood distribution have already provided a first useful way to predict stem profile from a simple process-based growth model for Norway spruce (Deleuze and Houllier 1995). Since partitioning and wood distribution are very sensitive to environmental changes, a more flexible model of carbon allocation is proposed here to describe partitioning and stem profiles.

4 Translocation According to Münch's Theory

To build a more mechanistic model we look at the underlying process of translocation as described by Münch's theory (Münch, 1930) and mathematically formulated by Smith et al. (1980). This theory is based on an experiment (Fig. 1) done by Ernst Münch in 1930. Let us consider two cells A and B, with semi-permeable membranes, filled with different sugar concentrations (higher in A) immersed in water and connected by a non-permeable tube. The concentration dif-

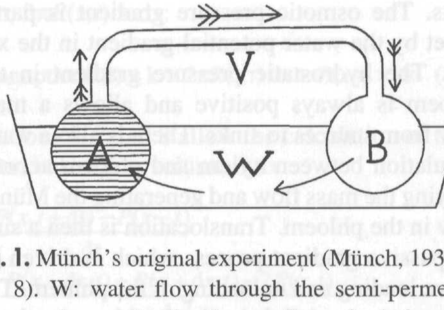

Fig. 1. Münch's original experiment (Münch, 1930, p. 8). W: water flow through the semi-permeable membrane of cells; V: mass flow of solution from cell A, with a high sugar concentration, to cell B, with a low concentration, through a non-permeable tube.

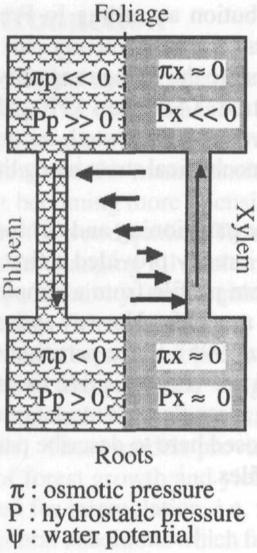

Fig. 2. Diagram illustrating the parallel flows of xylem and phloem sap, with hydrostatic pressure gradients. is the osmotic pressure, *P* the hydrostatic pressure and ψ the water potential. Indices *x* refers to xylem and *p* to phloem. ψ = *P* +

ference between A and B creates a difference of osmotic pressure and hence a difference of hydrostatic pressure, which then drives mass flow of sugar (V) from A to B. At the same time, water (W) enters cell A and exits cell B. This water flow accompanies the mass flow. The combination of these two flows is the Münch flow.

For a plant (Fig. 2) the phloem is described as a file of semi-permeable sieve cells with a gradient of sugar concentration between sources and sinks. The osmotic pressure gradient is partly offset by the water potential gradient in the xylem. The hydrostatic pressure gradient in the phloem is always positive and allows a mass flow from sources to sinks. There is also a water circulation between xylem and phloem accompanying the mass flow and generating the Münch flow in the phloem. Translocation is then a simple passive gradient process which is driven by active loading and unloading of the phloem. The strong structural link between phloem and xylem explains the direct response of translocation to changes in the water potential gradient and water availability. For instance, a water deficit decreases the pressure gradient and decreases the mass flow. Moreover the water flow between phloem and xylem decreases. Translocation is thus reduced by a water deficit (Roberts 1964, Esau 1969, Kuhns and Gjerstad 1988).

For the simpler model (see 5 below), we remember that translocation is a passive process, involving a concentration gradient, maintained by loading and unloading of the phloem. This process is directly connected to the water availability.

5 A Simpler Model of Translocation for a Plant with Two Compartments

Consider a plant consisting of two compartments: foliage and roots. W_i is their biomass and C_i their carbon labile concentration ($i = f$ for foliage and r for roots). The biomass compartments grow with a relative growth rate k_i and a conversion coefficient Y. We neglect senescence and respiration. To describe carbon partitioning we use the simplest gradient process which is diffusion-like, with a resistance Ψ. This approach was first described by Thornley (1972). According to the link between translocation and xylem water potential, we assume that the resistance Ψ depends on water availability. We consider a small amount of carbon in the foliage at $t = 0$, which is then partitioned by diffusion and used for biomass growth in each compartment. Dilution of sugar is neglected for this small biomass increment. Partitioning coefficients can then be calculated.

Growth and conservation equations in each compartment are:

$$\begin{cases} \dfrac{dC_f}{dt} = \dfrac{C_r - C_f}{\Psi} - k_f\,C_f \\ \dfrac{dW_f}{dt} = k_f\,Y\,C_f W_f \approx k_f\,Y\,C_f W_{fo} \end{cases} \tag{1}$$

$$\begin{cases} \dfrac{dC_r}{dt} = \dfrac{C_f - C_r}{\Psi} - k_r\,C_r \\ \dfrac{dW_r}{dt} = k_r\,Y\,C_r W_r \approx k_r\,Y\,C_r W_{ro} \end{cases} \tag{2}$$

At the beginning ($t = 0$), we assume that:

$W_f = W_{fo} \approx 1$; $W_r = W_{ro} \approx 1$; $C_f = \sigma_c$ and $C_r = 0$.

The system is linear for concentrations and could easily be solved. Solutions for biomasses are then deducted by integration. With this very simple model we can then calculate the analytical solutions for growth when σ_c has been completely consumed.

$$\begin{cases} \text{Lim}\left(\Delta W_f\right)_{t\to+\infty} = \dfrac{\psi\, k_f\, Y \sigma_c \left(\frac{1}{\psi} + k_r\right)}{k_f + k_r + \psi\, k_f\, k_r} \\ \text{Lim}\left(\Delta W_r\right)_{t\to+\infty} = \dfrac{k_r\, Y\, \sigma_c}{k_f + k_r + \psi\, k_f\, k_r} \end{cases} \quad (3)$$

Partitioning coefficients are then:

$$\begin{cases} \lambda_f = \dfrac{k_f\,(1 + \psi\, k_r)}{k_f + k_r + \psi\, k_f\, k_r} \\ \lambda_r = \dfrac{k_r}{k_f + k_r + \psi\, k_f\, k_r} \end{cases} \quad (4)$$

Allocation according to Warren-Wilson (Wyse 1986) would give partitioning coefficients as ratios of sink strengths (growth rates):

$$\begin{cases} \lambda_f = \dfrac{k_f}{k_f + k_r} \\ \lambda_r = \dfrac{k_r}{k_f + k_r} \end{cases} \quad (5)$$

Equations (5) is given by equations (4) when $\Psi = 0$: transport without resistance gives the same partitioning as the allocation of Warren-Wilson. The resistance Ψ introduces a disadvantage for the roots and measures the cost of transport from sources to sinks. Equations (5) describes two empirical features of allocation:

(i) partitioning depends on the intrinsic strength of each sink (k_i);

(ii) sinks which are nearer to the source are favored against the more distant sinks.

6 Translocation in the Stem

For a tree, a third compartment is introduced: the stem. To take account of the cambium in secondary growth, we assume that the stem is a continuous sink between foliage and roots. Carbon is assumed to be transported in the phloem. For conifers, phloem is assumed to have a constant cross-sectional area S distributed around the cambium. The radius of the cambium is assumed to be the radius of the stem $R(x,t)$ at distance x from the crown and time t, increasing from foliage to roots (Fig. 3). Translocation is described with the previous diffusion-type model, with a resistance r per unit length of phloem. $P(x,t)$ is the concentration of labile carbon in the phloem.

The model is derived from the mass balance of sugar in the elementary volume $S\,\mathrm{d}x$, at distance x and time t (Fig. 3).

$$S\,\mathrm{d}x\, P(x,\, t + \mathrm{d}t) = S\,\mathrm{d}x\, P(x,\, t) + P(\text{in}) - P(\text{out}) - \text{Consumption} \quad (6)$$

P(in) and P(out) are diffusion terms, proportional to the concentration gradient, with resistance $r\,\mathrm{d}x$.

$$\begin{cases} P(\text{in}) = \dfrac{P(x,t) - P(x-\mathrm{d}x,t)}{r\,\mathrm{d}x} S\,\mathrm{d}t \\ P(\text{out}) = \dfrac{P(x+\mathrm{d}x,t) - P(x,t)}{r\,\mathrm{d}x} S\,\mathrm{d}t \end{cases} \quad (7)$$

Consumption is assumed proportional (parameter k) to P and to the contact surface with cambium, $2\pi R(x,t) \times \mathrm{d}x$:

$$\text{Consumption}(x,t) = \mathrm{k} \times 2\pi R(x,t)\, \mathrm{d}x \times P(x,t) \times \mathrm{d}t \quad (8)$$

Equations 6, 7 and 8 allow the calculation of the carbon balance in volume $S\,\mathrm{d}x$:

$$\frac{P(x,t+\mathrm{d}t) - P(x-t)}{\mathrm{d}t} = \frac{P(x-\mathrm{d}x,t) + P(x+\mathrm{d}x,t) - 2P(x,t)}{r\,\mathrm{d}x^2} - \frac{\mathrm{k}\, 2\pi R(x,t)\, P(x,t)}{S} \quad (9)$$

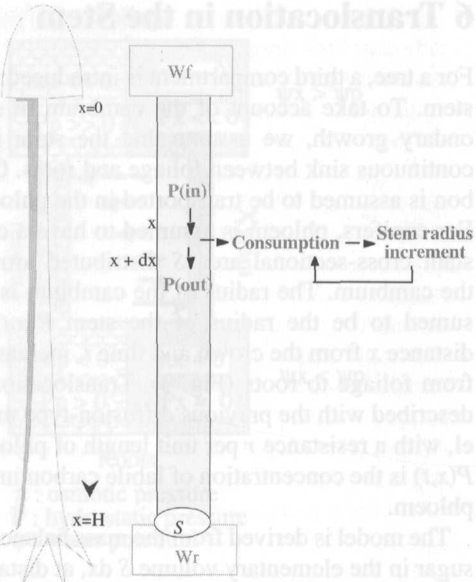

Fig. 3. Description of the stem between the foliage and the roots. Carbon is translocated in the phloem represented (on the right) by a cylinder with a constant area S, distributed around the stem (on the left). The elementary volume $S\,\mathrm{d}x$ is represented between x and $x + \mathrm{d}x$.

This leads to the parabolic partial differential equation:

$$\frac{\partial P}{\partial t} = \frac{\partial^2 P}{r\,\partial x^2} - \frac{2\,\pi\,k\,R\,P}{S} \tag{10}$$

Consumption of carbon results in a wood volume increment with density ρ (dry weight of carbon per unit fresh volume of wood) which is distributed around the cambium for xylem growth.

$$\frac{\partial(\pi R^2)}{\partial t} = k\,2\,\pi\,R\,P\,/\,\rho \tag{11}$$

which simplifies to

$$\frac{\partial R}{\partial t} = k\,P\,/\,\rho \tag{12}$$

Equations 10 and 12 provide the differential system of reaction–diffusion with two variables (P and R):

$$\begin{cases} \dfrac{\partial P}{\partial t} = \dfrac{\partial^2 P}{r\,\partial x^2} - 2\,\pi\,k\,R\,P\,/\,S \\ \dfrac{\partial R}{\partial t} = k\,P\,/\,\rho \end{cases} \tag{13}$$

7 Whole-Tree Model

The system of equations 13 is used to describe the dynamics of the stem in a whole-tree model. Foliage and root dynamics are described by equations similar to equations 1 and 2. Losses by respiration (r_i) and senescence (s_i) are also taken into account (Fig. 4). Dilution is still neglected. σ_c is the photosynthetic efficiency per unit of foliage biomass. Y is the conversion efficiency coefficient. k_i are the growth rates. Foliage (resp. root) labile carbon concentration is in equilibrium with concentration P at the top (resp. the bottom) of the stem.

$$\begin{cases} \dfrac{\partial C_f}{\partial t} = \sigma_c - \dfrac{S\,\partial P}{r\,W_f\,\partial x} - r_f - k_f\,C_f \\ \dfrac{\partial W_f}{\partial t} = \left(k_f\,Y C_f - s_f\right) W_f \end{cases} \tag{14}$$

$$\begin{cases} \dfrac{\partial P}{\partial t} = \dfrac{\partial^2 P}{r\,\partial x^2} - \dfrac{2\,\pi\,k\,R\,P}{S} - \dfrac{2\,\pi\,r_s\,R}{S} \\ \dfrac{\partial R}{\partial t} = k\,P\,/\,\rho \end{cases} \tag{15}$$

$$\begin{cases} \dfrac{\partial C_r}{\partial t} = \dfrac{S\,\partial P}{r\,W_r\,\partial x} - r_r - k_r\,C_r \\ \dfrac{\partial W_r}{\partial t} = \left(k_r\,Y C_r - s_r\right) W_r \end{cases} \tag{16}$$

This system can not be solved analytically but it can be discretized for numerical simulation. The discretization must be stable and we use a Crank-Nicholson scheme (Press et al. 1988) which is always stable for this system. With the Crank-Nicholson scheme and with constant parameters, smaller Δt and Δx only improve the accuracy of the results but increase the time resolution of simulations. We choose $\Delta t = 10^{-1}$ year and $\Delta x = 50$ cm. Simulations are done with Matlab software on a PC. Parameters are from the model of Deleuze and Houllier (1995) for Norway

Table 1. Summary of model parameters and variables.

Name	Meaning	Unit	Value
W_f	Foliage biomass	kgDW	Variable
W_r	Root biomass	kgDW	Variable
C_f	Carbon concentration in the foliage	kgC/kgDW	Variable
C_r	Carbon concentration in the roots	kgC/kgDW	Variable
k_f	Foliage growth rate	year^{-1}	9
k_r	Root growth rate	year^{-1}	30
k	Stem growth rate	m.year^{-1}	20
Ψ	Resistance between foliage and root	year	
r	Resistance along the phloem	year/m^2	4 e^{-9}
σ_c	Specific photosynthetic activity	kgC kgDW^{-1} year^{-1}	2.079
x	Distance from the crown	m	Variable
t	Time	year	Variable
S	Phloem cross sectional area	m^2	5 e^{-5}
$P(x,t)$	Photosynthates concentration in the phloem	kgC/m^3	Variable
$R(x,t)$	Stem radius	m	Variable
ρ	Dry weight of carbon per unit of fresh wood volume	kg/m^3	191.5
Y	Conversion coefficient	kgDW kgC^{-1}	0.6
r_f	Maintenance respiration coefficient of foliage	kgC kgDW^{-1} year^{-1}	0.1
r_r	Maintenance respiration coefficient of root	kgC kgDW^{-1} year^{-1}	0.1
r_s	Maintenance respiration coefficient of stem	kgC m^{-2} year^{-1}	0.01
s_f	Senescence coefficient of foliage	year^{-1}	0.2
s_r	Senescence coefficient of root	year^{-1}	0.5

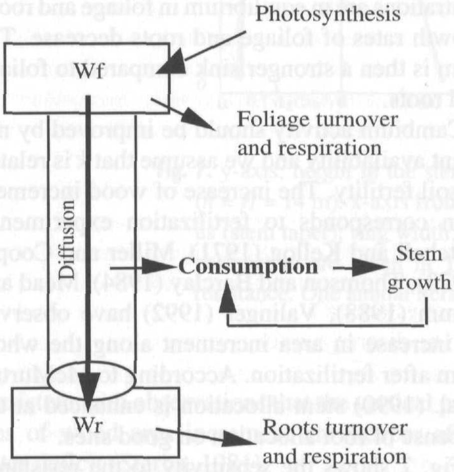

Fig. 4. Whole-tree model with 3 compartments: foliage W_f, roots W_r and stem between foliage and roots. Carbon gain from photosynthesis. Carbon losses from respiration, senescence and consumption. Carbon transport by diffusion.

spruce and given in Table 1. The initial state is for a 50-year old tree: $H_o = 14$ m; $W_{fo} = 12$ kgDW; $W_{ro} = 8.6$ kgDW; $R(x, t = 0) = 0.045x + 0.64$. Fig. 5 shows 5 years of simulation, but the stem height between root and crown basis is assumed to be constant.

The model generates various partitioning coefficients which are intermediate parameters cal

Table 2. Allocation coefficients after 5 years of simulation. Allocation of carbon or growth increment. (Carbon allocation includes senescence and respiration. Growth allocation is the net result of growth, allocation, senescence and respiration).

Allocation coefficient	Carbon allocation	Growth allocation
λ_f (foliage)	0.2235	0.0902
λ_s (stem)	0.4069	0.8146
λ_r (roots)	0.3696	0.0951

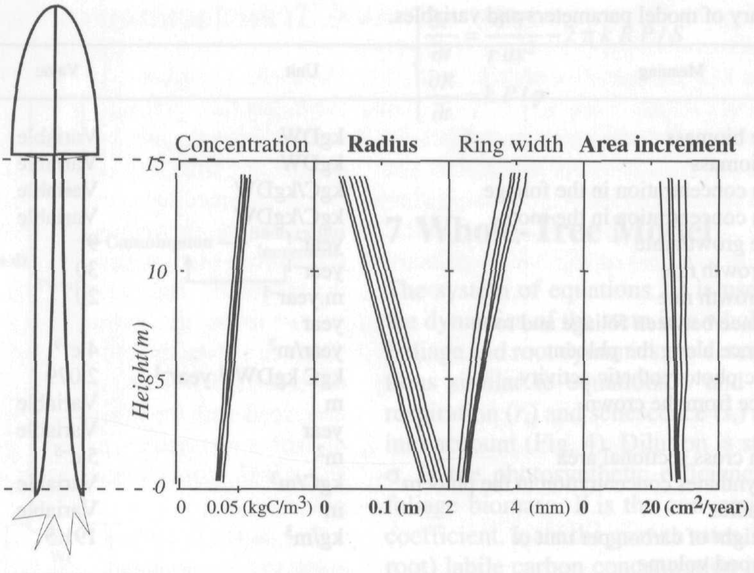

Fig. 5. y-axis: height in the stem between roots ($h = 0$) and crown basis ($h = H = 14$ m). x-axis from left to right: carbon concentration; radius (stem taper); ring width; basal area increment along the stem. Simulation for the initial model and 5 subsequent annual iterations. All parameters are given in Table 1.

culated through the growth simulations. Table 2 shows the different values after one year of simulation according to the definition of allocation: for instance partitioning of initial carbon uptake or partitioning of final growth. Other partitioning coefficients could be calculated. This model could be used to compare the different definitions of allocation.

In Fig. 5, we observe a steep vertical profile for sugar concentration which is compensated by the conical shape of the stem, and thus results in an approximately constant area increment of wood along the stem under the crown base: this consequence of our model in stable conditions is in agreement with Pressler's rule.

8 Sensitivity of the Model to Some Parameters

Fig. 6 shows the sensitivity of the model to the sink strength, the parameter k (each simulation is for one year). If the parameter k increases, stem growth increases along all the stem, whereas carbon concentration decreases. Because concentrations are in equilibrium in foliage and roots, growth rates of foliage and roots decrease. The stem is then a stronger sink compared to foliage and roots.

Cambium activity should be improved by nutrient availability and we assume that k is related to soil fertility. The increase of wood increment then corresponds to fertilization experiments: Mitchell and Kellog (1971), Miller and Cooper (1973), Thomson and Barclay (1984), Mead and Tamm (1988), Valinger (1992) have observed an increase in area increment along the whole stem after fertilization. According to McMurtrie et al. (1990) stem allocation is enhanced at the expense of root allocation on good sites.

Fig. 7 shows the sensitivity to the resistance parameter r. When the resistance is larger, stem profiles are steeper. Carbon is consumed more rapidly than it is transported. Concentration in the foliage increases whereas concentration in the roots decreases. With our assumption that r is related to water availability, these results are

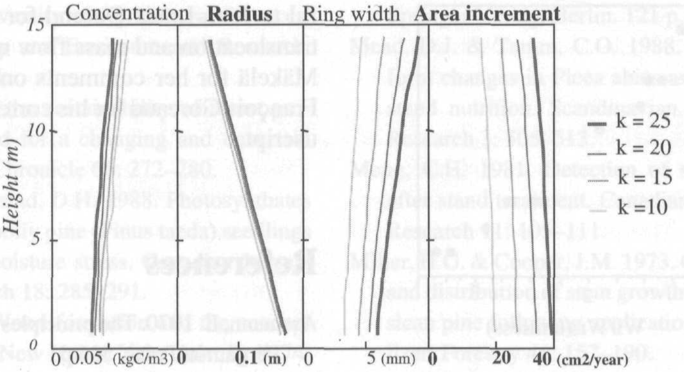

Fig. 6. y-axis: height in the stem between roots ($h = 0$) and crown basis ($h = H = 14$ m). x-axis from left to right: carbon concentration; radius (stem taper); ring width; basal area increment along the stem. All parameters are given in Table 1, except for parameter k of stem consumption. One annual iteration per value of parameter k.

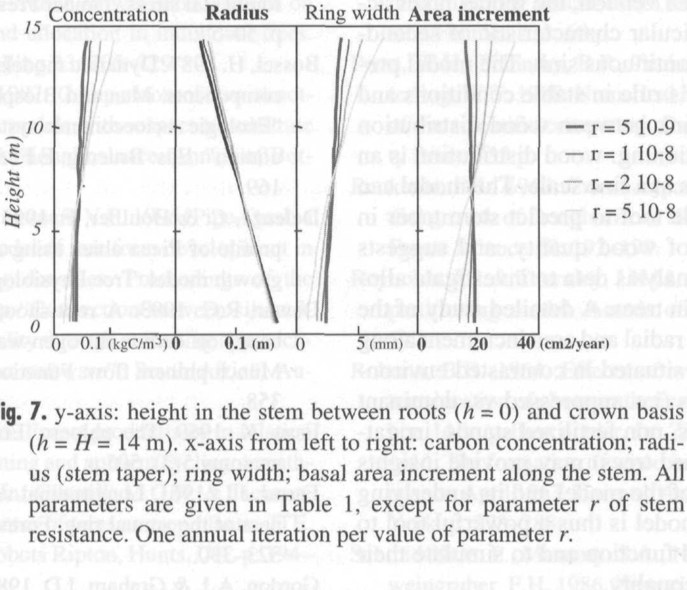

Fig. 7. y-axis: height in the stem between roots ($h = 0$) and crown basis ($h = H = 14$ m). x-axis from left to right: carbon concentration; radius (stem taper); ring width; basal area increment along the stem. All parameters are given in Table 1, except for parameter r of stem resistance. One annual iteration per value of parameter r.

consistent with observations that the vertical profiles of wood area increment are steeper after water deficit (Sterba, 1981).

These simulations show the strong relationship between stem profile and growth partitioning in the tree. Fig. 8 compares the profiles of wood area increment with the foliage:root ratio. Partitioning in the tree is therefore related to wood distribution along the stem.

9 Discussion and Conclusions

This model is simpler than the translocation mechanism described by Münch flow, but it is also based on a gradient process. It is consistent with the Warren-Wilson view of partitioning when $\Psi = 0$, but takes account of the advantage of nearest sinks when $\Psi > 0$. Therefore the model exhibits a strong link between plant morphol-

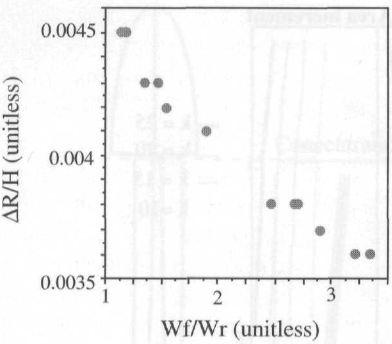

Fig. 8. Relationship between foliage:root ratio (W_f/W_r) and conicity of the stem wood increment ($\Delta R/H$) after one year of simulation, when the parameter r changes from 10^{-10} to 10^{-7}.

ogy and allocation pattern.

In the whole-tree version, the model takes account of the particular characteristic of secondary growth as a continuous sink. The model predicts the Pressler's rule in stable conditions and shows a strong link between wood distribution and growth partitioning: wood distribution is an allocation process at a fine scale. The model can serve as a flexible tool to predict stem taper in forestry models of wood quality, and suggests the use of stem analysis data to investigate allocation processes in trees. A detailed study of the vertical profile of radial and area increment along the stem of trees situated in contrasted environmental conditions (i.e. suppressed vs. dominant trees, fertilized vs. non fertilized stands, irrigated vs. non irrigated trees) may provide insights into the validity of the model and its underlying principles. The model is thus a powerful tool to link structure and function and to simulate their effects on timber quality.

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