# IMPLICATIONS OF THE PIPE MODEL THEORY ON DRY MATTER PARTITIONING AND HEIGHT GROWTH IN TREES

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December 1985
WP-85-89

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# PREFACE

IIASA's Acid Rain project is currently extending its model system, RAINS (Regional Acidification INformation and Simulation) to the possible damage caused by acid rain to forests. Like all submodels of RAINS, the forest impact submodel will be based upon a simple description of basic dynamics, while the complexity of RAINS originates in spatial and temporal extent and integration of disciplines. Building a simple model, however, often requires a thorough, understanding of the complexities of the system, so as to maintain the essential relationships of the real object in the model.

Our understanding of the response of forests to air pollution is still limited not only as regards the pathways of pollutant impact themselves, but also in relation to some basic phenomena of tree growth and development. One of the missing links in the chain from pollutants to damage is how the physiological processes, immediately affected by air pollution, interact at the whole-tree level, and how this interaction evolves as the tree grows bigger.

This paper describes a development of a dynamic individual-tree model which is based on requirements of metabolic balance and their interaction with tree structure. Because of its generality, the model can be applied to various situations, also giving insight into the impacts of a changing environment. An interesting contribution of the paper is that it provides a quantitative relationship between sensitivity to environmental stress, ecophysiological parameters and tree size.

Leen Hordijk
Project Leader

# ACKNOWLEDGEMENTS

The author wishes to acknowledge the contributions of Pertti Hari and Leo Kaipiainen to the ideas presented in this paper. Special thanks are due to Pekka Kauppi, Ram Oren and Risto Sievanen who have reviewed the manuscript and given their fruitful comments.

## ABSTRACT

A dynamic growth model is developed for forest trees where the partitioning of growth between foliage and wood is performed so as to fulfill the assumptions of the ***pipe model theory*** (Shinozaki et al. 1964a), i.e to maintain sapwood:foliage ratio constant. Partitioning of growth to feeder roots is treated using the principle of ***functional balance*** (White 1935, Brouwer 1964, Davidson 1969 and Reynolds and Thornley 1982). The model uses the time resolution of one year and it applies to the life-time of the tree. The consequences of the pipe model theory are examined by studying the life-time growth dynamics of trees in different environments as functions of length growth patterns of the woody organs. It is shown that there is a species-specific, environment-dependent upper limit for a sustainable length of the woody organs, and that the diameter of a tree at a certain height depends upon the rate at which that height has been achieved. These results are applied to the analysis of deceleration of growth, response to environmental stress and height growth patterns in a tree population. Further, the possible factors that allow certain coniferous species in the Pacific Northwest region to maintain an almost unlimited height growth pattern are discussed in relation to the pipe model theory.

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Annikki Mäkelä

## 1. INTRODUCTION

The pipe model theory by Shinozaki et al. (1964a) first theoretically formulated the observation that in trees, sapwood area is proportional to foliage biomass. The theory reasoned that each unit of foliage requires a unit pipeline of wood to conduct water from the roots and to provide physical support. Although the argument may be disputable, recent empirical observation strongly supports the existence of such a relationship. Constant ratios have been established both between sapwood and foliage area (or biomass) (Rogers and Hinckley, 1979; Waring, 1980; Kaufmann and Troendle, 1981), and sapwood areas of successive parts of the water conducting wood (Kaipiainen et al., 1985). The ratios appear fairly constant within species despite large environmental variation (e.g. Kaufmann and Troendle, 1981; Kaipiainen et al., 1985).

While the applicability of such constants to inventories of standing biomass has been widely recognized (Shinozaki et al., 1964b; Waring et al., 1982), less attention has been paid to the implications the maintenance of the structural balance may have to growth dynamics. Two observations are important from this viewpoint. First, since standing biomass is cumulative growth minus turnover, a balance between the rates of these two processes is required for maintaining the constant ratios between the standing biomass compartments. Secondly, as the tree grows higher, the build-up of new pipelines requires more and more growth resources per unit leaf biomass.

Varying the density of a tree stand causes variation in individual tree basal area and leaf biomass, but tree height remains more or less unchanged (Whitehead, 1978). A reason for this may be that the significance of the length variables for survival is not in their contribution to the internal balance of growth, but rather to the competitive ability for light and space.

A similar ratio has been observed between roots and leaves, with the difference that the ratio varies with the soil nutrient level. White (1935) observed that dry matter partitioning between the roots and shoots of grass and clover were dependent upon the light and nitrogen levels applied in laboratory experiments. This principle of functional balance was further developed and formalised mathematically by Brouwer (1964) and Davidson (1969), and a dynamic model of partitioning in non-woody plants was developed by Reynolds and Thornley (1982).

A dynamic growth model is developed for forest trees where the partitioning of growth between foliage and wood is performed so as to maintain the sapwood:foliage ratio constant. Partitioning of growth to feeder roots is treated using the principle of functional balance. The model uses the time resolution of one year and the time span of the life-time of the tree. Using the model, the consequences of the pipe model theory to the overall growth dynamics of trees are examined by studying the life-time growth dynamics of trees in different environments as functions of length growth patterns of the woody organs.

## 2. TREE MODEL WITH PARTITIONING OF GROWTH

### 2.1. Mass Balance Model of Growth

When regarded as assimilation of total growth resources and their distribution to different organs, plant growth can conveniently be analyzed with a mass balance model which incorporates the biomasses of the organs, $W_i$, the total growth rate, $G$, the turnover rates of the parts, $S_i$, and the *partitioning coefficients*, $\lambda_i$ ($i \varepsilon N$ = the set of indices of the parts). The latter are defined as the fraction of total growth allocated to part $i$,and they satisfy

$$\sum_{i \varepsilon N} \lambda_i(t) = 1, \tag{1}$$

for all times $t$. The growth rates of the biomass compartments are

$$\frac{dW_i}{dt} = \lambda_i G - S_i, \quad \text{for all } i \varepsilon N \tag{2}$$

i.e. net growth is the difference between gross growth and turnover.

Provided that the variables $\lambda_i$, $G$, and $S_i$ can be presented as functions of the state variables and identifiable parameters, Equations (2) constitute an operational dynamic model for tree growth. The following paragraphs are devoted to the derivation of the required relationships.

Following a customary approach, growth can be derived from the carbon metabolism of the tree. On an annual basis, it can be assumed that the carbon assimilated is totally consumed in growth and respiration. Denote annual photosynthesis ($kg\,\mathrm{C}\,a^{-1}$) by $P$, annual respiration ($kg\,\mathrm{C}\,a^{-1}$) by $R$, and the carbon content of dry matter by $f_C$. Annual growth $G$ ($kg$ dry weight $a^{-1}$) is therefore

$$G = f_C^{-1}(P-R). \tag{3}$$

Photosynthesis is assumed to be proportional to foliage biomass, $W_f$, and to the specific photosynthetic activity, $\sigma_C$ ($kg\,\mathrm{C}\,a^{-1}(kg$ dry weight$)^{-1}$), which depends upon environmental and internal factors:

$$P = \sigma_C W_f \tag{4}$$

Following McCree (1970), respiration is divided into growth respiration, $R_g$, and maintenance respiration, $R_m$:

$$R = R_m + R_g \tag{5}$$

Growth respiration $R_g$ is proportional to growth rate $G$

$$R_g = r_g G, \tag{6}$$

and maintenance respiration $R_m$ is proportional to the size of the maintained biomass compartment. Hence

$$R_m = \sum_{i \epsilon N} r_{mi} W_i \tag{7}$$

Above, $r_g$ and $r_{mi}$ are constant coefficients.

Turnover is customarily determined on the basis of specific turnover, $s_i$, which is the reciprocal of the average life-time of the organ:

$$S_i = s_i W_i \tag{8}$$

Equations (3)-(8) represent what can be called a standard procedure for determining total growth and senescence in growth models (Thornley, 1976; de Wit et al., 1978; Ågren and Axelsson, 1980). For the partitioning coefficients, such a standard does not exist. Section 2.2 treats the partitioning of growth in forest trees by using the pipe model theory and the principle of structural balance as premises.

## 2.2. Partitioning of Growth

### 2.2.1. Description of tree structure

Figure 1 depicts tree structure as a combination of five functionally different parts: foliage, feeder roots, stem, branches and transport roots. Foliage and feeder roots are considered simply as biomasses, $W_f$ and $W_r$, whereas the biomasses of the woody organs are derived from the geometric dimensions of the organs. Denote sapwood area at crown base by $A_s$, the total sapwood area of primary branches at foliage base by $A_b$ and the total sapwood area of transport roots at the stump by $A_t$. The length dimensions incorporated are tree height, $h_s$, crown radius, $h_b$, and transport root system radius, $h_t$. It is assumed that the *sapwood* biomasses of stem, $W_s$, branches, $W_b$, and transport roots, $W_t$, are obtainable from these variables through a simple algebraic operation. The assumption is then:

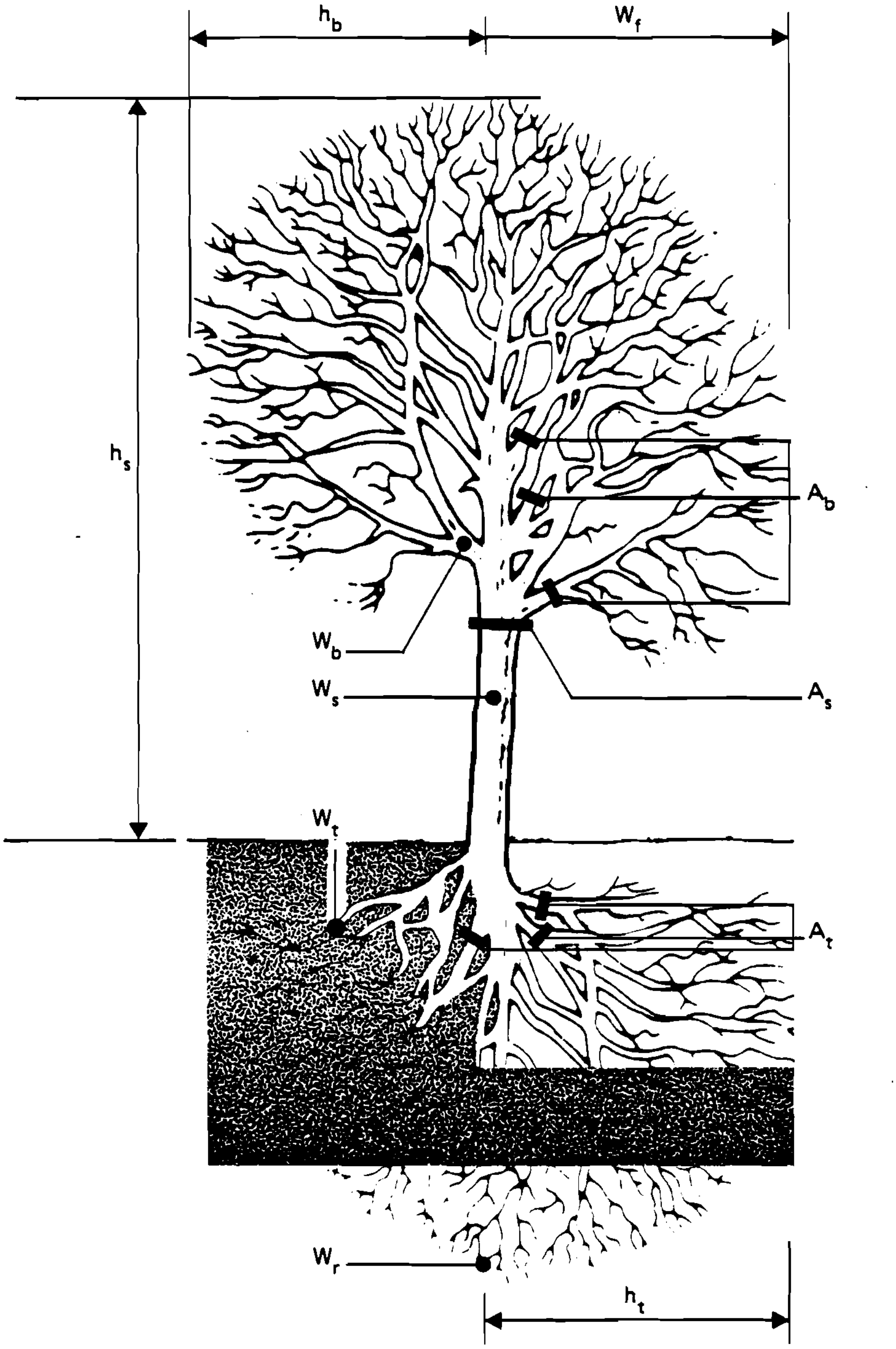

Figure 1. Variables describing tree geometry. For further explanation, see Table 1.

$$W_i = \varphi_i \rho_i h_i A_i , \quad i = s,b,t \tag{9}$$

where $\varphi_i$ is an empirical constant. This means that variation in the shape of the woody organs is allowed only as regards the ratio of sapwood area and the height/length of the organ. The variables are summarised in Table 1.

### 2.2.2. Foliage:wood ratio

The pipe model theory maintains that the sapwood area at height $x$ and the foliage biomass above $x$ are related through a constant ratio (Shinozaki et al., 1964a). According to Shinozaki et al (1964a), this applies to both stem and branches. More recent empirical results indicate, that (1) the ratio may be different for stem and branches, and (2) the transport roots obey a similar relationship (Kaipiainen et al., 1985). With these supplementary notions, the basic observation can be elaborated to yield the following three relationships.

(1) Stem sapwood area at crown base, $A_s$, is proportional to total foliage biomass $W_f$

$$\eta_s A_s = W_f \tag{10}$$

(2) The total sapwood area of primary branches (at foliage base), $A_b$, is proportional to total foliage biomass

$$\eta_b A_b = W_f \tag{11}$$

(3) The total sapwood area of transport roots at the stump, $A_t$, is proportional to total foliage biomass

$$\eta_t A_t = W_f \tag{12}$$

Table 1: Model variables

| Name | Meaning | Units |
|---|---|---|
| f | foliage | |
| r | feeder roots | |
| s | stem | |
| b | branches | |
| t | conducting roots | |
| Variables describing the state of the tree | | |
| $W_i$ | biomass (in case of wood:sapwood BM)<br>$i = f, r, s, b, t$ | (kg DW) |
| $A_i$ | sapwood area<br>$i = s, b, t$ | ($m^2$) |
| $h_i$ | height/length<br>$i = s, b, t$ | (m) |
| Other variables | | |
| $\lambda_i$ | partitioning coefficient<br>$i = f, r, s, b, t$ | |
| $G$ | total growth | (kg/a) |
| $P$ | photosynthesis | (kg C/a) |
| $R$ | respiration | (kg C/a) |
| $R_m$ | maintenance respiration | (kg C/a) |
| $R_g$ | growth respiration | (kg C/a) |
| $S_i$ | senescence of biomass<br>$i = f, r$ | (DW/a) |
| $D_i$ | senescence of sapwood<br>$i = s, b, t$ | ($m^2$/a) |
| $u_i$ | height growth rate<br>$i = s, b, t$ | (m/a) |

The constants $\eta_i$ are species specific parameters.

### 2.2.3. Foliage: feeder root ratio

According to an empirical relationship first established by White (1935), and further developed mathematically by Brouwer (1964) and Davidson (1969), the metabolic activities of the roots and the photosynthetic organs are in balance. Denote the specific photosynthetic activity by $\sigma_C$ ($kg\ C\ a^{-1}$ ($kg$ dry weight)$^{-1}$) and the specific root activity (of nitrogen uptake) by $\sigma_N$ ($kg\ N\ a^{-1}$ ($kg$ dry weight)$^{-1}$). The relationship can be expressed in the form

$$\pi_N \sigma_C W_f = \sigma_N W_r \tag{13}$$

where $\pi_N$ is an empirical parameter.

This requirement can be understood in terms of a balanced carbon and nitrogen ratio in the plant (Reynolds and Thornley, 1982). If the specific activities vary, like between growing sites, the relationship produces different foliage:feeder root ratios, thus explaining the variation in this ratio between growing sites.

### 2.2.4. Partitioning coefficients

Partitioning of growth between foliage, roots and wood follows from the requirement that the structural balances presented in Section 2.2 are satisfied. First, let us consider the foliage:root ratio constrained by Equation (13). Assuming that the balance holds initially, it can be maintained if and only if

$$\pi_N \sigma_C \frac{dW_f}{dt} = \sigma_N \frac{dW_r}{dt} \tag{14}$$

This equation relates the balance requirement with the partitioning coefficients which enter the equation through the time derivatives of $W_f$ and $W_r$. If these are substituted from Equation (2), the following relationship between $\lambda_f$ and $\lambda_r$ is obtained:

$$\lambda_r = \alpha_r \lambda_f + \beta_r \tag{15}$$

where

$$\alpha_r = \pi_N \frac{\sigma_C}{\sigma_N} \tag{16}$$

$$\beta_r = \frac{S_r - \alpha_r S_f}{G} \tag{17}$$

Similarly to Equation (14), the requirements of the pipe model theory can be maintained if and only if

$$\eta_i \frac{dA_i}{dt} = \frac{dW_f}{dt}, \quad i = s, b, t \tag{18}$$

In order to utilise this equation for the derivation of the partitioning coefficients of the woody organs, $\lambda_i$ ($i = s, b. t$), let us first relate the time derivative of $A_i$ to that of $W_i$. By Equation (9),

$$\frac{dW_i}{dt} = \rho_i \varphi_i \left(\frac{dA_i}{dt} h_i + \frac{dh_i}{dt} A_i\right), \quad i = s, b, t \tag{19}$$

On the other hand, $dW_i/dt$ is defined in terms of $\lambda_i$ by Equation (2). Combining (2) and (19) allows us to solve for the time derivatives of the sapwood areas, $dA_i/dt$, which thus become functions of the partitioning coefficients:

$$\frac{dA_i}{dt} = \frac{\lambda_i}{\varphi_i \rho_i h_i} G - D_i - \frac{u_i}{h_i} A_i \tag{20}$$

Above, we have denoted:

$$\frac{dh_i}{dt} = u_i, \quad i = s, b, t. \tag{21}$$

and

$$D_i = d_i A_i = \frac{1}{\varphi_i \rho_i h_i} S_i \tag{22}$$

Equation (2), with $i = f$, together with Equation (20) can now be substituted into Equation (18). This gives rise to the following partitioning coefficients $\lambda_i$:

$$\lambda_i = (\alpha_i \lambda_f + \beta_i) h_i , \quad i = s,b,t \tag{23}$$

where

$$\alpha_i = \rho_i \varphi_i \eta_i^{-1} \tag{24}$$

$$\beta_i = \alpha_i \frac{\eta_i D_i + \eta_i \frac{u_i}{h_i} A_i - S_f}{G} \tag{25}$$

where $i = s,b,t$.

This gives a general growth partitioning pattern between foliage and wood as a function of the lengths of the woody organs.

## 2.3. Summary of the Model

It follows from the above derivation that tree growth can be described in terms of length growth and one of the dependent variables $W_f$, $W_r$, $A_s$, $A_b$ and $A_t$ only. If foliage biomass is selected as a reference, the model reads as follows:

$$\frac{dW_f}{dt} = \lambda_f G - s_f W_f \tag{26a}$$

$$\frac{dh_i}{dt} = u_i, \quad i = s,b,t \tag{26b}$$

where

$$\lambda_f = \frac{1 - \beta_r - \sum_i \beta_i h_i}{1 + \alpha_r + \sum_i \alpha_i h_i} \tag{27}$$

$$G = Y^{-1}(\sigma_C W_f - \sum_{i=f,r} r_{mi} W_i - \sum_{i=s,b,t} r_{mi}\,\varphi_i\,\rho_i\,h_i\,A_i) \qquad (28)$$

$$Y = f_C + r_g \qquad (29)$$

and $\alpha_i$ and $\beta_i$ are defined as in Equations (15), (17), (24) and (25) for $i = r,s,b,t$. Additionally,

$$W_r = \alpha_r W_f, \qquad A_i = \frac{1}{\eta_i} W_f, \qquad i = s,b,t. \qquad (30)$$

The variables of the model are listed in Table 1, and Table 2 gives a summary of its parameters.

In order to fully understand the partitioning of dry matter in trees, the determination of the length growth pattern should be understood. Since, for the reasons pointed out in Section 1, it is difficult to relate length growth to biomass growth directly, we shall consider the growth rates of the length variables as unknown "strategies" that can vary. Below, the behaviour of the model is analyzed as a function of these strategies.

### 2.4. Extension of the Model to Changing Environment

So far it has been assumed that the structural ratios between the state variables, Equations (10)-(13), are constant over time. Actually, the metabolic activities $\sigma_C$, $\sigma_N$, and - as will be discussed later - also the parameters $\eta_i$, may respond to environmental changes such as shading and fertilization during the life-time of the tree. If the change is faster than the response time of the tree, it is impossible even approximately to maintain the balance. However, the tree may be able to change the partitioning coefficients so as to eventually reach a new balance in the new situation. The present model manifests this behaviour if we reduce the assumption that the balance equations (10)-(13) hold at every moment of time, but maintain the

Table 2. Parameters

| Names | Meaning | Unit |
|---|---|---|
| $\sigma_C$ | foliage specific activity | kg[C]/kg[DW]a |
| $\sigma_N$ | root specific activity | kg[N]/kg[DW]a |
| $f_C$ | carbon content of dry weight | kg[C]/kg[DW] |
| $\pi_N$ | N:C ratio of dry weight | kg[N]/kg[C] |
| $\eta_s$ | foliage DW:stem sapwood ratio | kg[DW]/m$^2$[SW] |
| $\eta_b$ | foliage DW:branch sapwood ratio | kg[DW]/m$^2$[SW] |
| $\eta_t$ | foliage DW:transport root sapwood ratio | kg[DW]/m$^2$[SW] |
| $\rho_s$ | stemwood density | kg/m$^3$ |
| $\rho_b$ | branchwood density | kg/m$^3$ |
| $\rho_t$ | rootwood density | kg/m$^3$ |
| $\varphi_s$ | form factor of stem | unitless |
| $\varphi_b$ | form factor of branch system | unitless |
| $\varphi_t$ | form factor of root system | unitless |
| $s_f$ | foliage specific turnover rate | 1/a |
| $s_r$ | feeder root specific turnover rate | 1/a |
| $d_s$ | stem sapwood specific turnover rate | 1/a |
| $d_b$ | branch sapwood specific turnover rate | 1/a |
| $d_t$ | root sapwood specific turnover rate | 1/a |
| $r_m$ | specific maintenance respiration | kg[C]/kg[DW]a |
| $r_g$ | specific growth respiration | kg[C]/kg[DW] |

partitioning coefficients derived from those equations. The dynamics of all the state variables are included using the original differential equations, Equation (2). A partitioning model with similar adaptive behaviour has already been presented by Reynolds and Thornley (1982) for the shoot-root ratios in grass.

The analysis of the model in Section 3 is carried out using the time invariant form, but some of the considerations in Section 4 make use of the possibility that the parameters vary in time.

## 3. PROPERTIES OF THE MODEL

### 3.1. Root-Foliage Relationships

Let us define the ***productive biomass***, $W_P$, as follows:

$$W_P = W_f + W_r \tag{31}$$

The partitioning coefficient of the productive part is

$$\lambda_P = \lambda_f + \lambda_r \tag{32}$$

Let us define the specific growth rate, $\bar{g}$, as the growth rate per productive biomass, and denote the specific turnover rate of productive biomass by $s_P$. The net growth rate of $W_P$ is then

$$\frac{dW_P}{dt} = \lambda_P \bar{g} W_P - s_P W_P \tag{33}$$

The quantities $\bar{g}$ and $s_P$ can be reduced to the original parameters through the differential equations of $W_f$ and $W_r$. This yields

$$s_P = (1 + \alpha_r)^{-1} (s_f + \alpha_r s_r) \tag{34}$$

$$\bar{g} = [\sigma - r_{mP} - \sum_i r_{mi}\, \bar{\alpha}_i\, h_i\,]\, Y^{-1} \tag{35}$$

where the parameters $\sigma$, $r_{mP}$ and $\bar{\alpha}_i$ correspond to $\sigma_C$, $r_{mr}$ and $r_{mf}$ and $\alpha_i$, respectively, with the difference that they are defined as activities per unit productive biomass instead of unit foliage or root. The relationships are

$$r_{mP} = (1+\alpha_r)^{-1}(r_{mf} + \alpha_r\, r_{mr}) \tag{36}$$

$$\bar{\alpha}_i = (1+\alpha_r)^{-1}\alpha_i\,, \quad i = s, b, t \tag{37}$$

$$\sigma = (1+\alpha_r)^{-1}\sigma_C \tag{38}$$

The specific activity of the productive part becomes, when the original parameters are substituted for $\alpha_r$:

$$\sigma = \frac{\sigma_C\, \sigma_N}{\sigma_N + \pi_N\, \sigma_C} \tag{39}$$

which is a Michaelis-Menten type function in both $\sigma_C$ and $\sigma_N$. The dependence is such that if $\pi_N\, \sigma_C \gg \sigma_N$, then root activity is restricting growth and small changes in $\sigma_C$ have little impact on the total productivity. If $\pi_N \sigma_C \ll \sigma_N$, then $\sigma_C$ is limiting. If both terms are of the same order of magnitude then respective changes in either one have equal effects. Environmental variation affecting root and foliage activity can be brought into the model through this relationship.

### 3.2. Length Variables and Growth

The relative growth rate of the productive part, $R_P$, is defined as follows

$$R_P = \frac{1}{W_P}\frac{dW_P}{dt} \tag{40}$$

This is readily obtainable from Equation (33):

$$R_P = \lambda_P\, \bar{g} - s_P\,, \tag{41}$$

Let us define $h$ and $u$ as

$$h = \frac{\sum_i \bar{\alpha}_i h_i}{\sum \bar{\alpha}_i}, \quad u = \frac{\sum_i \bar{\alpha}_i u_i}{\sum \bar{\alpha}_i} \tag{42}$$

and let

$$\bar{\alpha} = \sum_i \bar{\alpha}_i \tag{43}$$

Assume that length growths are small in comparison with the lengths themselves, such that

$$\frac{u_i}{h_i} \ll d_i \tag{44}$$

This means that the term $u_i / h_i$ is negligible in the parameter $\beta_i$, Equation (25). This assumption is reasonable especially in the late stage of growth. Assume, further, that $d_i$ and $r_{mi}$ are independent of $i$, and drop the subscripts. Denote

$$\Phi = (\sigma - r_{mP})Y^{-1} - s_P \tag{45}$$

$$\bar{\beta} = (d + r_m Y^{-1})\bar{\alpha} \tag{46}$$

$R_P$ can then be written as a function of $h$ as follows:

$$R_P = \frac{\Phi - \bar{\beta} h}{1 + \bar{\alpha} h} \tag{47}$$

The relative growth rate is thus a function of the metabolic and structural parameters and the generalized length $h$. The results can be summarized as *Lemma* 1 below.

Lemma1.

1. If $h < \frac{\Phi}{\bar{\beta}}$, then $R_P > 0$.

2. If $h = \frac{\Phi}{\beta}$, then $R_P = 0$.

3. If $h > \frac{\Phi}{\beta}$, then $R_P < 0$.

This means that if the lengths of the woody organs continue to grow after Equation (46) has been fulfilled, the relative growth rate of foliage and roots goes negative and the tree starts to die off. However, if length growth ceases before the state $R_P < 0$ has been reached, growth will continue exponentially at the rate $R_P$ which thus remains constant.

The time development of the productive biomass depends exponentially on the relative growth rate:

$$W_P(t) = W_P(0) \exp \{ \int_0^t R_P(t) dt \} \tag{48}$$

With an exchange of variables, the integral can be expressed in terms of $h$:

$$W_P(t) = W_P(0) \exp \{ \int_0^{h(t)} R_P(h) \frac{1}{u} dh \} \tag{49}$$

This expression contains information on the relationship between the growth rates of the biomass and length variables. This can be summarized as the following *Lemma*:

Lemma2.

Given a fixed set of parameter values, the size of the productive part at any length $h$ is a function of the rate at which that length has been achieved: the faster the preceding growth rate $u$, the smaller the size at the length $h$.

The result can also be interpreted *vice versa*. If the height and length growth rates are fixed, then variation in the parameter values causes differences in the size of foliage and roots.

## 4. SOME IMPLICATIONS OF THE MODEL

### 4.1. Deceleration of growth

When young, trees grow exponentially in all dimensions, then gradually slow down to reach a constant growth rate, and the growth finally ceases slowly. Although all parts of the tree seem to follow the same basic pattern, their relative time scales vary. Dominant trees can maintain considerable basal area growth long after the slowdown of height growth (*cf.* Koivisto, 1959).

It is widely accepted that the decline in growth in old trees is a whole-plant phenomenon rather than a consequence of the aging of individual tissues (Noodén, 1980), but the mechanisms of decline are not fully understood. It has been pointed out that the proportion of stem to crown gradually increases with age and size and, consequently, the ratio of carbohydrates produced to that consumed in respiration decreases (Jacobs, 1955). There is also evidence of increasing difficulty of material translocation between the roots and the crown (Kramer and Kozlowski, 1979; p. 611). Particularly, difficulties in water relations have been argued to cause severe water deficits and death of leaves and branches (Went, 1942).

The result of Lemma 1 provides some further insight into this behaviour. Since net growth of roots and foliage cannot be maintained if the woody parts exceed a critical size, survival requires that the length growth rates are decelerated. If this action is postponed until very close to the critical limit - which would be expected because rapid dimensional growth is an advantage in competition for light and nutrients - only a small growth potential will remain. Nevertheless, a fraction corresponding to the turnover of sapwood must continuously be allocated to the growth of the woody organs.

The model thus explains the deceleration of growth as a consequence of the fact that maintenance and growth requirements of the woody parts increase faster than the productive potential. This is ultimately due to the assumption that sapwood and foliage grow in constant proportions, which makes the fraction of wood in total tree biomass increase whenever there is length growth. In the absence of length growth, all the organs would continue to grow in constant proportions.

A numerical example is worked out below so as to study to what extent the processes described by the present model can be responsible for the slowdown of growth in trees. Let us consider a Scots pine tree (*Pinus sylvestris*) under boreal conditions. Table 3 summarizes the necessary parameter values for such a tree. The source of the value is indicated in the table. Maximum sustainable tree heights have been calculated for a range of nutrient uptake rates, corresponding to different growing sites, and for a range of different trunk-branch-root configurations. The results are summarized in Figures 2 and 3. This shows tree heights of the correct order of magnitude. However, the parameter values are rough estimates only, and result is sensitive especially to the maintenance requirement of living woody tissue.

Table 3. Parameter value

| Name | Value | Source |
|---|---|---|
| $\sigma_C$ | 2 | Agren and Axelsson 1980 |
| $\sigma_N$ | 0.04 | guess |
| $\pi_N$ | 0.01 | estimates based on elemental contents according to various sources |
| $f_C$ | 0.5 | |
| $r_g$ | 0.25 | Agren and Axelsson 1980 |
| $\eta_s$ | 600. | Kaipiainen *et al.* 1985 |
| $\eta_b$ | 450. | Kaipiainen *et al.* 1985 |
| $\eta_t$ | 2400. | Kaipiainen *et al.* 1985 |
| $\rho$ | 400 | Kärkkäinen 1977 |
| $\varphi_s$ | 0.75 | estimates based on tree from measurements according to various sources |
| $\varphi_b$ | 0.70 | |
| $\varphi_t$ | 1.00 | |
| $s_f$ | 0.25 | corresponds to average life time of 4 years |
| $s_r$ | 0.8 | Persson 1980 |
| d | 0.01 | guess |
| $r_m$ | 0.05 | Agren and Axelsson 1980 |
| $r_{mp}$ | 0.10 | Agren and Axelsson 1980 |

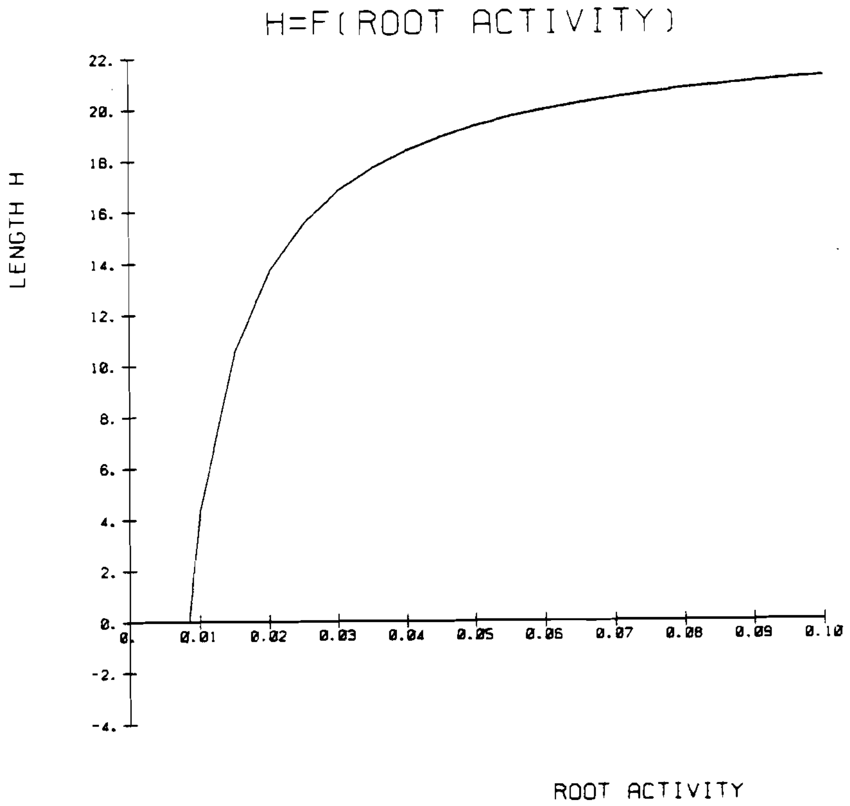

Figure 2. Maximum sustainable average length of woody organs *h* (Equation 42) as a function of root activity $\sigma_N$.

## 4.2. Response to Environmental Stress

Many environmental stress factors cause a slowdown of metabolic activities and/or accelerate the turnover of plant tissue. Drought, for example, first decreases photosynthesis through stomatal closure, and if prolonged, may lead to shedding of leaves so as to decrease the transpiring surface. The same is true of the increasing anthropogenic stress load. Atmospheric air pollution has been reported to decrease specific photosynthesis and accelerate foliage aging, and soil acidification increases fine root mortality and decreases specific nutrient uptake rate by leaching nutrients.

Such stress factors can be incorporated in the dynamic extension of present model (Section 2.4) as changes in the corresponding parameter

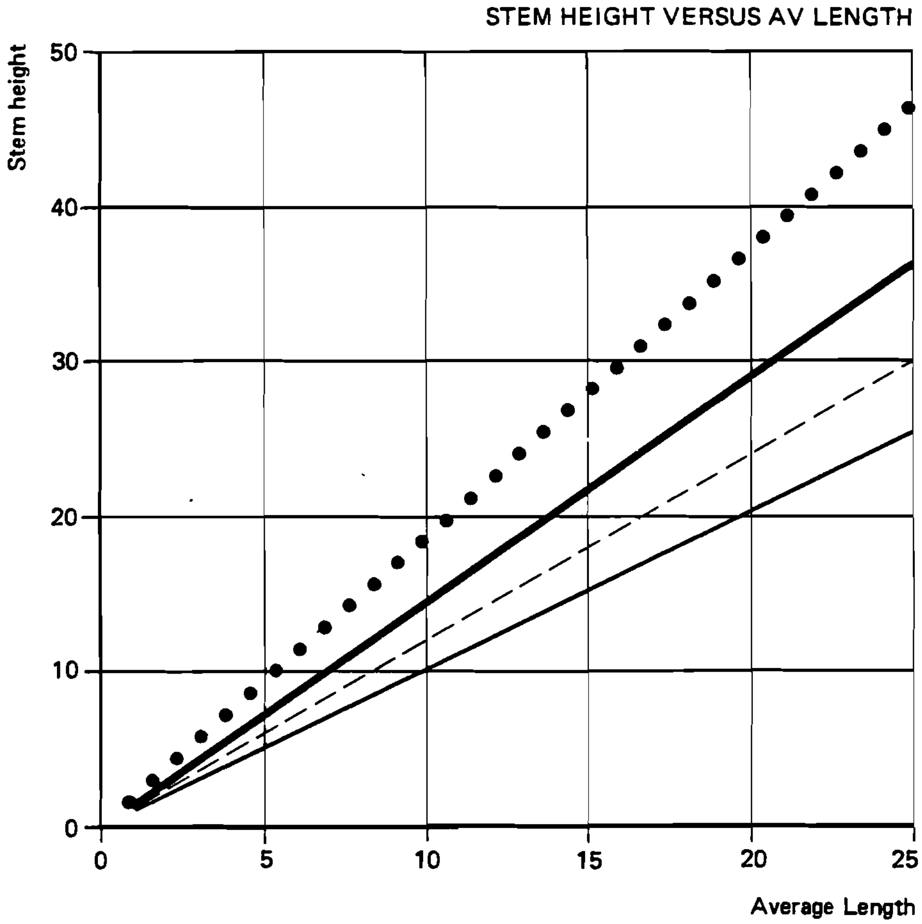

Figure 3. Stem height as a function of average length using different stem: branch: root length ratios. All curves have $h_b = \alpha h_s$, $h_t = 2\alpha h_s$, and $\alpha$ varies as follows:

●●● $\alpha = 0.2$,
▬ $\alpha = 0.4$,
---- $\alpha = 0.6$,
— $\alpha = 0.8$.

values. Hence, a decrease in the specific activities $\sigma_C$ and $\sigma_N$, or an increase in the specific turnover rates of foliage and roots, $s_f$ and $s_r$, may be involved. All these changes have a similar impact on the relative growth rate of the productive part: $R_P$ decreases. We shall study in more detail the conditions under which the tree will not survive the stress.

In terms of the model, the tree survives as long as it maintains a positive level of productive biomass. This condition will be violated if the long-term average of the relative growth rate is negative. By Equation (46), relative growth rate is positive only if

$$\Phi > \bar{\beta} h_0 \tag{50}$$

If the opposite occurs frequently the tree will die because of a decline in root and foliage biomass.

Equation (50) states that the immediate reaction of a tree to a decrease in growth potential depends on the size $h$ of its woody organs. Again, the result can be attributed to the fact that in the model, maintenance and growth of woody parts increase faster than growth potential. Since $h$ does not, normally, decrease in time, the model implies that age increases the susceptibility of trees to stress factors that suppress productivity.

The model implies that the long-term response of a young tree initially satisfying condition (49) largely depends on its ability to adapt its height and length growth to the new situation. If adaptation occurs, the environmental change solely means a smooth decrease in growth rates and maximum sizes of the affected trees. Catastrophic behaviour will enter, however, if the tree insists in following its normal growth patterns. This would suggest that species with different capacities of environmental flexibility of height growth could manifest different reactions to long-lasting environmental stresses.

### 4.3. Height Growth

Tree height, relative to its neighbours, is an important indicator of foliage productivity because it affects the amount of shade cast on the tree by the rest of the canopy. The specific photosynthesis of the shorter trees will be reduced, and they will probably also have a higher turnover rate of foliage, both factors decreasing their productivity relative to the well-to-do neighbours. It therefore appears that the only means of survival in a stand is to keep up with the height growth of the rest of the canopy. Indeed, Logan (1965,1966a,1966b) has shown by experiments that the height growth rates of seedlings shaded to different extents vary considerably less than the corresponding foliage growth rates (Logan, 1965,1966a,1966b).

The suppressed trees have nevertheless a lower productive potential than the dominant ones. According to the result of Lemma 2, this means that they are allocating a considerably larger fraction of their growth resources to the trunk than the other trees. The fact that suppressed trees are smaller as regards crown, roots and basal area can thus be readily interpreted in terms of the present model.

According to Lemma 1, the suppressed trees with lower potential productivity reach the point where they can no longer grow taller, much earlier than their dominant neighbours. But slowing down height growth in a suppressed situation means more shade and less photosynthetic production, and therefore the relative growth rate is bound to turn negative no matter which height growth pattern they have in the end. The model hence explains the mortality of suppressed trees as a consequence of not being able to avoid one of the two processes reducing growth potential, i.e. shading and relative increase of wood in tree biomass.

Lemma 2 also applies to an opposite situation where there is no light competition at all, i.e. a tree growing in the open. If it maintains the same height and length growth patterns as the densely growing trees it will have a larger share of growth to be allocated to foliage and roots and more massive individuals will result. This is consistent with the observation that open-grown trees maintain large crowns although they do not grow considerably higher than within-stand trees.

## 5. DISCUSSION

The present results can be summarized as follows. Provided that (1) the pipe-model theory is adequate, and that (2) sapwood compensation is required due to turnover, the growth and maintenance requirements of the woody parts increase faster than the photosynthetic potential and therefore sooner or later start to limit growth. Under disturbances in productivity, these requirements may even make the system unstable, an important result with respect to the consequences of possible environmental change. The implications of the model on the height growth patterns of trees give some further insight into the competitive processes in a tree stand.

It is interesting that the summarizing form of the model, Section 2.3, essentially reduces the dynamics of tree growth to that of diameter and height, the standard variables used for the description of individual tree growth in a variety of empirical-statistical stand growth models (cf. Botkin et al., 1972; Shugart, 1984). The structural constraints thus provide a way of connecting the mass balance approach (Equation (2)) with the more conventional tree growth models. Moreover, if development of biomass can be derived from that of geometric dimensions, large data sources become available for the verification of models. That helps to solve one of the major problems of the mass balance approach (cf. Mäkelä and Hari, 1985).

The tree model used in the so-called gap models of forest stands (cf. Shugart, 1984) very much resembles the present one, with the properties that (1) leaf area is proportional to basal area, and (2) increasing height provides a limitation to growth. An important difference is, however, that in the gap models maximum height is a species-specific constant rather than a variable depending on site conditions. When applied to environmental change the gap models do not, therefore, show the unstable behaviour described in Section 4.2. Instead, they account for the increased mortality under environmental stress with the aid of a stochastic dependence of mortality on growth rate (West et al., 1980).

So as to assess the applicability of the results, let us review the premises of the derivation. The key assumption is that sapwood area and foliage biomass occur in constant ratios. Although many empirical studies seem to confirm this (see Section 1), more detailed consideration may yield contradicting observations. Following the argument that sapwood serves as a water conducting medium, it is expected that variation of those environmental factors that affect the availability, conductance and transpiration of water will also cause variation in the parameters $\eta_i$. In order to incorporate this in the model, we could attempt to define $\eta_i$ in terms of the environmental variables. Let us denote the water conductivity of sapwood by $\sigma_W$ (kg water/year/m$^2$ sapwood), and the efficiency of water use by $\pi_W$ (kg water transpired/kg C assimilated). A balance requirement analogous to the one applied to the foliage-root ratio (Equation (13)) would then become

$$\sigma_W A = \pi_W \sigma_C W_f \tag{51}$$

implying that

$$\eta = \frac{\sigma_W}{\pi_W \sigma_C}. \tag{52}$$

So far our empirical data do not allow, however, a proper test of this relationship.

As pointed out in Section 4, the turnover rates of the different organs play an important role in the resulting tree dynamics. Especially if height and foliage growth is slow, it is the turnover rate of sapwood that essentially determines the growth requirements of the woody organs. It seems plausible that sapwood turnover is related to the pruning of branches, which slows down in the later stage of canopy development. According to the model results, this would increase net productivity and thus postpone the attainment of equilibrium. A better understanding of the turnover processes of sapwood therefore seems crucial for the further development of the model.

As was pointed out earlier, many recent observations support the ideas of the pipe model theory at least roughly, suggesting that an accurate correspondence with measurements can be obtained merely with minor improvements, such as the time dependence of certain parameters, and perhaps the incorporation of the relationship in Equation (52). However, since the applicability of the model totally depends upon the adequacy of the pipe model structure, let us critically review the underlying hypotheses and compare them with a tentative alternative.

The pipe model theory is consistent with the idea that it is the conductivity of the pipeline that restricts the availability of water to the foliage (Shinozaki et al., 1964a). One could also assume that storage capacity is a critical parameter. Since storage capacity is proportional to volume, sapwood volume instead of area then becomes the critical parameter to match with the size of the foliage. This implies that tree height no longer supplies an entirely negative feedback to growth, but a steady height growth can be maintained.

The requirement that conductivity rather than storage capacity is restricting presumes that the trees either (1) cannot store water or recharge the sapwood after exhaustion, or (2) do not occur in environments where long dry and moist periods alternate, making storage capacity profitable. Condition (1) seems to be approximately true of many hardwood species with a ring porous conducting structure, whereas the coniferous conducting structure would be more appropriate for the development of storage (Waring and Franklin, 1979). However, in the dominant region of conifers, the boreal and oroboreal zones, the main growth limiting factor is temperature instead of water (e.g. Kauppi and Posch, 1985), which means that condition (2) is fulfilled.

As an interesting exception to this pattern, Waring and Franklin (1979) have discussed the evergreen coniferous forests of the north-western coast of the American continent. They draw attention to both the climate with wet winters and dry summers, and the recharge ability of the conifers' sapwood. They argue that these two factors, together with longevity and sustained height growth, contribute to the long-lasting high productivity of these forests. The present analysis goes even further by suggesting that also the longevity and the ability of sustaining height growth can be consequences of the unusual water economy. If this is the case, the giant trees should not have a constant foliage:sapwood ratio. For the time being, we may only speculate: Perhaps it was the capability of overcoming the restrictions of the pipe-model structure that enabled the coniferous forests of the Pacific Northwest to become one of the world's greatest accumulators of biomass.

This study has given some insight into the role of length growth patterns in the dynamics of tree growth. The length growth pattern itself was not defined, however. This approach was chosen because length growth, although fairly well understood in general terms, is still missing a dynamic connection to the environment and total growth. Lemmas 1 and 2 show that under the assumptions of the pipe model theory, the growth of a tree is very sensitive to its length growth pattern. In the highlight of the fairly stable and regular growth patterns that occur in reality, this result indicates that we are missing an additional balancing mechanism between length and diameter - or biomass - growth. As indicated in Section 1, such a balancing mechanism seems likely to involve interactions between trees. If this is true, an analysis of the whole stand is required in order to understand the length growth of individual trees. In this respect, some new insight has been gained by looking at height growth patterns as evolutionary consequences of intra-specific competition, with the aid of game theory (Mäkelä, 1985). The present study further emphasizes the need for such integrated analyses as means of increasing our understanding of the factors that regulate the development of tree geometry.

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