

# A Functional Model of Tree Growth and Tree Architecture

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A new approach for modelling plant growth using the software AMAPpara is presented. This software takes into consideration knowledge about plant architecture which has been accumulated at the Plant Modelling Unit of CIRAD for several years, and introduces physiological concepts in order to simulate the dynamic functioning of trees. The plant is considered as a serial connection of vegetative organs which conduct water from the roots to the leaves. Another simple description of the plant as a network of parallel pipes is also presented which allows an analytical formulation of growth to be written. This recurring formula is used for very simple architectures and is useful to understand the role of each organ in water transport and assimilate production. Growth simulations are presented which show the influence of modifications in architecture on plant development.

**Keywords** ecophysiology, plant architecture, water transport, assimilate production, growth, mathematical models, computer simulations

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## 1 Introduction

Interest in modelling and simulation of plant growth has been increasing for many years. Morphological models using computing concepts (L-systems) have been developed in order to describe vegetative structures in three dimensions (Prusinkiewicz and Hanan 1989, Kurth 1994). Other models, based on the architectural description of plants (Hallé and Oldemann 1970, Edelin 1987), depend on stochastic rules to describe bud activity (Jaeger and Reffye 1992). Some simulation programs also take into account interactions between the plant and its environment during growth (Blaise 1991, Mech and Prusinkiewicz 1996). On the other hand, several studies have approached the modelling of growth through the carbon allocation process in different parts of the plant (see Cannell and Dewar 1994). In these simulation approaches, the functional relationship between tree growth and assimilate production are taken into particular consideration. Most of the methods are based on the Shinozaki "pipe model theory" (Shinozaki et al. 1964), e.g. the carbon-balance model of Valentine (1985) or that of Mäkelä (1986). More recently, the software LIGNUM proposed a finer description of the vegetative units' assembly for simple architectural models (Perttunen et al. 1996). Some interesting new formalisms for modelling the interactions between plant architecture, competition and carbon allocation have been implemented in the software GROGRA (Kurth 1996). However, these approaches do not include the calculation of the water flow circulating from the roots to the leaves in the hydraulic architecture, and usually neglect the description of the root system. To better blend the morphological and allocational approaches to modelling tree growth and form, we have developed the software AMAPpara (Reffye et al. 1996). The AMAPpara model aims to link the knowledge of tree architecture (Hallé et al. 1978) used at the Plant Modelling Unit of CIRAD with the physiological processes of water transport and carbon allocation in the whole plant.

The purpose of this paper is to present the capacities of the model in order to simulate the implication of hydraulic architecture on resource allocation and consequent plant development. The new concepts of tree growth modelling used

in AMAPpara (Fourcaud et al. 1997) will be presented. The influence of each organ (leaves, growth units, etc.) on the water transport and the assimilate production is taken into consideration. Furthermore, some analytical relationships, based on a pipe model description, will be given in order to interpret the behaviour of the model. The response of the simulated plants to hydraulic (sapwood resistivities) and external (pruning) parameters will be shown for well known tree architectural models.

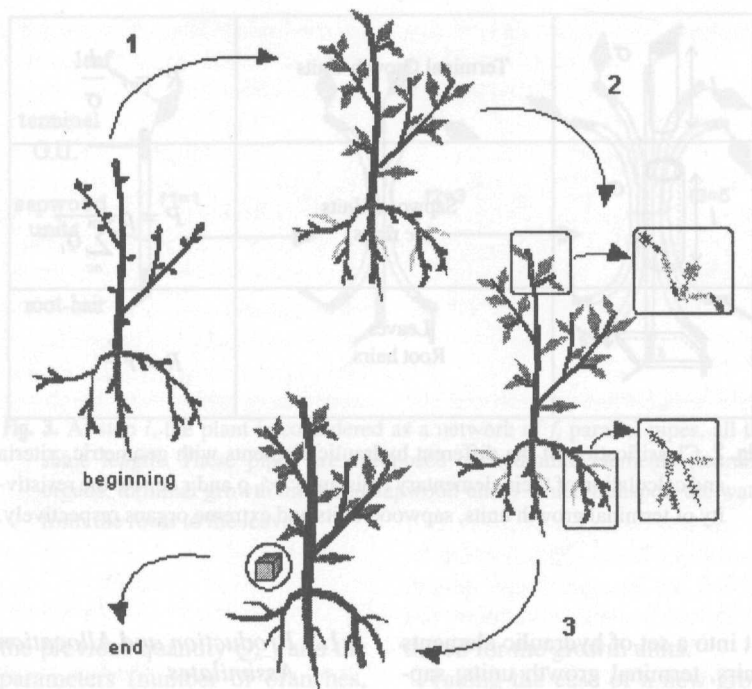
## 2 New Concepts for Plant Growth Modelling in AMAPpara

A new approach has been developed to simulate plant growth with the software AMAPpara (Fourcaud et al. 1997). The underlying model incorporates a physiological principle and allows dynamic growth to be simulated. Indeed, the plant is considered as a hydraulic structure, transporting water from the roots to the leaves, and producing assimilates via photosynthesis. These assimilates are used by the buds and the cambium to build the vegetative material (primary and secondary growth). It is assumed that there is a proportional relationship between accumulated assimilate production and transpiration during a cycle of growth. This hypothesis appears to correspond to agronomic observations during a cycle of growth. An analytical formulation of growth has also been derived. One of the main objects of these theoretical formulae is to better understand the behaviour of the plant and the role of the functional parameters during growth.

The model is actually run in a stepwise fashion, each calculation corresponding to a cycle of growth i.e. to the period which is necessary to fabricate a growth unit (G.U.) (1 year for a tree).

### 2.1 Description of a Cycle of Growth in AMAPpara

For each cycle of growth, three main stages are distinguished (Fig. 1):



**Fig. 1.** A cycle of growth is composed of three stages which describe the elementary functioning of the plant: 1) production of new growth units by the buds, 2) transport of water into the hydraulic structure, 3) production and allocation of assimilates within the plant.

- first, new growth units are built by the primary growth organs of the aerial and below-ground parts of the plant;
- secondly, the plant transports water from the roots to the leaves via the active rings of the sapwood;
- thirdly, assimilates are made by the leaves during photosynthesis, and carbon is allocated to different organs of the plant.

## 2.2.1 Allometric Relations

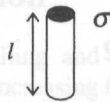
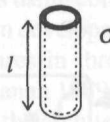
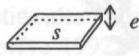
### 2.2.1.1 Production of New Growth Units

At the beginning of the current step, the plant disposes of global reserves of assimilate which have been accumulated in the previous step. These assimilates are redistributed to each primary growth organ which uses them to fabricate the inter-nodes and leaves constituting the growth units of the cycle. The volume and the shape (see section 2.2.1) of these new vegetative elements

are functions of the quantity of dry matter which has been used to build them. These characteristic parameters are obtained by measurements according to the protocol used in the previous versions of the software AMAP (Jaeger and Reffye 1992). In the same way, the newly obtained topology depends on the architectural model (Halle et al. 1978) of the simulated plant.

### 2.2.1.2 Transport of Water into the Plant

The plant draws up soil water from its roots and transports it via the conductive sapwood rings up to the leaves. For each step of the calculation (one cycle of growth), it is assumed that a stable laminary water flow in the plant can represent its functioning for this period. Hydraulic equilibrium of the plant is computed using an assembly method (Fourcaud et al. 1997). The

	<p>Terminal Growth Units</p>	$R' = r' \frac{l}{\sigma}$
	<p>Sapwood Units (<i>nc</i> rings)</p>	$P = \rho \sum_{nc} \frac{l}{\sigma_i}$
	<p>Leaves Root hairs</p>	$R = r \frac{e}{s}$

**Fig. 2.** Classification of the different hydraulic elements with geometric criteria and calculation of their elementary resistance:  $r'$ ,  $\rho$  and  $r$  denote the resistivity of terminal growth units, sapwood units and extreme organs respectively.

structure is split into a set of hydraulic elements (leaves, root hairs, terminal growth units, sapwood) that are classified according to geometric characteristics and that each possess their own resistance (Fig. 2). The connection table of the elementary units of which the plant is composed allows the hydraulic equilibrium to be written as a linear system:

$$[C]\{P\} = \{E\} \tag{1}$$

where

$[C]$  is the conductance matrix of the whole structure, which is built by assembling the elementary conductances  $C_{ij} = 1/R_{ij}$

$\{E\}$  is the water potential vector of the extreme organs (leaves and root hairs)

$\{P\}$  is the unknown vector of water pressure at the discretisation nodes (connection point between two vegetative elements)

For each node  $i$ , the pressure  $P_i$  is set by resolving the linear system (1). Darcy's rules (2) then allow the water flow  $\Psi_{ij}$  in each hydraulic element  $ij$  to be computed.

$$\Psi_{ij} = C_{ij}(P_j - P_i) \tag{2}$$

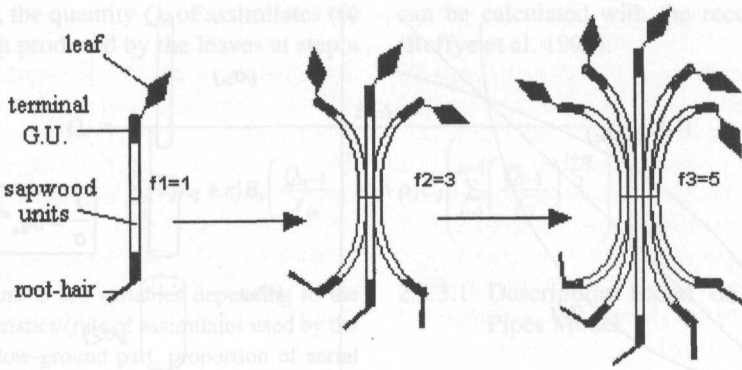
### 2.1.3 Production and Allocation of Assimilates

An empirical linear relationship between the quantity of water evaporated by the leaves  $\Psi_{ij}^{leaf}$  and the quantity of assimilates  $q_{ij}^{leaf}$  produced locally is used to take into consideration the photosynthate accumulated during the cycle. These photosynthates migrate and are laid down all along the tree using a uniform allocation rule (Reffye et al. 1993). Then, each quantity of assimilates  $q_{ij}^{leaf}$  which circulates along a pathway, length  $L$ , gives an amount  $q_{ij}^{leaf}/L$  locally. One part is used by the cambium for cell division (secondary growth) and the other part is kept to maintain respiration and to constitute the reserves for primary growth at the beginning of the next step.

### 2.2 An Analytical Formulation Based on a Pipe Description

In order to write an analytical formulation of growth, the plant can be seen as a network of parallel pipes (Shinozaki 1964) in which water is transported from the roots to the leaves. The aim of this theoretical model is to write a recursive formula in order to calculate the global quantity of assimilates  $Q_n$  produced by the plant at step  $n$ , as





**Fig. 3.** At step  $i$ , the plant is considered as a network of  $f_i$  parallel pipes, all the same length. These pipes are composed of hydraulic elements (extreme organs, terminal growth units and sapwood units) which transport the water from the roots to the leaves.

a function of the previous quantity  $Q_{n-1}$  and the architectural parameters (number of branches, length, etc.).

Consider a very elementary plant that can be described as such a network of pipes. Each pipe has the same length and it is composed of three kinds of hydraulic elements: extreme organs (one leaf at the top and one root hair at the bottom), terminal growth units (one T.G.U. at each extremity) and active sapwood units (Fig. 3).

These hydraulic units are classified with the geometrical criteria used in the AMAPpara simulation model presented follow (Fig. 2). In order to simplify the equations, the number  $nc$  of conducting sapwood rings is reduced to  $nc = 1$  in this theoretical pipe description (external ring).

### 2.2.1 Allometric Relations

The evolution of the shape of the terminal growth unit is one of the most important factor for the functional model presented here. Indeed, a bud disposing of a given local quantity of assimilates (i.e. a given G.U. volume) can build a long and thin cylindrical growth unit or a short and large one. This phenomenon is well known in forestry sciences, in particular in the case of space competition (Valinger 1993, Hara et al. 1991). This is the reason why a shape relation has been intro-

duced for the growth units.

Taking the case of a new growth unit which expands at step  $n$  with a local quantity  $q_n$  of assimilates. Let

- $h$  be the length of the G.U.
- $\sigma$  be the cross section area of the G.U.
- $v = h\sigma$  be the volume of the G.U.

Allometric relations between the length  $h$  and the section of this growth unit are given as a function of the quantity  $q_n$  by the following equations:

$$v = aq_n \quad (3)$$

$$\frac{h}{\sigma} = bq_n^\alpha \quad (4)$$

where

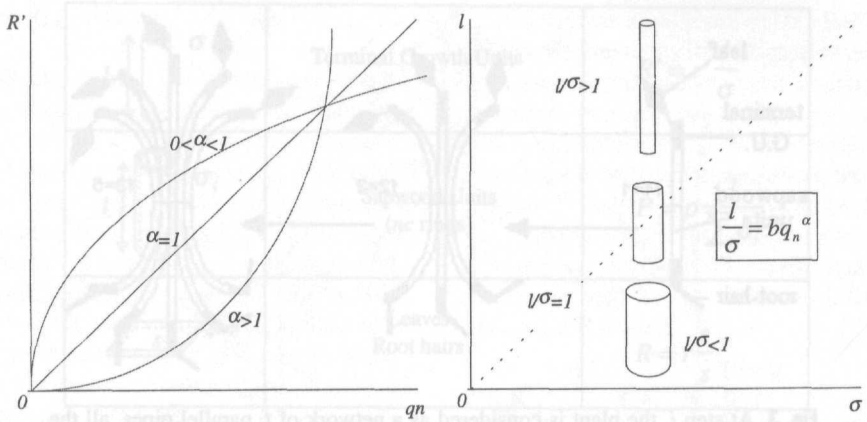
$a$  is the proportion of assimilates allocated to the axis of the growth unit

$b$  and  $\alpha$  are two shape coefficients

The size of extreme organs (leaves and root hairs) is also proportional to the local quantity  $q_n$  and considered to have a constant thickness  $e$ .

The surface  $s_n$  of leaves or root hairs can be written as

$$s_n = (1-a) \frac{q_n}{e} \quad (5)$$



**Fig. 4.** Growth unit resistance  $R'$  versus local quantity of assimilates  $q_n$  for different shape coefficients  $\alpha$ . This resistance depends on the shape ratio  $f_j$  linked to  $q_n$  and  $\alpha$  by relation (4).

**2.2.2 Quantity of Assimilates Produced during a Step of Growth**

At step  $n$ , the global quantity of assimilates  $Q_n$  which is available for the plant growth is considered to be proportional to the water flow calculated at the leaves surface, i.e. linked to the parameters of the hydraulic architecture. Considering the resistance of each parallel pipe, this quantity  $Q_n$  can be written as (Reffye et al. 1996):

$$Q_n = \frac{E_n \Delta t}{\sum_{j=1}^2 \frac{1}{f_{jn}} \left[ \frac{r_j}{s_{jn}} + r'_j \frac{h_{jn}}{\sigma_{jn}} + \rho_j \sum_{i=1}^{n-1} \frac{h_{ji}}{\sigma_{jn-1}} \right]} \quad (6)$$

- where
- $x_{ji}$  indicates that the variable  $x$  is related to the aerial part ( $j = 1$ ) or below-ground part ( $j = 2$ ) and concerns an element which has been appeared at step  $i$
- $E_n \Delta t$  is the water use efficiency during the period  $\Delta t$  and represents the environmental conditions of growth
- $f_n$  indicates the number of pipes constituting the hydraulic structure at step  $n$
- $r, r'$  and  $\rho$  are the hydraulic resistivities of extreme organs, terminal growth units and sapwood units respectively

Three main terms appear at the denominator of the formula (6):

$$R = \sum_{j=1}^2 \frac{r_j}{s_{jn}} \quad (7)$$

$$R' = \sum_{j=1}^2 r'_j \frac{h_{jn}}{\sigma_{jn}} \quad (8)$$

$$P = \sum_{j=1}^2 \rho_j \sum_{i=1}^{n-1} \frac{h_{ji}}{\sigma_{jn-1}} \quad (9)$$

For each pipe, these terms represent the hydraulic resistances of the extreme organs, the terminal growth units and the set of sapwood units respectively. The global hydraulic resistance of the network is determined by multiplying the resistance of a pipe by the factor  $(1/f_{jn})$ .  $R, R'$  and  $P$  play a very important role in the behaviour of plant growth (linear growth, inhibition of growth, etc.) as it will be shown in the following parts of this paper.

Relation (8) shows the privileged role played by the shape factor  $h/\sigma$  (cf. relation (4)) on the hydraulic model, and more particularly the sensitivity of the resistance of the terminal growth units to the shape coefficient  $\alpha$  (Fig. 4).

According to the allometric relations (3) & (4) and to the increase in the number  $f_n$  of pipes

during growth, the quantity  $Q_n$  of assimilates (6) which has been produced by the leaves at step  $n$  can be calculated with the recurrence formula (Reffye et al. 1996):

$$Q_n = \frac{E_n \Delta t}{\left[ \sum_{j=1}^2 r_j A_j + r'_j B_j \left( \frac{Q_{n-1}}{f_{jn}} \right)^{1+\alpha} + \rho_j C_j \left( \sum_{i=1}^{n-1} \left( \frac{Q_{i-1}}{f_{ji}} \right)^{\frac{1+\alpha}{2}} \right)^2 \right]} \cdot Q_{n-1} \quad (10)$$

where  $A$ ,  $B$  and  $C$  are variables depending to the plant characteristics (rate of assimilates used by the aerial and below-ground part, proportion of aerial assimilates used to build the leaves, growth units shape, etc.)

The three denominator factors (7), (8) and (9) can be written again:

$$R = \sum_{j=1}^2 r_j A_j, \\ R' = \sum_{j=1}^2 r'_j B_j \left( \frac{Q_{n-1}}{f_{jn}} \right)^{1+\alpha}, \text{ and} \quad (11) \\ P = \sum_{j=1}^2 \rho_j C_j \left( \sum_{i=1}^{n-1} \left( \frac{Q_{i-1}}{f_{ji}} \right)^{\frac{1+\alpha}{2}} \right)^2$$

### 2.2.3 Description of the Hydraulic Structure with Pipes

The previous study has shown that it is useful to describe hydraulic structures as an equivalent network of parallel pipes in order to write an analytical formulation of growth applicable to most tree architectures. It is assumed that the environmental conditions (aerial potential, below-ground potential) are homogeneous and that an uniform allocation of assimilates is used. For some cases, the transformation requires approximations due to the necessity to ensure the compatibility of the section area along the pipes when they branch, but it has been shown that the results obtained with the analytical relations are very close to the AMAPpara simulations (Fourcaud et al. 1996). Some decomposition samples are given below, corresponding to different hypotheses for the architecture description.

#### 2.2.3.1 Description Based on the Separated Pipes Model

An elementary splitting of separated pipes is established for trees with symmetrical aerial and below-ground parts. Assuming that the terminal leaf (root-hair) has only one functional cycle (one functional leaf (root-hair) at the extremity of the axis), this decomposition allows the hydraulic equilibrium of the tree to be written as the previous recurrence formula (10).

In some cases (Leeuwenberg), this decomposition is trivial (Fig. 5a) and the theoretical formulation (10) gives accurate results.

However, in other cases (Rauh, Massart) the structure cannot be strictly split into parallel pipes starting from each leaf and having the same cross-sectional area. Local errors are induced by this kind of decomposition, due to the incompatibilities of the cross-sectional areas at some terminal axis level (Fig. 5b). Therefore, the analytical formulation (10) generates an inaccurate model for the tree growth calculation. Nevertheless, it has been shown that the induced errors are not significant (Fourcaud et al. 1997) and that this model is very acceptable.

#### 2.2.3.2 Generalisation of the Separated Pipes Model

It is useful to generalise the previous formulae to a symmetrical plant with several functional cycles (several functional leaves (root-hairs) per annual growth unit). The generalised model assumes that all the leaves (root-hairs) are fixed at the extremity of the terminal growth units. Then, the recurrence formula (10) becomes:

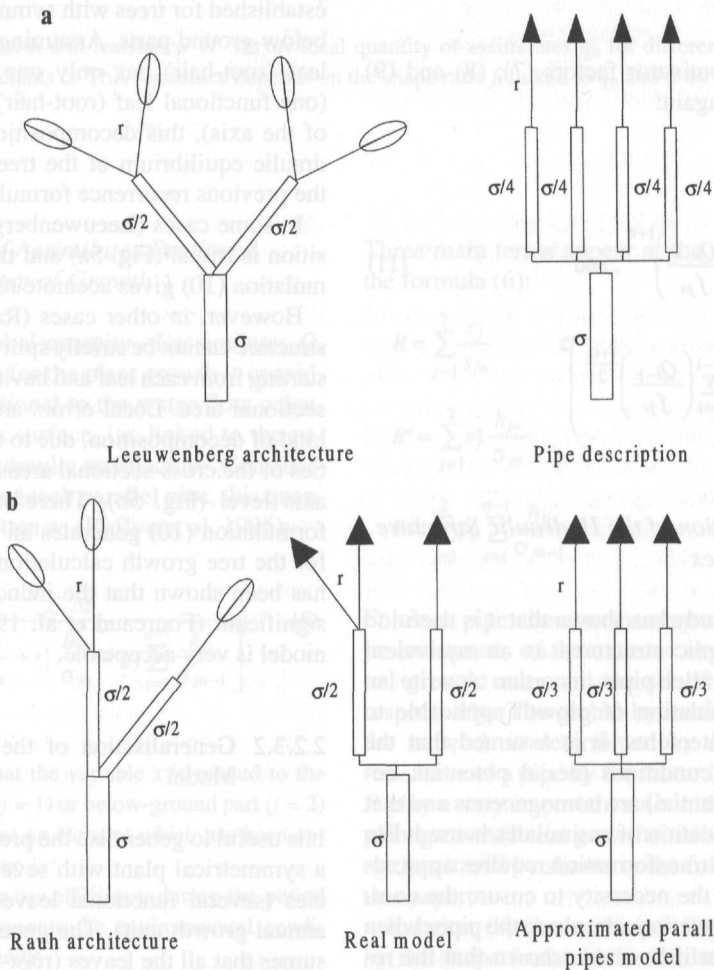
$$Q_n \approx \frac{E_n \Delta t}{\sum_{j=1}^2 \left[ \frac{f_{jn}}{F_{jn}} \left( r_j A_j + r'_j B_j \left( \frac{Q_{n-1}}{f_{jn}} \right)^{1+\alpha} \right) + \rho_j C_j \left( \sum_{i=1}^{n-1} \left( \frac{Q_{i-1}}{f_{ji}} \right)^{\frac{1+\alpha}{2}} \right)^2 \right]} \cdot Q_{n-1} \quad (12)$$

where  $F_{1n}$  and  $F_{2n}$  are the total number of leaves and root-hairs respectively

it gives the influence of the number of functional organs on the growth.

This formulation is of course an approximate relation for all the considered architectures, but

According to relations (10) and (12), it appears that the ratio  $Q_{n-1}/f_{jn}$  is one of the most important quantities to explain plant growth be-



**Fig. 5.** a) Splitting of the aerial part of a Leeuwenberg hydraulic architecture into a network of parallel pipes. The compatibility of section areas is assured for all the axes of the plant, b) Splitting of the aerial part of a Rauh (or Massart) hydraulic architecture into a network of parallel pipes. The cross-sectional area compatibility is not assured for the terminal axis due to the asymmetrical distribution of terminal growth units.



behaviour (height and volume increasing) in connection with plant architecture. This ratio expresses the relationship between the photosynthetic production of the plant at time  $n-1$  and the number of new organs elaborated at time  $n$  with  $Q_{n-1}$ : it thus describes the link between the physiological activity and the architectural development. Many examples can be found in Reffye et al. (1996) showing the effects of this factor on simulated plant growth behaviour. The influence of branch number variation on plant functioning is explained below.

### 3 Results of Simulations

The consequences of the hypothesis of proportionality between photosynthesis and transpiration on vegetative architecture will be presented using several examples.

The behaviour of simulated plant growth is very sensitive to physiological and environmental parameters, in particular to sapwood resistivity and the pruning of branches. The following samples show these influences in terms of height, assimilate production and tree shape for several plant architectural models.

In all these examples, we assume that the environment is homogeneous. The plants have been simulated by the new version of the software AMAPpara and validated with the analytical formulae (10) or (12), in the simplest cases of architecture.

#### 3.1 Free Growth

The behaviour of a plant with free growth, i.e. growth without external constraint, is shown for two types of hydraulic structures. First, no sapwood resistance to water transport is considered. Second, plant growth is simulated using hydraulic resistance in the sapwood rings.

##### 3.1.1 No Water Resistance in the Sapwood

###### 3.1.1.1 The Corner Model

The growth of Corner architectural models have

been simulated during 20 cycles. Five functional cycles have been considered for the metameres. The growth units shape parameters (relationship between volume and local quantity of available assimilates and the ratio between cross-sectional area and length) (cf. relations (3) and (4)) have been changed for each. The results (Fig. 6) generalise those already published in a previous article (Reffye et al. 1996). The beginning of growth is characterised by an exponential increase of the assimilate production. After five cycles, this production slows down and the terminal growth unit volume is stabilised. The dilation of the terminal growth unit according to the quantity of available assimilates, allows growth to be modulated. It appears that the linear relationship hypothesis between photosynthesis and transpiration could induce cyclical or chaotic phenomena. These phenomena can be observed by looking at the production curves presented for each plant.

Transpiration and size variation of growth units could explain the appearance of meristem axial production rhythms.

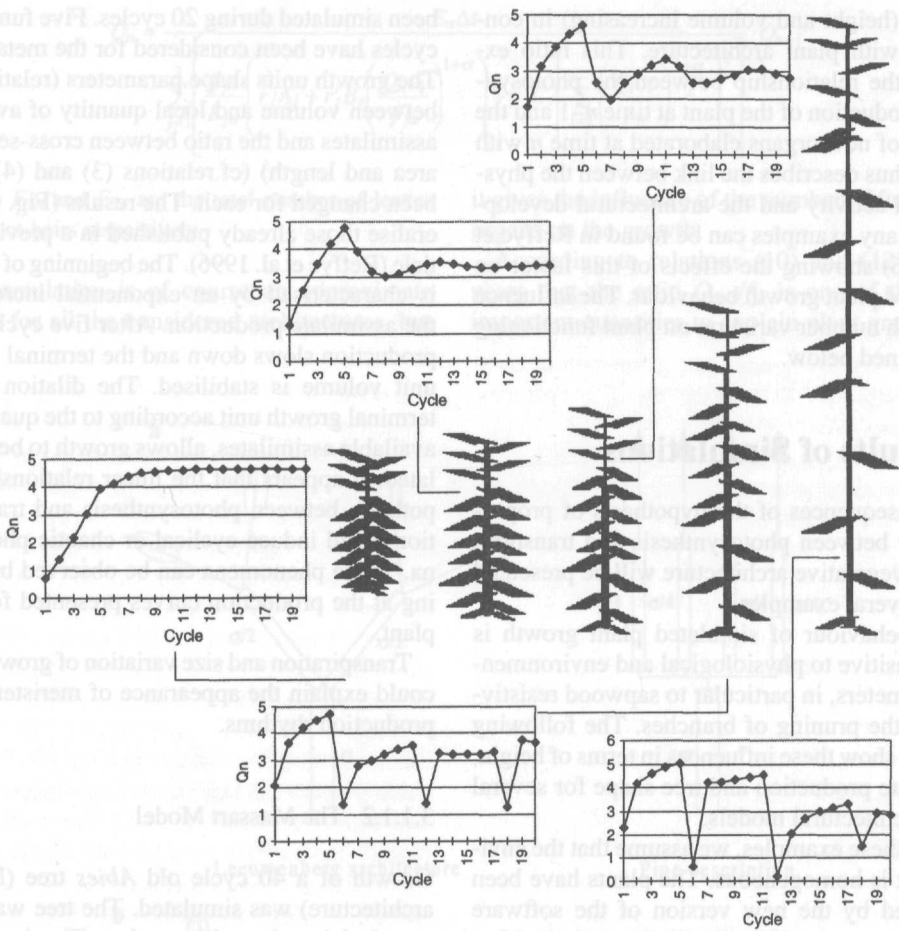
###### 3.1.1.2 The Massart Model

Growth of a 40 cycle old *Abies* tree (Massart architecture) was simulated. The tree was composed of three branching orders. The duration of life (self-pruning) of order 2 branches was limited to 15 cycles. The tree then formed a crown where a constant volume could be observed during growth (Fig. 7).

This linear growth can be demonstrated using the formula (12) with sapwood resistivity equal to zero. Indeed, the assimilate production reaches a limit value  $Q_l$  which can be written as

$$Q_l = \left( \frac{E_n \Delta t - r_1 A_1 \frac{f_{1n}}{F_{1n}} - r_2 A_2 \frac{f_{2n}}{F_{2n}}}{\frac{1}{F_{1n}} \frac{r_1 B_1}{f_{1n}^\alpha} + \frac{1}{F_{2n}} \frac{r_2 B_2}{f_{2n}^\alpha}} \right)^{\frac{1}{1+\alpha}} \quad (13)$$

using the same notations as in the first part of the paper.



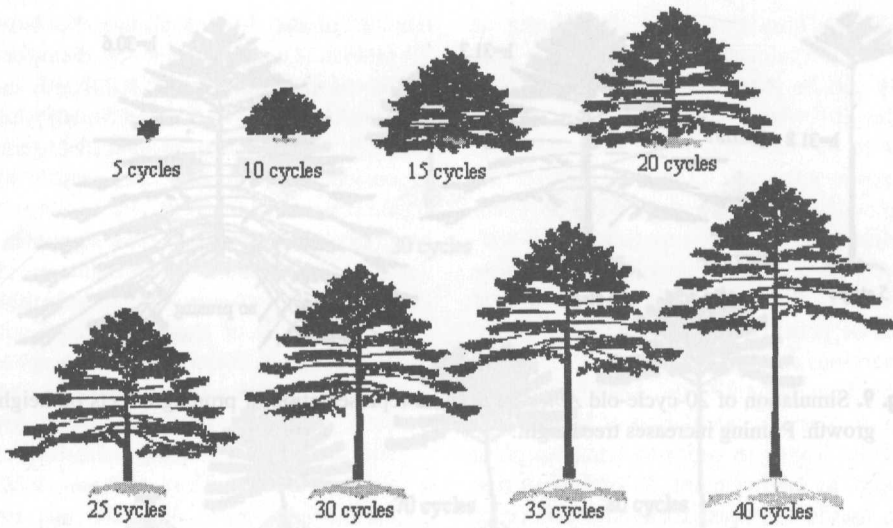
**Fig. 6.** Simulation of a 20-cycle-old Corner architecture for five different shape coefficients of the growth units. From left to right  $\alpha = 0$ ,  $\alpha = 1$ ,  $\alpha = 2$ ,  $\alpha = 3$  and  $\alpha = 4$ . Only the erect leaves are active (5 functional cycles).

### 3.1.2 Water Resistance in the Sapwood

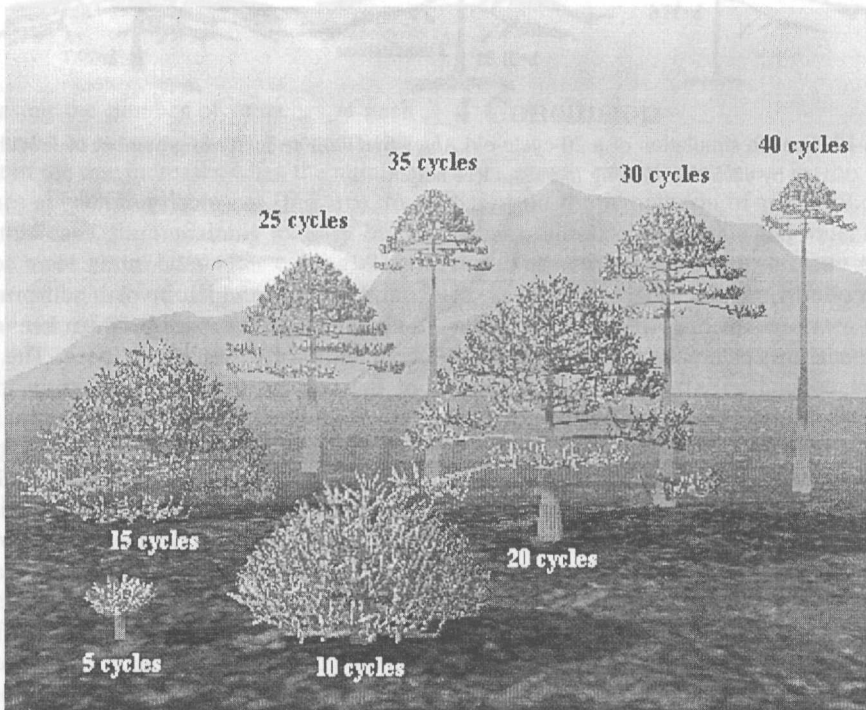
The hydraulic resistance in the conductive rings of the sapwood plays an important role in significantly moderating or decreasing the growth during simulation. Water is drawn up inside a longer and longer network of sapwood pipes. In the following samples, the influence of a relatively low sapwood resistivity on plant growth behaviour will be shown.

#### 3.1.2.1 The Rauh Model

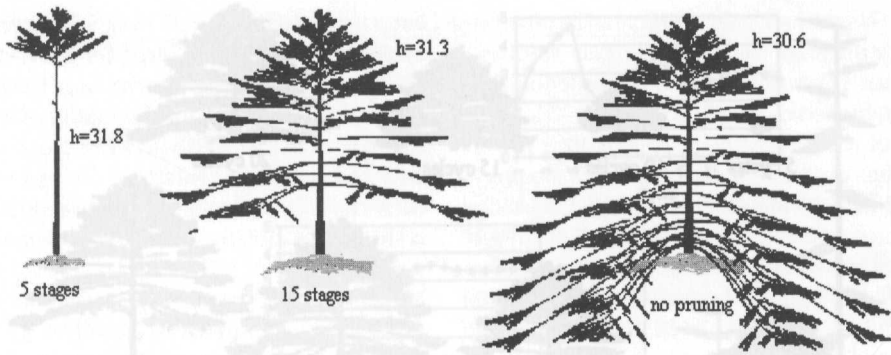
Growth of a 40 cycles old *Pinus* tree (Massart architecture) was simulated. The number of branching orders was 4, and the duration of the life of second order axis was limited to 12 cycles. Unlike the previous samples, it was considered that the sapwood presents a resistance to water circulation. Nevertheless, the sapwood resistivity parameter used was 4000 times smaller than that of the leaf. A significant decrease of the crown volume could then be observed (Fig. 8).



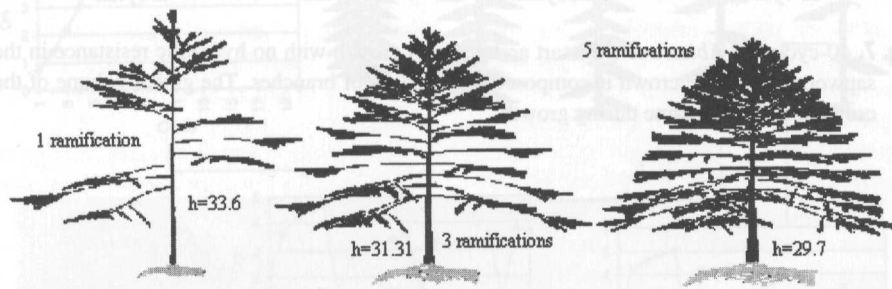
**Fig. 7.** 40-cycle-old *Abies* tree (Massart architecture) growth with no hydraulic resistance in the sapwood rings. The crown is composed of 15 stages of branches. The global volume of the crown remains the same during growth.



**Fig. 8.** 40-cycle-old *Pinus* tree (Rauh architecture) growth with hydraulic resistance in the sapwood rings. The crown was composed of 12 stages of branches. Its global volume decreased during growth.



**Fig. 9.** Simulation of 20-cycle-old *Abies* trees and a representation of pruning effects on height growth. Pruning increases tree height.



**Fig. 10.** Growth simulation of a 20-cycle-old *Abies* tree with an increasing number of branches carried by each tier. Cutting increases tree height.

### 3.2 Controlled Growth

The software allows external interventions (pruning, cutting, coppicing) to be performed on trees. The reserves of assimilates are uniformly distributed in the peripheral rings. These reserves can be allocated to the latent buds which will expand after cutting.

This simulation will be illustrated with three samples corresponding to different interventions.

#### 3.2.1 Pruning of a Massart Model

The growth of the previous *Abies* tree was calculated with three different durations of life for second order branches (Fig. 9). These simulations could correspond to the effect of different

stand densities which involve self-pruning due to competition for space between trees or to root competition for water and space. The decrease of the number of branch stages in the crown induced an increase of the tree height, i.e. pruning favours height. This phenomenon has already been shown by the software GROGRA (Kurth 1996). Data from pruning experiments on walnut and wild cherry trees, not yet published, have been carried out at CIRAD and appear to validate this result.

#### 3.2.2 Cutting of a Massart Model

The growth of 20 cycle old *Abies* trees was re-used. The life duration of second order axes was 15 cycles. Three simulations have been carried

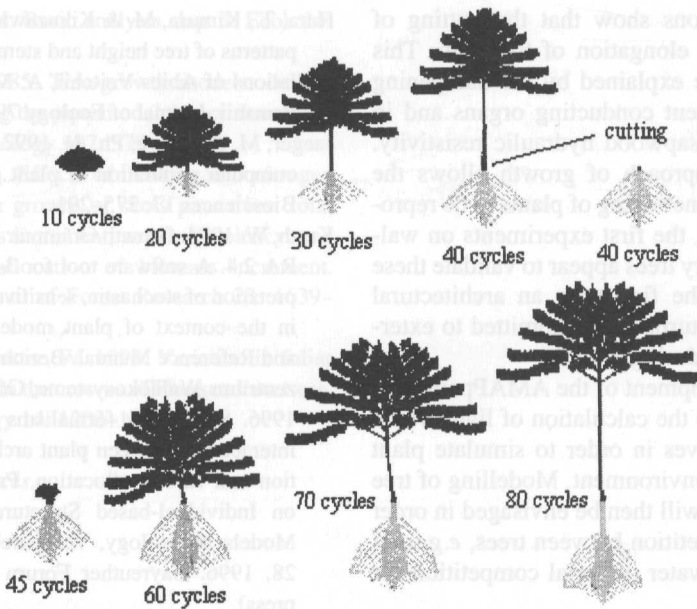


Fig. 11. Copping simulation of a coffee tree. The trunk has been cut at cycle 40, and the growth of the aerial part has become more vigorous.

out increasing the number of branches at each tier (1, 3 and 5 axes at each tier). It appears that the height of the tree increases when the number of branches at each tier decreases (Fig. 10). Indeed, in this case, the remaining axillary buds dispose of more assimilates after cutting. This behaviour can be theoretically explained by the dampening role of the parameters  $Q_{jn}/f_{jn}$  in relation (12).

### 3.2.3 Copping of a Roux Model

The growth of a coffee tree was simulated during 80 cycles. At cycle 40, the plant was cut at the base of the aerial part. A more vigorous growth resumption could be observed after the cutting of the plant (Fig. 11). This phenomenon is characterised by bigger crowns, e.g. the upper part of the 60 cycle old tree is the same age as the 20 cycle old tree, but its volume is larger.

This vigour comes from a better developed root system which is more efficient for the drawing up of water.

## 4 Conclusion

The growth model presented in this paper is based on the hypothesis of proportionality between assimilate production and water transpiration. The new version of the software AMAPpara uses the knowledge of plant architecture accumulated at CIRAD and incorporates hydraulic calculation of water transport into the tree.

Analytical formulae allow the computer simulations to be validated and the behaviour of plant growth to be understood according to the environmental parameters. The model is able to reproduce correctly the sigmoidal form of the vegetative morphogenesis. Even a low sapwood resistivity involves a slowing down of growth after a certain period of time. This hypothesis has already been formulated by Waring (1994).

The presented simulations identify precisely the relationships existing between the global hydraulic conductivity of the tree and growth behaviour in terms of assimilate production and structure height. The behaviour of the model is very sensitive to cutting processes (pruning, cop-



ping). Simulations show that the cutting of branches favours elongation of the stem. This sensitivity can be explained by the dampening role of the different conducting organs and in particular to the sapwood hydraulic resistivity. This dynamic approach of growth allows the morphogenetic functioning of plants to be reproduced. Moreover, the first experiments on walnut and wild cherry trees appear to validate these results. This is the first time an architectural model can be perturbed and submitted to external interventions during growth.

The next development of the AMAPpara software will involve the calculation of light which arrives at the leaves in order to simulate plant adaptation to its environment. Modelling of tree growth in stands will then be envisaged in order to simulate competition between trees, e.g. root competition for water or aerial competition for light and space.

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Le Dizès, S., Cruziat, P., Lecoq, A., Sinoquet, N., Le Roux, X., Bolandier, P. & Jacquet, P. 1997. A model for simulating structure-function relationships in walnut tree growth processes. *Silva Pennica* 31(3): 313–328.

An ecophysiological growth-process model, called INCA, for simulating the growth and development of a young walnut tree (*Juglans regia* L.) during three or four years, is presented. This tool, currently under development, aims at integrating architectural and physiological knowledge of the processes involved, in order to give a more rational understanding of the pruning operation. The model describes a simple three-dimensional representation of tree crown, solar radiation interception, photosynthesis, respiration, growth and partitioning of assimilates to leaves, stems, branches and roots. It supports the hypothesis that the tree grows as a collection of semi-autonomous, interacting organs that compete for resources, based on daily sink strengths and proximity to sources. The actual growth rate of organs is not predetermined by empirical data, but reflects the pattern of available resources. The major driving variables are solar radiation, temperature, topological, geometrical and physiological factors. Outputs are hourly and daily photosynthate production and respiration, daily dimensional growth, starch storage, biomass production and total number of different types of organ. The user can interact or override any or all of the input variables to examine the effects of such changes on photosynthate production and growth. Within INCA, the tree entities and the surrounding environment are structured in a frame-based representation whereas the processes are coded in a rule-based language. The simulation mechanism is primarily based on the rule chaining capabilities of an inference engine.

**Keywords** structure-function relationships; carbon; growth; frame-based representation; rule-based representation; simulation; pruning; walnut tree.

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