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## **TreeRing 3: A Simulation Model of Conifer Ring Growth and Cell Structure**

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### **Abstract**

TreeRing, version 3, is a process model of daily cambial activity simulating the ring width, cell number, cell size, wall thickness and ring-width index of growth variations in conifer tree rings. Input data are daily precipitation and temperature, actual cell measurements for trees growing in the simulated area and the annual ring-width index. Input parameters define mathematical constants and initial data for the equations describing the processes governing daily changes in the tree water balance, photosynthesis, carbon allocation, crown growth and cambial activity. Outputs from the whole-tree processes along with limiting environmental conditions of temperature, water stress, and available sucrose (carbon) govern the initiation of cambial activity, rates of cell division, cell enlargement, wall thickening and growth cessation. Derivatives of crown growth represent net growth regulator flux. The growth rate, cell size, wall thickness and state (dividing, enlarging, maturing, or dead) of each tracheid is calculated for each day of the year. Data are stored in tabular form and selected information is plotted on the screen as the simulation progresses through time. Actual measurements from a tree in the simulated forest are compared to the simulated annual ring widths, cell numbers, cell sizes, wall thicknesses and ring-width indices (a replicated time series portraying the relative ring-width response of many trees in the forest); and the statistics of comparison are calculated at the end of each simulation run. A variety of initial conditions and input measurements including altitude, tree height, sapwood and heartwood, root depth and spread, soil characteristics, stored sucrose, and needle retention are used to estimate crown surface, proportion of leaves, stems, and roots, living and growing masses, carbon allocation and water balance. An iteration subroutine can be used to cycle through simulations while varying one parameter at a time and minimizing the residual variance to allow fine tuning of the model. Simulations account for 50 percent or more of the variance in actual cellular and ring measurements from a single tree. This percentage is near the upper

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limit calculated from dendrochronological evidence. Limitations and some applications of the current model are described.

### Introduction

Dendrochronological research throughout the last two decades has made many significant advances in statistical tools and models applied to analyzing the characteristics in tree rings and their relationships to climate (Fritts 1976, Cook and Kairiukstis 1990). These approaches make assumptions which may or may not fit the systems to which they apply. Perceptive scientists can question whether these models provide the most accurate descriptions of tree growth behavior over time and space. Long-term planners require assurance that the statistical estimates will be applicable to future conditions that may lie outside the range of past conditions on which model calibrations are based. As a result, there is growing interest in the questions of “Exactly how do trees record environmental information in the structure of their growth rings in both temperate and tropical environments?” and “Will these relationships be altered by the anticipated global changes?”

Industrial research on wood quality has focused primarily on measures of stem volume and form as indirect measures of wood quality, because until recently direct measurements of wood properties have not been cost effective (Downes *et al.* 1997). However as vertical integration between forest growers and users improves, forest growers will be under increasing pressure to supply wood of known or defined quality. New technology has been developed that makes measurements of wood quality rapid and cost effective (Evans *et al.* 1995). This allows users of plantation forests to start exploring methods of growing quality wood suited to particular end uses. Several projects are currently underway which investigate relationships between growth and wood property development as a function of changing genotype or silviculture (Downes personal communication). The challenge for tree growers in this industry is to understand how wood properties, including cell size and wall thickness, vary as a function of environmental and genetic conditions that influence growth processes in trees (Downes *et al.* 1997). While the current emphasis is still on volume production, market demands will increasingly drive growers to understand the relationships between growth rate, wood quality and product performance.

Many empirical and process based models of forest productivity are being developed or are in use (e.g. Battaglia and Sands 1998, McMurtrie *et al.* 1994, Landsberg and Hingston 1996). Whereas empirical models look for mathematical or statistical relationships between cause and effect, process-based models endeavor to understand the physiological relationships between cause and effect. Consequently the latter tend to be more

complicated and, at this time, less accurate. However empirical models cannot deal adequately with changing environmental and management conditions (Battaglia and Sands 1998).

A reductionist approach to understanding living systems, although desirable, is not always possible. Investigating cambial dynamics is one of those areas where it is impossible. Process modeling provides an alternative approach. TreeRing, version 3, is such a model that describes cambial activity mathematically. It essentially incorporates our current understanding in a way that can predict outputs of ring and cell attributes which can be tested. If the model successfully predicts reality then we can assume our understanding is close to reality until we find those conditions where the model fails. This then gives us the opportunity to refine our knowledge base. There is, to our knowledge, only one other process-based model of wood property development (Deleuze and Houllier. Submitted). As the focus in industry shifts from being driven by growth alone, to also being driven by wood properties, this type of model will need to be incorporated into existing commercially-used models which at present predict only annual increments of tree growth. In addition the process of model development itself can improved understanding of how environmental factors influence plant processes important to cell division and cell-wall growth. Such clarification is not only important to the forest products industry but it can 1) provide dendrochronologists with a biological basis for constructing more accurate and reliable statistical tools for tree-ring analysis and 2) lead to new and more powerful dendrochronological applications (Fritts and Shashkin 1995).

This paper describes the TreeRing model of xylem growth which operates at daily time steps. We use knowledge of basic physiological processes to characterize the tree growth system controlling cell division, enlargement and maturation at daily time steps. This model is unique in that biomass is converted to cell and wood properties which in turn can be compared to wood properties of trees growing in the forest environment. Thus the actual xylem cell anatomy in past tree rings are used to measure the real tree response to past environmental conditions and in turn to assess the precision of the model estimates. This is accomplished by 1) reading the anatomical measurements from a tree in the simulated environment during each run of the model, 2) plotting them along with the model estimates and 3) calculating a number of statistics that provide an objective comparison. Discrepancies between the measured and simulated ring widths, cell numbers in the ring, cell sizes, wall thickness and tree-ring index are immediately apparent. The characteristics of discrepancies are used to identify inadequacies in the model and to suggest what model changes will lead to the greatest improvement.

Our approach is to start with a simple linear model and increase its complexity in a step-wise fashion. At first we described the growth of only a single radial file of cells and assume that the living crown, stem and root mass

are constant through time (Vaganov 1990, Fritts et al. 1991). In a more recent version of the model (Fritts and Shashkin, 1995), the effects of prior environmental conditions were modeled using the dynamics of food storage, growth efficiency and differences in respiration of the various tissues in the tree (Fritts et al. 1997). In the present version the algorithms have been refined. The model is adapted for operation in the Southern as well as the Northern Hemisphere. Outputs from new imaging technology, SilviScan (Evans 1994, Evans et al. 1995) are used with software written by Downes to scan and transform image and xray information to files of cell sizes and wall thicknesses for input to the model for verification. Heartwood, sapwood and other measurements derived from the wood samples are used to estimate a number of model parameters.

This version of the model does not yet consider crown and branch growth and changing photosynthetic capacity from one year to the next. These calculations are needed 1) to capture fully the autoregressive and low frequency behavior of ring widths through time and other acknowledged changes in growth (Cook and Kairiukstis 1990) and 2) to describe the changes in ring structure of the seedling as it grows into a sapling and then a closed canopy or reaches the understory, codominant, mature and over-mature stages finally ending with death.

### The Model

The growth rate of a tree is determined by the amount of available carbon (glucose) produced by photosynthesis and by the rate that the carbon is transformed into biomass. More than 30% of the carbon produced by annual photosynthesis is used for the maintenance of living cells and tissues (maintenance respiration) and the rate of consumption largely depends upon temperature (Linder & Axelsson, 1982; Ryan & Warning, 1992; Ryan et al., 1996). The amount of assimilated carbon used for wood growth depends upon the allocation of the carbon to foliage, roots and stem as well as the growth conditions at the time (Gholtz, 1980; Gower et al, 1992, 1995; Snowdon & Benson, 1992).

There are four interrelated blocks simulating 1) the microclimate and other input calculations, 2) photosynthesis along with photosynthate allocation and utilization by foliage, stem and roots, 3) water balance in the soil, the tree, and the stomates and 4) cambial growth and development (Fig. 1). Cambial growth includes separate modules of cell division, enlargement and wall thickening. The model tracks the changing physiological conditions for each day and for each growing tracheid element passing through one of the growth modules until the cells protoplasm disappears and the cell wall becomes a structural component of the wood (Fig. 2).

The rates of processes in these four blocks are influenced by both regulating and limiting factors where: 1) Regulating factors include growth promoters and inhibitors largely in the actively growing crown (Larson 1969, 1994, Catesson 1994, Savidge 1994, Romberger, 1963). 2) Limiting factors include only external environmental or internal biophysical conditions that limit the rates of growing processes that occur. In TreeRing, these regulating and limiting factors are applied to particular trees growing in dendrochronologically limited sites. The values of both regulating and limiting factors may be different for the different processes and are normalized in that they range from a minimum value (most limiting condition) of 0 to a maximum value (unlimiting condition) of 1. The collective effect of these regulating and limiting factors is expressed as the product of those factors that are most likely to be limiting to a particular process. For example, the effect of limiting factors to growth ( $g$ ) is described as a function  $g_i(T, s, w)$  where  $T$  is temperature,  $s$  is substrate (sucrose) and  $w$  is water stress (a function of stomatal resistance). The regulating factors are expressed as control functions ( $C_t$ ,  $C_{tm}$ ) related to the growth of new foliage and conditions in the crown. The controlling effects of  $C_t$  and  $C_{tm}$  begin when the rate of foliage growth declines below two specified critical rates.

### I. Microclimate

The calculation of microclimatic values is based on microclimatic model developed by Running (Hungerford et al. 1989, Running et al. 1987). The absolute humidity and incoming short-wave radiation are derived from climatological principles (Hungerford et al. 1989, Running et al. 1987, Nicolov and Zeller 1992), and average daytime temperature is calculated from the maximum and minimum temperatures (Running et al 1987). Vapor pressure deficit is calculated from the equation relating air temperature to saturation vapor pressure for use in potential evaporation calculations (Running et al. 1987, Murray 1967, Bristow 1992). We use the daily minimum temperature to be equal to dew point as suggested by Running et al. (1987) and Hungerford et al. (1989). Finally, the estimated dew point for the site is combined with the estimated daily air temperature to calculate the average vapor pressure deficit.

Incoming solar radiation on a horizontal surface is estimated using the algorithm based on meteorological conditions developed by Nivolov and Zeller (1992). Daily potential radiation is a function of latitude, solar declination, sunrise/sunset hour angles and the day of the year (Klein 1977). The amount of solar radiation received at the earth's surface is less than that at the top of the atmosphere because of scattering and absorption by components of the atmosphere. This attenuation of radiation is expressed as a linear function of undepleted solar radiation at the top of the atmosphere and the average cloudiness (Hungerford et al. 1989, Bristow and Campbell 1984). The model is applied to the growth of *Pinus ponderosa* at 478 m higher than the weather

station at Chiricahua National Monument in southeastern Arizona. The temperatures are corrected for the elevation difference using a lapse rate of  $-0.006\text{ }^{\circ}\text{C}/\text{m}$ ., but no correction was used for elevational differences in precipitation.

In addition to the microclimatic estimations, simple allometric relationships are used to transform readily available information from the study trees into 1) leaf mass, 2) mass of the living tissues in the stem, 3) mass of living roots and 4) the number of cambial initials in the stem. These estimates of living tissues are in turn used to calculate maintenance respiration, growth dynamics of the foliage and roots, photosynthesis, transpiration and absorption of water from the soil by roots. The number of cambial initials determines the initial radial growth mass in the stem. The calculations start with information on the tree height, diameter breast height, the radial size of the dead bark, living phloem and sapwood that is used to calculate the cross-sectional areas for 1) the tree stem at breast height, 2) bark and dead phloem, 3) live phloem, 4) sapwood, 5) heartwood, 6) an average ring, and 7) mass and area of leaves (Callaway et. al 1994, Grier and Waring 1974, Gholz 1980). Mass of the sapwood and mass of the ring are calculated when the cell size and wall thickness measurements are obtained using density of the wood measured by SilviScan (Evans 1994). Root mass is calculated from the root/shoot ratio (Kramer and Boyer 1995, Ryan et. al 1996).

## II. Water Balance

The processes governing water movement through the soil, into the roots, through the plant and into the atmosphere are highly interrelated (Boyer 1985, Ellsworth and Reich 1992, Gates 1980, Johnson et al. 1991, Kramer and Kozlowski 1979, Noble 1974, Penman and Schofield 1951, Zahner 1955, 1968, Zimmermann 1983). Transpiration is the dominant factor because evaporation of water produces the water potential gradient in the plant that drives the water movement. It controls the rate of absorption and produces diurnal water deficits in the leaves as well as through out the entire plant. This influences the water status of guard cells on the leaf surface, and the stomates change in size as they regulate the flux of carbon dioxide into leaves and the rate of photosynthesis in the plant. Water deficits can also affect enlargement of cells in the cambium and cell division can be reduced or even stopped. Stomatal resistance is the most important control of transpiration rate and the tree water balance (Cowan 1977, Farquhar and Raschke 1978, Gates 1980, Jarvis et al. 1966, Jarvis and Stewart 1979, Kramer and Kozlowski 1979, Kramer and Boyer 1995, Luo and Strain 1992, Shulz and Hall 1982, Whitehead and Jarvis 1981).

The potential transpiration by leaves is given by

$$(1) \quad tr^p = \frac{dr}{R_{min}},$$

where  $tr^p$  is potential transpiration [ $\text{kg H}_2\text{O m}^{-2} \text{ s}^{-1}$ ],  $\delta p$  is the water vapor density deficit [ $\text{kg m}^{-3}$ ],  $R_{min}$  is the minimum resistance of leaves to water diffusion [ $\text{m s}^{-1}$ ], which is parameter  $p_4$  (All parameters and options are included in the model input files.)

The water vapor deficit is determined from equation 2,

$$(2) \quad dr = r_a \cdot 0.622 \cdot \frac{e_s - e}{P_{atm}},$$

where  $r_a$  is air density [ $\text{kg m}^{-3}$ ],  $P_{atm}$  is the atmospheric pressure [mbar],  $e$  is the water vapor pressure at temperature  $T$ ,  $e_s$  is the saturated water vapor pressure at the same temperature calculated as follows:

$$(3) \quad e(T) = 6.1078 \cdot e^{\frac{17.269T}{237.3+T}}, \quad e_s = e(T_{min})$$

The total potential transpiration from the crown is

$$(4) \quad Tr^p = tr^p \cdot D \cdot sM_l$$

where  $M_l$  is the foliage mass [kg],  $D$  is day length, and  $M_l$  is the surface area of the foliage [ $\text{m}^2$ ].

The potential rate of water absorption by the roots is described as

$$(5) \quad w_{max} = q \cdot f(\mathbf{q}) \cdot m_r,$$

where  $w_{max}$  is the potential rate of water absorption by roots from a unit of soil volume [ $\text{kg m}^{-3} \text{ day}^{-1}$ ],  $q$  is the “activity” of root [ $\text{kg H}_2\text{O kg}^{-1} \text{ day}^{-1}$ ]  $p_{18}$ ,  $f(\mathbf{q})$  is a normalized function describing dependence water uptake on soil water content,  $\mathbf{q}$ , per unit of soil volume [ $\text{kg/m}^{-3}$ ]. This function takes a trapezoidal form (similar to the temperature-dependence curve eq.(12)) with parameters  $\mathbf{q}_f$  - field capacity,  $p_{13}$ ,  $\mathbf{q}_{min}$  - wilting point,  $p_9$ ,  $\mathbf{q}_1$ - $\mathbf{q}_2$  - the range of the optimal soil moisture,  $p_{10}$ , and  $p_{11}$ ,  $\mathbf{q}_{max}$  - saturation when water uptake is limited by soil oxygen,  $p_{12}$ .

If the root system has mass  $M_r$ , the tree occupies a soil volume,  $v_s$ , with a surface area,  $A_s$ ,  $p_{15}$ , and a depth,  $h$ ,  $p_{14}$ , ( $v_s = A_s \cdot h$ ) the potential water absorption by roots of the tree will be

$$(6) \quad W_{max} = q \cdot f(\mathbf{q}) \cdot M_r \cdot v_s = q \cdot f(\mathbf{q}) \cdot M_r$$

The tree water balance is calculated depending upon the potential rates of absorption -  $W$ , loss of water due to transpiration -  $Tr$ , and resistance of the leaves -  $R$  and is described as  $W = Tr$ , where  $Tr = \min\{Tr^p, W_{max}\}$  and  $R = R_{min} \cdot \max\{1, Tr^p / W_{max}\}$ .

If photosynthesis is not limited by  $\text{CO}_2$ , resistance is controlled by the rate of photosynthesis and is increased to value  $R^c > R$ . In that case

$$(7) \quad W = Tr = \min\{Tr^p R_{\min}/R^c, W_{\min}\} \quad R = R_{\min} \cdot \max\{1, Tr^p/W_{\max} R_{\min}/R^c\}$$

The content of water in the soil of volume  $v_s = A_s h$  is calculated each day as

$$(8) \quad \frac{d\Theta}{dt} = A_s \cdot \min(P(t)a_1, a_3) - W - a_2\Theta$$

$$q = \frac{\Theta}{v_s}, \quad \theta_w \leq \theta \leq \theta_f$$

where  $\Theta$  is the water content in soil volume  $v_s$  [kg],  $\theta$  is soil moisture [ $\text{kg m}^{-3}$ ],  $P(t)$  is the precipitation [ $\text{mm day}^{-1}$ ],  $P(t)(1-a_1)$  is the interception of precipitation by the crown,  $P(t)a_1$  is the precipitation that goes into the soil. If  $P(t)a_1$  is greater than the value  $a_3$ , there will be surface runoff equal to  $P(t)a_1 - a_3$ . Additional loss of water occurs when the soil water content exceeds field capacity,  $\theta_f$ .  $a_2Q$  is the rate of drainage of water from the soil.

### III. Photosynthesis.

The control of daily photosynthetic rates by external and internal factors is a complicated relationship. The chemical reactions of photosynthesis depend upon the availability of light and carbon dioxide, while the rates of these reactions are temperature dependent. Leaf temperature is determined by the energy budget of the leaf, which relates radiation, air temperature, wind speed and humidity to the temperature of the leaf (Gates 1980). When stomates close, carbon dioxide becomes limiting under conditions of water stress increasing the resistance to diffusion of carbon dioxide into the leaf. Different factors may limit photosynthesis at different times during the day. In the morning, increasing light enables photosynthesis to begin, the stomates open, and rising temperatures accompanied by increasing light intensity cause photosynthetic rates to increase. During midday, whenever water loss is greater than water absorption, stomatal apertures may decrease and temporary closure may take place, especially when osmotic concentrations of solutes in the guard cells are low. The degree of stomate opening and the rate of photosynthesis are highly correlated because the aperture controls the  $\text{CO}_2$  diffusion rate (Bowes 1991, Campbell et al. 1988, Harley et al. 1992, Wong et al. 1979, Farquhar and Sharkey 1982).

It is important for the model to distinguish seasonal variations in the photosynthetic rates in the tree crown caused by leaf development, metabolic activity and changing environmental conditions. In this version of the model, the rate of daily net photosynthesis depends upon:

- light (the average daily incoming radiation for the latitude of the site),
- average daytime temperature of the air,
- carbon dioxide inside the leaves which is dependent upon the condition of the stomates.

There are several approaches to modeling whole-leaf photosynthesis (Berry and Farquhar 1978, Buwalda 1991, Chartier and Prioul 1976, Farquhar and von Caemmerer 1982, Gates 1980, Hall 1979, Johnson and Thornley 1984, Running and Coughlan 1988, Running and Gower 1991).

The rate of photosynthesis is described in the model by the following system of equations

$$(9) \quad p = \frac{C_a - C_i}{R^*}$$

$$p = P_{\max} f_c(C_i) f_T(T) f_I(I) ,$$

where  $C_a$  is the concentration of CO<sub>2</sub> in the air [mM m<sup>-3</sup>],  $C_i$  is concentration of CO<sub>2</sub> inside the leaf [mM m<sup>-3</sup>],  $R^* = IR$  (where  $I$  is the transformation coefficient from water resistance into CO<sub>2</sub> diffusion resistance) is the resistance of leaves to diffusion of CO<sub>2</sub> [s m<sup>-1</sup>],  $p$  is the photosynthetic rate [mM CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>],  $f_c$ ,  $f_T$  and  $f_I$  are normalized functions of dependence of photosynthesis on  $C_i$ , temperature  $T$ , incoming irradiation  $I$ ,  $p_{\max}$  is the maximum of photosynthetic rate,  $p_{56}$ .  $R^c = R^c = IR$  where  $I$  is the transformation coefficient from water resistance,  $R$ , to CO<sub>2</sub> diffusion resistance  $R^c$ .

The dependence of photosynthesis on  $C_i$  is approximated by the linear function

$$(10) \quad \begin{aligned} &0 & , & C_i < a \\ f_c(C_i) &= (C_i - a)/(b - a) & , & a < C_i < b \\ &1 & , & C_i > b \end{aligned}$$

where  $a$  and  $b$  are constants  $p_{26}$  and  $p_{27}$ .

With an average light flux, the function for  $I$  ([J m<sup>-2</sup> s<sup>-1</sup>] corresponding to photosynthetically active radiation),  $f_I$ , is a Michaelis-Menten type curve

$$(11) \quad f_I = I/(I+I^*),$$

where  $I^*$  is the Michaelis-Menten constant  $p_2$ . The temperature dependency of photosynthesis is

$$(12) \quad f_T = \begin{cases} 0 & , T < T_{\min} \\ (T - T_{\min}) / (T_1 - T_{\min}) & , T_{\min} \leq T \leq T_1 \\ 1 & , T_1 \leq T \leq T_2 \\ (T_{\max} - T) / (T_{\max} - T_2) & , T_2 \leq T \leq T_{\max} \end{cases}$$

where  $T_{\min}$ ,  $T_1$ ,  $T_2$ , and  $T_{\max}$  are constants  $p_{21} - p_{24}$ .

From equations (9) and (10) the rate of photosynthesis is

$$(13) \quad p = P_m(T, I) \frac{C_a - a}{b - a + P_m(T, I) R^c}, \quad \text{if } P_m R^* \geq C_a - b$$

$$p = P_m(T, I), \quad \text{if } P_m R^* \leq C_a - b,$$

where  $P_m(T, I)$  is  $P_{\max} f_T(T) f_I(I)$ . For conditions when the  $\text{CO}_2$  inside the leaf is not limiting the rate of photosynthesis ( $p = p_m(T, I)$ ), the leaf resistance increases according to the equation

$$(14) \quad R^c = (C_a - b) / p_m(T, I) / \lambda, \quad (R^c \leq R_{\max})$$

Daily photosynthesis for the entire crown is

$$(15) \quad P = p \cdot D \cdot \sigma \cdot M_1,$$

where  $D$  is the day length [s],  $\sigma$  is the coefficient for transforming foliage mass into surface area [ $\text{m}^2 \text{kg}^{-1}$ ],  $M_1$  is the mass of foliage [kg].

#### IV. Growth

##### A. Leaf Growth.

The leaf is an organ of limited growth and limited life span. The increase in dry mass of leaves is a highly complex series of biochemical events, and numerous attempts have been made to model it (Dale 1988, Thornley et al. 1981). The growth and morphogenesis of the leaf primordium and the unfolding of the associated lamina are intimately associated with both cell enlargement and cell division. While the volume increase of their primordia includes some cell size increase, it largely reflects the increase in the number of cells, and this number ultimately determines the size of leaves even though cell sizes can vary greatly (see Dale, 1988).

The foliage produced during the current year has mass  $M_{10}(t)$ , the one year-old leaves have mass  $M_{11}(t)$  etc. The mass of meristematic cells is proportional to the potential mass of new foliage  $M_{10}^*$ ,  $M_{1m} = \eta l M_{10}^*$ . The dynamic of foliage growth is

$$(16) \quad \begin{aligned} \frac{dM_{10}}{dt} &= \mu_1 M_{1m} - \lambda_{10} M_{10} \\ \frac{dM_{li}}{dt} &= -\lambda_{li} M_{li}, \end{aligned}$$

where  $\lambda_{li}$  is the rate of leaves lost at age  $i$ ,  $\mu_1$  is the rate of new foliage growth by the foliage meristem. The photosynthetic active foliage is  $M_1 = \sum M_{li}$ . The rate of leaf growth is

$$(16a) \quad \mu_1 = \mu_{10} (1 - M_{10}/M_{10}^*) F_1(s, l, T, W),$$

where  $M_{10}^*$  is the potential mass of new foliage,  $F_1$  is a normalized function relating the growth rate to limiting conditions of substrate concentration, temperature and water balance.

## B. Root Growth

The root system is treated as a carbon sink using substrate during the growing process as it produces new mass (surface area) enabling water uptake from the soil. Water uptake is a function of the mass of living cells in the fine roots while growth of these roots is a function of the root meristematic tissue. The growth of roots is simulated in the model as

$$(17) \quad \frac{dM_r}{dt} = \mu_r M_{rm} - \lambda_r M_r$$

where  $\mu_r$  is the rate of fine root production by the root meristem which varies as a function of limiting factors,  $M_{rm} = \eta_r M_r$  is the mass of root meristem.

$$\mu_r = m_r F_r(sr, T, W) \quad \text{and } \lambda_r \text{ is the rate of mortality of roots.}$$

For this current version of the modelled dynamic of root and foliage growth, we suggest that the mass of root, foliage,  $M_1$ , and potential mass of new foliage,  $M_{10}^*$ , can be considered constant and equal to  $M_r$ .

### C. Stem Growth

The term stem includes all parts of the tree in which the growth is secondary growth in the cambium. This includes branches, the main stem and coarse roots. The living cells in the stem include various cellular types such as ray cells, parenchyma, living phloem cells and the population of cambial initials. The average life span of the initial cell is many years and all cells in the radial file are clones of this one initial cell (Iqbal and Ghouse, 1990). It is assumed that the ratio of cambial initials to all other living cells is constant (the number or mass of cambial initials is constant and proportional to the mass of all living cells in the stem,  $M_s$ ).

The differentiation of mature tracheids elements is modeled for one radial file which is assumed to be characteristic for all radial files in the tree. Growth in the radial file involves division of the cambial initials and xylem mother cells in the cambial zone, followed by enlargement and wall thickening in zones of enlargement and maturation. As a cell grows, sugar is converted to cell wall material. This consumption of sugar is included as one of the carbon sinks along with the growth and respiration of all other living cells of the tree.

The production of new xylem cells is related in part to the mass of cambial initial cells. The number of cells,  $n_i$ , in the radial file includes the:

initial cell,	
xylem mother cells	- $n_c$ ,
elongating cells	- $n_e$ and
maturing cells	- $n_m$ .

Each cell in the radial file is characterized by values of several parameters. The controls to these are input parameters  $Cmb_j$  in file CAMBINI.

$j$  - is the position of each cell in the radial file. The initial cell is position 1 and those derived from it are numbered by their actual position in the file at the current time.

$x_j$  - is the cell size in the radial direction. The tangential cell size is assumed constant and is entered as a parameter of the model.

$w_j$  - is the cell wall area in cross section.

Cell size is the most important characteristic in determining the behavior of each cell. While in the cambium zone, each cell increases in size until it reaches a maximum size and divides (moves through the cell cycle). The resulting daughter cells are one half the maximum cell size after each cell division. The innermost cells in the

cambial zone lose their ability to divide and enter the enlargement phase where the cell size continues to increase but at a diminishing rate. When the rate of size increase reaches a critical low value, the cell loses its ability to enlarge and enters the zone of maturation where cell wall thickening and wall synthesis continue until the cell dies.

### 1. Cell division

Unless the cambium is dormant, all cambial cells pass through the phases of the cell cycle: G1, S, G2 and M. The size of each cell when it enters a particular phase, is  $D_{G1}$ ,  $D_s$ ,  $D_{G2}$  and  $D_m$  (see  $Cmb_{11}$  -  $Cmb_{14}$ . These parameters refer to those in the input file CMB61.PAR). However, the rate of division varies as a function of the growth rate of cambium cells ( $Cmb_{10}$ ) while the cell is in phase G1. Growth rates (duration) while the cell passes through all other phase are constant and specified by input parameters. The duration of the full cell-cycle will be:

$$\frac{D_{G1} - D_m / 2}{V_c} + \frac{D_m - D_{G1}}{Cmb_{10}} .$$

However,  $V_c$  is not constant but changes with position in the cellular file, varying limiting conditions and controlling factors which change through time. As a result duration of the cell-cycle can not be expressed as a simple equation.

The rate of growth is a function of cell position,  $j$ , and is related to limiting conditions and numbers of other growing and maturing cells as follows:

$$(18) \quad V_c = [Cmb_7 - (10 - j) \cdot Cmb_6 \cdot \frac{x}{x + x^*}] \cdot Cmb_2 \cdot F_c(s_s, T, w) \cdot \left[ \frac{1}{Cmb_{37}} + \left( j - \frac{1}{Cmb_{34}} \right) \cdot (C_t) \right]$$

where  $Cmb_7$  is the rate of enlargement in position  $j$  (Fig. 3);  $Cmb_6$  is the slope regulating the increasing growth rate of cambial cells across the cambial zone;  $x$  is the sum of the cell size in the division, enlargement and maturation zone;  $x^*$  ( $Cmb_{18}$ ) is the ring width of growing cells (mKm) when the slope of the division rate is  $\frac{1}{2}$  the maximum value;  $Cmb_2$  is a scalar of growth rate;  $Cmb_{37}$  is a scalar for the rate of enlargement; and  $Cmb_{34}$  is the sensitivity of enlargement to  $C_t$  ranging from 1-10.

The relationship between the rate of growth  $Cmb_7$  and  $x^*$  of the differentiating cells is used to control the rate of division of the cambial initial and mother cells at the beginning of the growing season through a feed back loop;  $F_c$  is a normalized function ranging from 0 to 1; and  $C_t$  is the control from the crown.

The cell leaves the zone of cell division and enters into the enlargement stage if  $V_c < V_{min}$  (Relationship 2, Fig 3) and the cell is in the G1 phase of the cellular cycle. If the cell is in any other phase, the cell continues to divide until it completes the division process. The function  $V_{min}$  (Relationship 2) is determined as

$$(19) \quad V_{min} = Cmb_2 \exp(Cmb_8 (j+Cmb_9)) = Cmb_2 \exp(Cmb_8 \cdot Cmb_9) \cdot \exp(Cmb_8 \cdot j)$$

where  $Cmb_2$ ,  $Cmb_8$  and  $Cmb_9$  are coefficients of the equation.

Cell division will stop reversibly (the cambium becomes dormant) for all cells in phase G1 if  $V_c < V_{cr}$  (Relationship 3, Fig 3).

## 2. Cell enlargement

The exact mechanisms that control cell enlargement and its variation over time are not known (Haigler 1994, Catesson 1994, Fukuda 1994, Savidge 1994). However, there are many observations of cell size variations and cell enlargement including experimental data from trees growing under controlled conditions (Larson 1969, 1994, Wodzicki 1971, Zahner 1968, Creber and Chaloner 1984). In addition, there is considerable information available concerning the molecular control of enlargement and the influence of growth regulators (Savidge 1994, Fukuda 1994).

For trees growing on dendrochronologically selected stress sites, temperature, water supply and perhaps substrate availability may be the most important limiting conditions (Larson 1969, 1994, Wodzicki 1971, Zahner 1968). Based upon studies in roots, the rate of enlargement can be divided into accelerating and decelerating phases (Pritchard 1994). Limiting conditions have the least effect on the first and the greatest effect on the second phase of growth when it is decelerating. Thus, we assume in our model that limiting conditions have the greatest effect on growth rate and potential cell size in the later stages of cell enlargement.

There has been much discussion over the years as to what factors control the transition from large earlywood cells to smaller latewood cells (see Larson 1969). Environmental factors may hasten or delay this transition, but it does not appear to be directly connected to environmental changes but rather to the physiology of the growth

process itself, related to new xylem tissue and hormone production primarily in the crown (see Larson 1969, Creber and Chaloner 1984). Since the specific action of these growth regulators is not well known, we simply have modeled the transition from earlywood to latewood as a function of growth and development of foliage in the crown.

As in the cell division module, the enlargement phase of growth is described as a function of limiting factors  $g_e(T, s, w)$  and a controlling factor  $C_t$ . The relative importance of these factors are not necessarily the same as those in cell division. In addition the rate of enlargement in the model,  $V_e$ , decreases with increasing cell size. This relationship is a linear function (Relationship 1, Fig 4).

The dynamics for enlargement of cells is described as

$$(20a) \quad \begin{aligned} \frac{dx}{dt} &= V_e \\ \frac{dV_e}{dt} &= -k_e V_e \end{aligned} ,$$

$$x \text{ at } t=0 = x_0 \text{ and } V_e \text{ at } t=0 = V_{e0}$$

where  $x$  is radial cell size [ $\mu$ ];  $V_e$  is the growth rate [ $\mu \text{ day}^{-1}$ ];  $V_{e0}$  is the initial growth rate calculated as

$$Cmb_{22} \cdot Cmb_{37} \cdot \left(1 - \frac{x_0}{Cmb_{21}}\right)$$

where  $Cmb_{22}$  is the maximum growth rate of the cambial cell in position 10 (see equation 18);  $Cmb_{37}$  is a scalar mentioned above;  $x_0$  is the initial radial size when the cell entered the zone of enlargement; and  $Cmb_{21}$  is the maximum radial size.  $K_e$  is:

$$(20b) \quad k_e = k_{e \min} \left[ b_{35} + (1 - Cmb_{35}) \cdot C_t \right] \cdot \left[ y + (1 - y) \cdot F_e \right] ,$$

where  $Cmb_{35}$  ranges from 1-10 expressing the sensitivity of the enlargement process to  $C_t$ ,  $F_e$  is a normalized function ranging from 0 to 1 and

$$y = \frac{k_{e \max} - k_e}{k_{e \max} - k_{e \min}} , \quad k_{e \min} \leq k_e \leq k_{e \max}$$

where:

$$K_{e\min} = \frac{Cmb_{22} - Cmb_{24}}{Cmb_{21}}$$

$$K_{e\max} = \frac{Cmb_{22} - Cmb_{24}}{Cmb_{23}}$$

where  $Cmb_{21}$  and  $Cmb_{22}$  are described above,  $Cmb_{24}$  is  $V_{ecr}$ , the critical rate when the enlarging cell enters the zone of maturation (Relationship 2, Fig 4) and  $Cmb_{23}$  is in the minimum mature radial cell size. The cell stops enlarging and enters the zone of maturation when  $V_e \leq V_{ecr}$ .

### 3. Cell maturation.

The dynamics of cell wall synthesis and wall thickening are similar to those controlling cell enlargement (Fig 5).

The rate of cell wall synthesis is

$$(20c) \quad \begin{aligned} \frac{dw_j}{dt} &= V_m \\ \frac{dV_m}{dt} &= -k_m V_m, \quad V_m(t=0) = V_{m0} \end{aligned} \quad \begin{aligned} w_j(t=0) &= 2.0y_o(x_j + x_t - 2y_o) \end{aligned}$$

where  $w_j$  is the cell wall area of the  $j$ -th cell [ $\mu^2$ ],  $V_m$  is the rate of cell wall synthesis [ $\mu^2 \text{ day}^{-1}$ ],  $y_o$  is initial cell wall thickness [ $\mu$ ],  $x_t$  is the tangential cell size [ $\mu$ ],  $V_{m0}$  is the initial rate of wall synthesis, and  $k_m$  is a function through which the process is controlled. This function is

$$(20d) \quad k_m = k_{m\min} \left[ (Cmb_{36} - 1) \cdot (Ctm + 1) \right] \left[ y + (1 - y) \cdot F_m \right],$$

where  $Cmb_{36}$  ( $V_{mcr}$ ) is the critical level of the rate of wall thickening (Relationship 2, Fig 1-6) when the

synthesis irreversibly stops;  $C_{tm}$  is the crown control;  $y = \frac{k_{m\max}}{k_{m\min}}$ ; where:

$$k_{m\min} = \frac{Cmb_{31} - Cmb_{27}}{P_{area} - P_0}$$

$$k_{mmax} = \frac{Cmb_{31} - Cmb_{27}}{P_{min} - P_0}$$

$P_0$  is initial area of the cell wall:

$$P_0 = 2 \cdot Cmb_{29} \cdot (x + Cmb_{28} - 2 \cdot Cmb_{29})$$

where  $Cmb_{29}$  is the initial wall thickness;  $x$  is the radial cell size; and  $Cmb_{28}$  is the tangential cell size.

$$P_{min} = 2 \cdot Cmb_{33} \cdot (x + Cmb_{28} - 2 \cdot Cmb_{33})$$

where  $Cmb_{33}$  is the minimum wall thickness.

An estimate of the potential area of the wall,  $P_{area}$ , is

$$P_{area} = 2 \cdot wall_j \cdot (x + Cmb_{28} - 2 \cdot wall_j)$$

However,  $P_{area}$  cannot be larger than  $Cmb_{32}$ , the maximum wall thickness for the particular species and site measured from wood samples, but must maintain a minimum lumen area,  $Cmb_{30}$ . When wall thickening stops, the cell dies and becomes a part of the fully differentiated ring.

If one plots the relationships between cell wall area or wall thicknesses for each cell in a large number of rings expressed as a function of radial cell size (see figure 5 in Fritts et. al. (1997)) and keeps track of the relative sequence of each cell within its particular ring, two clusters of points are visible. The first cluster of points appears on the lower right of the plot and corresponds to cells from the earlywood portion of the ring. The second cluster of points is in the upper left corresponding to cells from the latewood in the rings. In the plots of wall thickness as a function of radial cell size, the points for earlywood cluster around a horizontal line, indicating that wall thickness is completely independent of cell size during earlywood formation. The scatter in points around this horizontal line is most likely the error in measurement, random variations from one cell to the next, or possibly some limiting conditions at that time. In the plot of cell wall area, the points fall along a slope indicating that this measurement is dependent on cell size (also see Wimmer 1991). However, the slope for earlywood is markedly less than the slope of the relationship for latewood cells.

Since wall area is more related to cell size than wall thickness, we use wall area and express it as a linear function of cell size where  $sl_{\min}$  is the minimum slope of the relationship for earlywood and  $sl_{\max}$  is the maximum slope expressing the relationship with cell size for the latest part of the latewood. The possible effects of limiting conditions on the wall thickness of the earlywood appears so small, that we include no limitation until latewood begins to form. The slope is steeper for latewood,  $sl_{\max}$ , and is reduced if environmental conditions become limiting. This implies that limiting environmental conditions can reduce the rate of cell wall thickness only during the phase of latewood development. It is well known that limiting conditions such as temperature or moisture are related to the color, appearance and density of the latewood ( Denne and Dodd, 1981 ).

#### V. The Substrate Dynamics In The Tree

Different approaches have been used to deal with the tree carbon balance (Gifford and Evans 1981, Hesketh and Jones 1975). Some have used allometric relationships (Monsi and Marata 1970, Patefield and Austin 1971, Sheehy et al. 1979); some use a “nutritional control” that is based on the “functional equilibrium” between organs (de Wit et al. 1970); and some use transport gradients and resistances (Thornley 1976) to model allocations within the tree. We assume in the model that substances are translocated rapidly within a day by diffusion processes (Canny 1973) and that the maintenance respiration is proportional to the weight of the living biomass following Thornley (1970 ).

The substrate, sucrose, is produced by photosynthesis and is consumed by maintenance respiration and growth of new tissues throughout the tree. Maintenance respiration is dependent upon temperature and of course substrate availability (Amthor 1989, Buwalda 1991, Kramer and Kozlowski 1979).

$$(21) \quad Rm_i = \beta_{oi} \frac{s_i}{s_i + s_i^*} e^{\beta_{li} T} M_i, \quad i=l,s,r$$

where  $Rm_i$  is the rate of maintenance respiration [ $\text{mM CO}_2 \text{ d}^{-1}$ ],  $\beta_{oi}$  is the substrate uptake for maintenance respiration, parameters  $rmt_i$  where  $i$  varies from 1-3 in units of mass per day [ $\text{mM CO}_2 \text{ kg}^{-1} \text{ d}^{-1}$ ],  $s_i^*$  is a Michaelis-Menten constant,  $\beta_{li}$  is the temperature constant.

We follow Chung and Barnes (1977), Williams et al. (1987) and assume that the respiration required for growth is proportional to the growth increment of new foliage (leaves), roots and stem

$GR_l = \alpha_{gl} \mu l M_l m$  growth respiration by leaves

$GR_r = \alpha_{gr} \mu r M_r m$  by roots,

$GR_c = a_{gc} \cdot r_w \cdot N \cdot (\sum_{n_c} V_c + 2 \cdot x_t \cdot d)$  by cambium,

(22)  $GR_e = a_{ge} \cdot r_w \cdot N \cdot \sum_{n_e} V_e$  by enlarging cells,

$GR_m = \alpha_{gm} \cdot \rho_w \cdot N \sum_{n_m} V_m$  by maturing cells,

where  $\alpha_{gl}$  and  $\alpha_{gr}$  is quantity of substrate assimilation per units of growth per day [ $\text{mM CO}_2 \text{ kg}^{-1}$ ],  $\alpha_{gc}$ ,  $\alpha_{ge}$ ,  $\alpha_{gm}$  are the substrate assimilation per units of cell wall mass [ $\text{mM CO}_2 \text{ kg}^{-1}$ ],  $\rho_w$  is the specific gravity of cell wall [ $\text{kg } \mu^{-3}$ ] and  $N$  is the number of cellular files or cambial initials per tree. If 1 kg of wood tissue is equal  $0.375 \text{ kg } ^\circ\text{C}$  or  $3.125 \cdot 10^4 \text{ mM CO}_2$  the coefficient of efficiency is

$$\frac{3.125 \cdot 10^4}{a_{gi}}$$

where  $a_{gi}$  is the value from  $GR_{ci}$ ,  $i$  varies from 1-5. The dynamics of substrate content in the leaves is

$$(23) \quad \frac{dS_l}{dt} = P - Rm_l - GR_l - \xi_{ls}(s_l - s_s),$$

in the stem is

$$(24) \quad \frac{dS_s}{dt} = \xi_{ls}(s_l - s_s) - Rm_s - GR_c - GR_e - GR_m - \xi_{sr}(s_s - s_r),$$

and in root is

$$(25) \quad \frac{dS_r}{dt} = \xi_{sr}(s_s - s_r) - Rm_r - GR_r,$$

where  $S_i$  is substrate content [mM CO<sub>2</sub>],  $s_i$  is substrate concentration [mM CO<sub>2</sub> kg<sup>-1</sup>],  $\xi_{ls}$  and  $\xi_{sr}$  are coefficients of diffusion for the substrate from leaves to the stem and from the stem to the roots [kg t<sup>-1</sup>].

## VI. The Growth Control Functions.

The growth rates in the crown and the three cambial zones depend upon temperature, substrate concentration and tree water balance. The same functions are used in all four cases but coefficients vary depending upon the relative importance of each condition on the particular process. The relationship is

$$(26) \quad F_i = f_i(T) \frac{s_i}{s_i + s_i^*} \min\left(1, \frac{R_i^*}{R^w}\right), \quad i=1,c,e,m,r$$

where  $s_i$  is substrate concentration,  $s_i^*$  is a Michaelis-Menten constant, gc1 - gc5,  $R^w$  is the resistance determined from water balance,  $R_i^*$  are the coefficients p46 - p50,  $f_i(T)$  is the temperature function (see eq.(12)).

The values  $C_t$  describing “hormonal control” for the cambium and zone of enlargement and  $C_{tm}$  for maturation are determined in the model through the dynamic of new foliage growth

$$(27a) \quad C_t = \text{MIN}\left(\frac{z}{z_t^*}, 1\right)$$

$$(27b) \quad C_{tm} = \text{MIN}\left(\frac{z}{z_m^*}, 1\right)$$

where  $z_t^*$  and  $z_m^*$  are p28 and p29 and  $z$  is  $\frac{m}{m_0}$  (see Eq. 16a).  $z$  is an average for an interval of 1 or more days p7. If p7 is positive the average is unweighted, if negative the average is weighted around the central value. Therefore, at any moment  $t$ ,  $C_t$  is the weighted or unweighted average for the period  $(t-\Delta t, t)$ .  $C_t$  and  $C_{tm}$  are compared each day to several critical values. If  $C_t \leq p_{28}$ , latewood begins to form; if  $C_t \leq p_8$  crown growth stops. If  $C_{tm} \leq p_{29}$  wall thickening begins. The net effect of these controls are portrayed on the computer screen along with the temperature and precipitation input and the daily rates of selected plant processes (Fig. 1-7).

## VII. Other Calculations

Starting with March 1 (northern hemisphere), growth can begin following the day when the sum of temperature (in °C) over some interval of time (a parameter of the model) becomes greater than an assumed constant threshold value (Cannell and Smith 1986, Hanninen 1990, Landsberg 1974, Lindsay and Newman 1956, Valentine 1983) and resistance is lower than an assumed threshold value. This was added as dendrochronological observations made by Christopher Baisan (private communications) suggesting that at times of severe water stress, growth may not begin until soil moisture is replenished during the summer rainy season. This is consistent with the observations of Shepherd (1964) in *Pinus radiata*.

The calculation of all growth processes in the model begins when time  $t > t_{beg}$ . Leaf growth ends when the growth rate is less than a specified threshold; and the cambial division stops when leaf growth stops. The enlargement and maturation phases continue until their rates fall below the critical values specified in the parameter file.

A number of standard statistics are calculated to help evaluate the similarities and differences between the simulations and actual measurements of ring width, cell numbers, cell sizes, wall thicknesses and ring indices. The means, standard deviations, correlation and regression coefficients, standard error and other statistics are calculated following Ezekiel (1941), but they may be found in most textbooks on basic statistics.

An iteration procedure is designed to optimize any selected parameter or contiguous group of parameters keeping all of the other parameters constant. The residual variance is minimized between the simulated and actual measurements of one or more attributes 1) ring widths, 2) cell numbers, 3) cell sizes, 4) wall thicknesses for a single core, and 5) ring-width index. Different statistics of the residual can be minimized which allow one to use different optimization strategies. These include 1) absolute value of the mean, 2) standard deviation + absolute value of the mean, 3) 1- correlation squared or 4) standard deviation + absolute value of the mean residual / standard deviation of the measurements. The mean minimizes only the mean residual so that the actual and simulated means can be brought into line; the standard deviation minimizes the variance of the residual; the correlation gives equal weight to all controls but does not consider differences in the mean values; and the last statistic attempts to scale the variance in terms of the variance in the independent variable for that attribute so that the statistics of the residuals weigh each variable equally. The values of these statistics can be used singly or the sum of the statistics for attributes 1-4 or 1-5 can be calculated to control the iteration. The statistics of the ring-width index, if run for a different interval of time, will be calculated for a different time period than those of the other attributes and these values can be summed to control the iteration process.

## VIII. Discussion and conclusions

TreeRing 3 is only a beginning in the immense task of developing a simulation model for cambial activity (Larson 1994) in both conifer and angiosperm species. However, the statistics provide an objective confirmation that the simulations can explain over 50 percent of the variance in ring width, cell numbers and cell sizes. Wall thickness estimates are less precise but explain more than 40 percent of the variance. Results from analysis of variance and correlation statistics of between and within tree ring-width variance (Fritts 1976) confirm that measurements from a single core, analogous to a single radial file of model estimates, is not likely to account for a great deal more than 50 percent of the larger scale stand variance. Therefore, we conclude that the basic form of the model produces reasonable and reliable estimates of ring width, cell number, cell size and wall thickness measurements obtained from the modeled trees in spite of the many model inadequacies. The model is ready to be refined and developed further depending upon the particular application to be made.

Most of the mathematical equations will be changed in future versions and many of the assigned parameters are little more than intelligent guesses based upon a reading of the literature. Many values must be changed when the model is applied to different sites and species. There is a great need for more field investigation and controlled experiments not only to measure the parameters but also to evaluate how well the model captures the dynamics of growth as it progresses over the season and from one year to the next.

The initial impetus behind the model was the need for a more fundamental approach to some important dendrochronological questions. It assumes that the cell information is placed in the correct year in which the ring grew using either dendrochronologically dated materials or plantation grown trees with known history. The model implies that some variations in climatic factors have affected the growing trees by limiting growth-controlling processes (Fritts 1976). We developed the model using only daily maximum and minimum temperature and precipitation so the model could be applied to any area around the world where standard daily climatic records were available and the rings could be precisely dated.

Certainly some processes such as photosynthesis as described by Farquhar and von Caemmerer (1982) can be more precisely described using hourly or minute by minute records of environmental conditions. Very few environmental records with hourly detail are available so that hourly time steps would have to be generated from daily information. It can be easily argued that such detail contributes other errors and, since the model generates cell features that integrate and average the effects of environmental conditions over a number of days, any precision lost is trivial.

A stand or higher level model is certainly possible, but its development will depend upon our capacity to generalize the specific ring and cell features from actual wood measurements. Validation using dendrochronological indices based upon replicated samples is a first step and is already included in version 3.

The focus has been on the development of tree-ring structure. Our attempts to describe photosynthesis, water relations and assimilation are practical and pragmatic means to obtain reasonable daily inputs for the growth models. We solicit help and would welcome the opportunity to incorporate any more sophisticated and better researched models of these processes that can generate daily values for a single tree. By linking TreeRing or elements of it to existing or future models of forest productivity should not only improve the estimates of tree-ring structure, but the host model could benefit by using the estimates of cell structure as rapid and objective validation of the overall model precision.

#### IX. Some Applications

Some general applications of the model are described in the Introduction. A few of the many possible applications are described here. The specific form of each application will of course depend on the interests and creativity of the investigators who use it.

Applications of the model to studies of wood and fiber quality are readily apparent. The model could suggest climatic conditions and site characteristics that would yield wood and fiber of a desired quality. The pulp and paper industry in Australia is interested in using the model for future planning in purchasing the appropriate land for growing pulp and paper of a desired quality. Similar interest has been expressed in North America and South Africa.

The rings of trees are a rich source of environmental information on past climate variations, stand conditions and events as well as biochemical changes occurring in past years. The model output can suggest specific ring and wood features and biochemistry that are related to environmental and climatic conditions and have specific environmental interpretations. The model can serve as an experimental tool for examining a variety of hypotheses using the past record in tree-ring structure.

Geochemical changes in wood can be modeled, studied and compared to field measurements. Current investigations on monthly variations in stable isotopes throughout the year could be assisted by an expanded

model with compartments for different fractionations of carbon, hydrogen or oxygen along with coefficients of fractionation for different processes in the carbon cycle.

The ring structure serves as a history of tree productivity and the model can be incorporated in forest productivity models and modeled ring structure compared to measurements from trees growing in the modeled forests. The statistical comparison between modeled and measured wood quality could be a powerful validation tool for such ecological models.

Considerable interest centers around a model for hardwood species. The existing model can serve as a basis by making changes in a step-by-step manner, first constructing simple representations of hardwood anatomy, then expanding them to include more detail.

Last but not least, the model equations clarify our understanding of the processes affecting cambial activity, cell structure and radial growth. The equations are explicit, can be criticized and replaced with improvements. Thus it is a formal medium allowing concrete discussion and debate for further developments and refinements. The TreeRing model represents a first step in an effort to create a simulation model of cambial growth and the development of wood structure.

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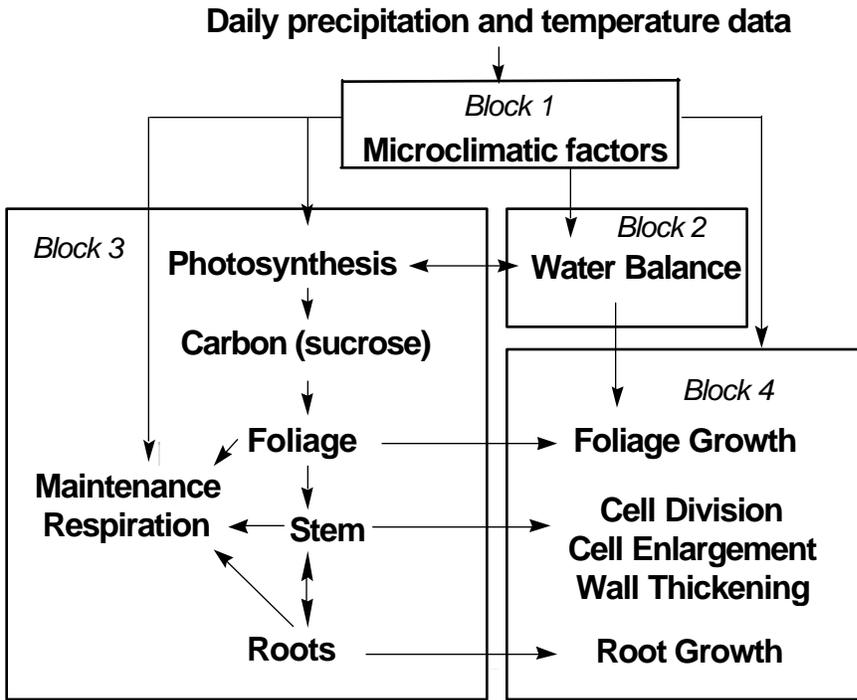


Figure 1. Organizational diagram of the model showing the four basic blocks and the modules they contain.

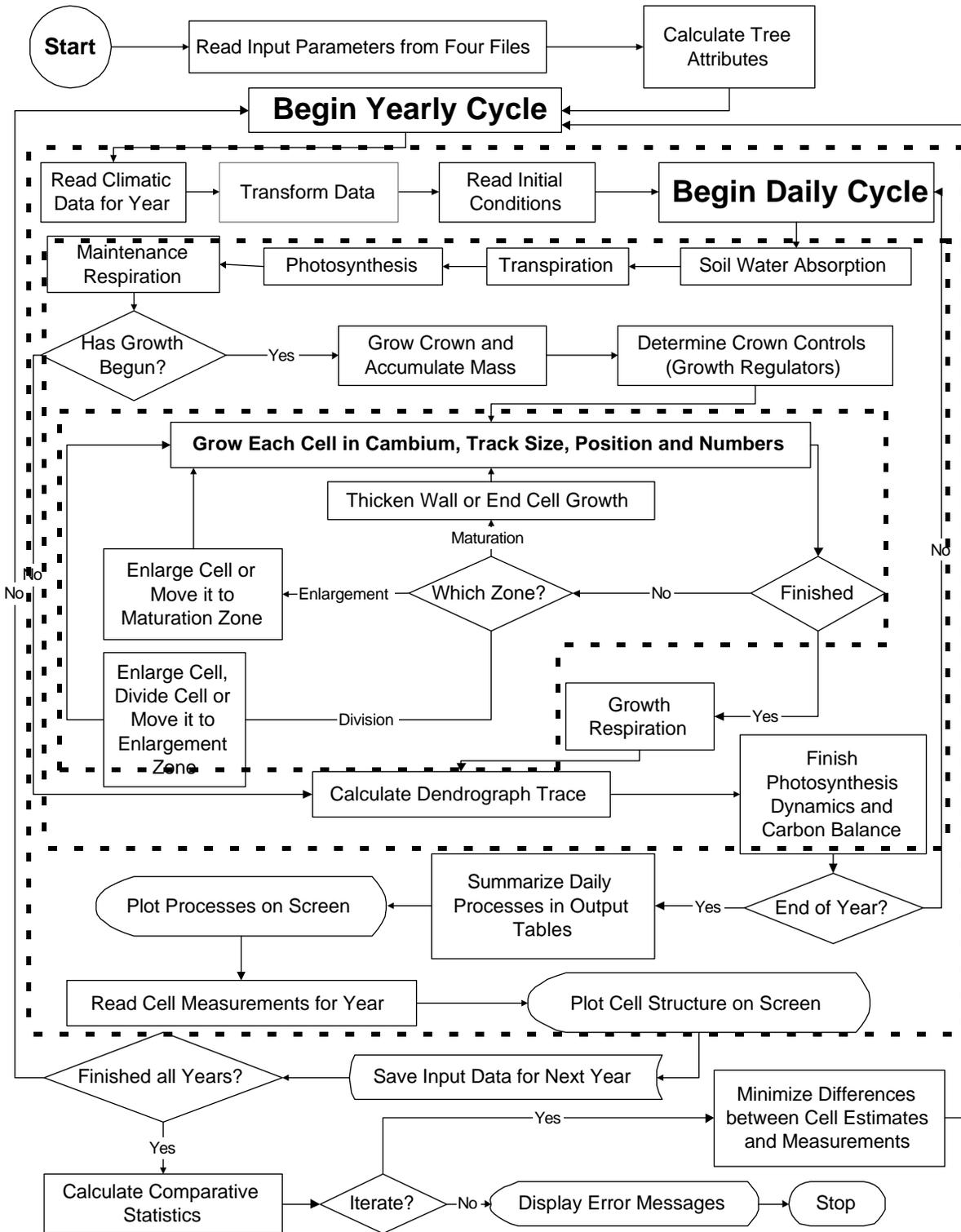


Figure 2. A flow chart outlining the operation of the model. The outer dashed block encloses the annual cycle; the middle block encloses the daily cycle; the inner block encloses the cambial block that grows each cell according to limiting conditions, its size or position in the array and its zone of growth.

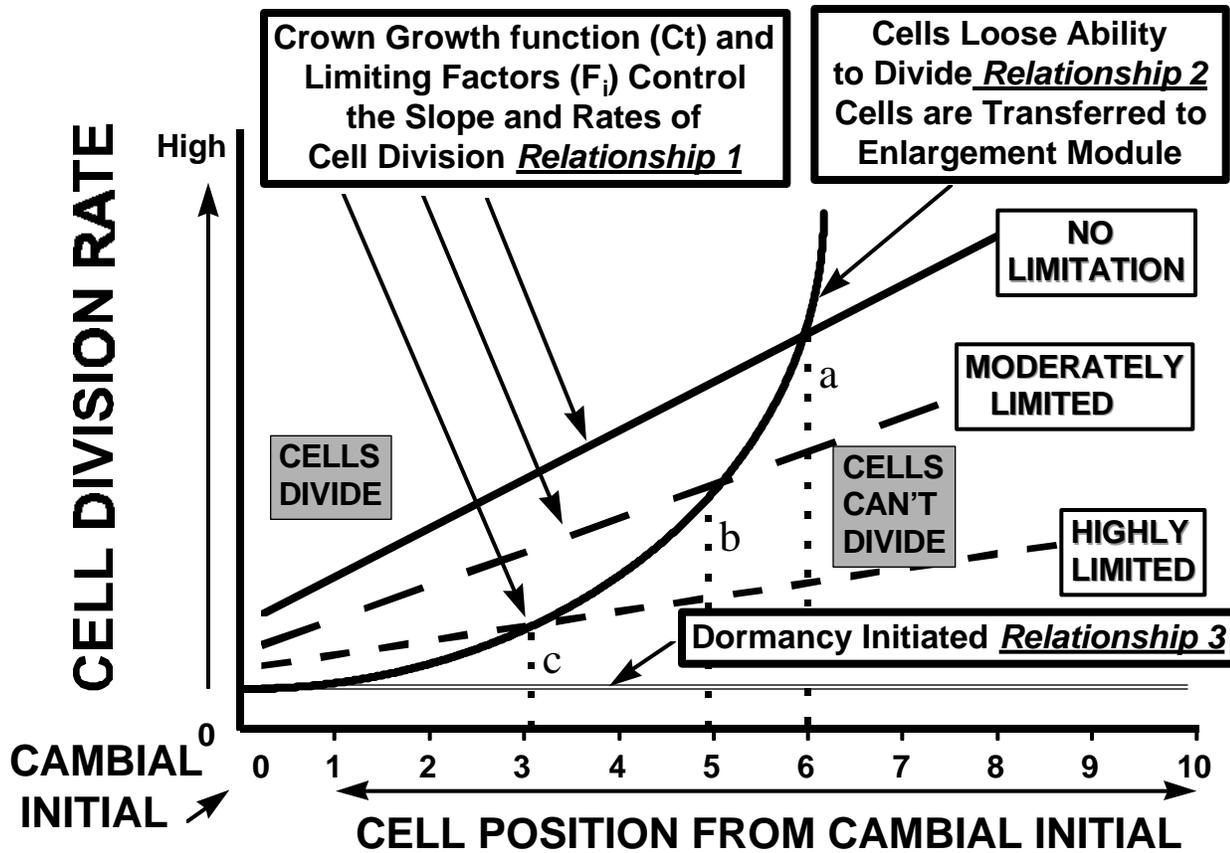


Figure 3. A diagram of the functions that control cell division. Rate of division is a linear function of cell position,  $J$ , starting with the cambial initial at position 0. The higher the order of the position, the greater the division rate. However, the change in rate with position is great under conditions that are unlimiting to division. The change in rate diminishes with increasing limitation represented by the change from solid to dashed sloping lines. A second relationship corresponding to the curved line controls the ability of the cell to divide (cells move to the enlargement module when their position exceeds the area inside the curved line). A third relationship, a horizontal line, determines the rate at which the cambium becomes dormant. In this example, under no limitation, 6 cells are dividing (see dotted line a) and the rate of division is high; under moderate limitation, 5 cells are dividing (see dotted line b) and the rate of division is moderate; under highly limited conditions, only 3 cells are dividing (see dotted line c) and the rate of division is low.

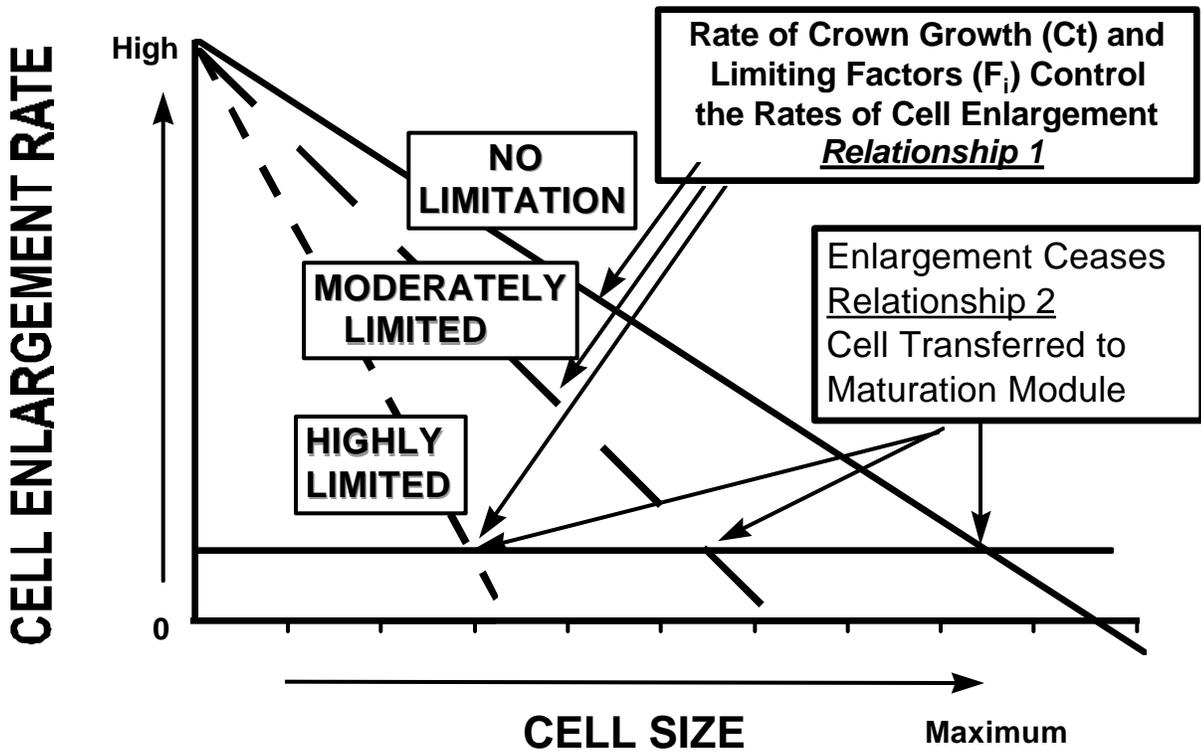


Figure 4. A diagram of the functions that control cell enlargement. The rate of enlargement is an inverse linear function of cell size. A cell enters this zone with maximum enlargement rate and the slope of *relationship 1* increases with increasingly limited conditions. As conditions become more limiting, the cell remains in the zone for a shorter duration of time and the cell is smaller. If the crown growth rate is rapid, the slope of the line is gradual and large cells are formed. If the crown growth rate decreases below a threshold value, the slope becomes steeper and small cells are produced. When the enlargement rate reaches a critical rate, *Relationship 2*, the cell loses its capacity to enlargement and moves to the zone of maturation.

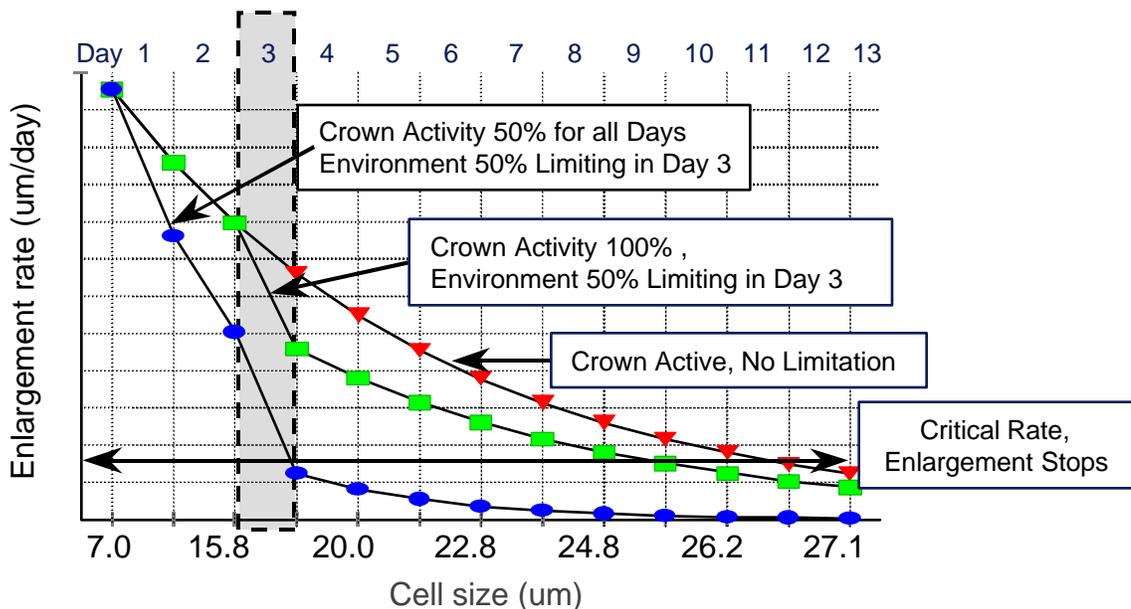


Figure 1.5 Enlargement rates decrease each day as a function of cell age, crown activity and environmental conditions. Three scenarios are shown. The line with red triangles shows the gradual decrease in cell enlargement rate with no limitation. The line with green rectangles is the same as solid line for days 1 and 2. In day 3 crown activity is unlimiting but environment is 50% limiting and the rate declines rapidly. After day 3 there is no limitation and the rate declines gradually as in upper line but at lower rates. The line with blue ellipses represents the rate changes when crown activity is 50% limiting for all days and environment becomes 50% limiting only in day 3. Dashed lines with shading surround rate changes for day 3 when environment became 50% limiting for only that one day.

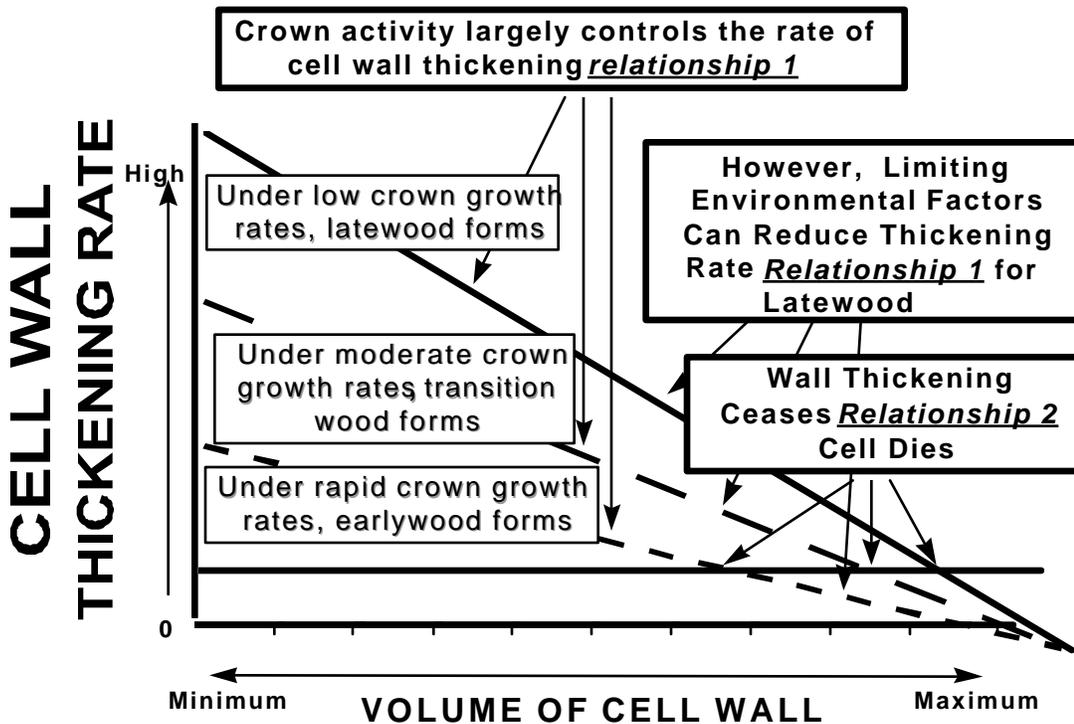


Figure 6. A diagram of the functions that control cell-wall thickening. Crown activity largely controls wall thickening, relationship 1. If crown growth is rapid, the rate of wall thickening is low and declines with increasing volume of the cell wall and earlywood is produced. When the rate of crown growth diminishes past a threshold condition, the initial wall thickening rate increases reaching maximum rate under very low crown growth rates. Only under conditions of latewood formation can environmental factors reduce the rate of wall

thickening. When the wall thickening rate is lower than a critical rate, thickening stops, the protoplasm disappears and the tracheid cell dies.

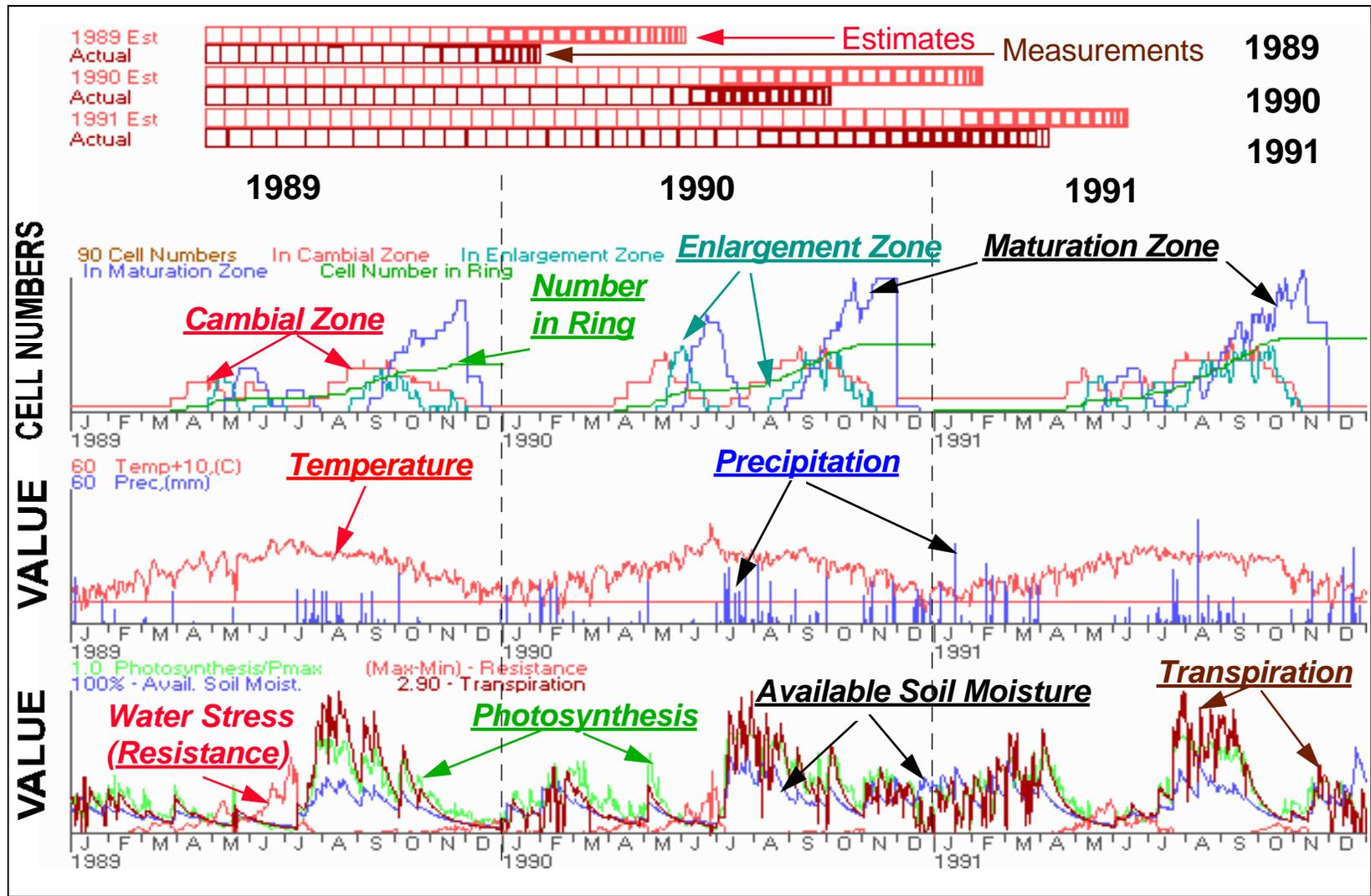


Figure 7. An example of the output generated on the computer screen except this version is rendered in black and white instead of color. The estimated and measured cell sizes and wall thicknesses for 1989-1991 are shown in the diagram at the top. Cell numbers in different cambial zones, daily climatic conditions and rates of several whole-tree process are shown in the three panels below.

6/9/98 TreeRing - Fritts, Shashkin and Downes