Climatic variation and tree-ring structure in conifers: empirical and mechanistic models of tree-ring width, number of cells, cell size, cell-wall thickness and wood density

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ABSTRACT: Variations in tree-ring structure are simulated with (1) an empirical model using monthly climatic data as statistical predictors and (2) a mechanistic model using daily climatic data as growth limiting conditions. The empirical model calibrates standardized ring-width and density chronologies of tree-rings with monthly temperature, precipitation or Palmer Drought Severity Index. The empirical model can be used with any tree-ring and climatic data set to evaluate linear, curvilinear or interactive relationships, to examine different types of calibration procedures, to calculate growth response to climatic factors, to compare the responses of different data sets, to examine a number of environmental questions about climatic change and to detect possible effects of altered environmental conditions on growth such as those caused by air pollution. The empirical model is applicable to any species and site where there is a tree-ring chronology and a climatic record of sufficient length. The mechanistic model uses mathematical equations to simulate processes affecting cell size, cell-wall thickness and wood density variations for individual rings using precipitation, temperature and humidity measurements. Limiting conditions are estimated from temperature, day length and a calculated water balance. The mechanistic model has been validated for *Pinus sylvestris* L. from dry sites in south Siberia and for *P. ponderosa* Laws. from southern Arizona. The results from both models are instructive as to what factors are important to the growth of different ring structures and when these factors become limiting. While the models will be developed further, they have already contributed to an understanding of tree-ring and climate relationships and have provided a number of answers to certain environmental questions. The empirical model is used in tandem with the mechanistic model to obtain important insights on relationships that the mechanistic model calculations lack.

INTRODUCTION

Trees monitor environmental conditions that limit their biological processes, and this information is stored in the structure of the annual ring (Fritts 1976, Schweingruber 1988). Dendrochronology is a developing science dealing with annual and seasonal variations in tree-ring structures that have been precisely dated and arranged in annual time series (Fritts 1976, Schweingruber 1988).

Dendrochronological data are now recognized as important sources of information on (1) past, present

and future climatic changes (Fritts 1976, Hughes et al. 1982, Brubaker & Cook 1983, Briffa et al. 1990, Cook & Kairiukstis 1990), (2) ecological changes in forest communities (Fritts & Swetnam 1989), (3) past geomorphic variations including earthquakes (Scuderi 1984, Jacoby et al. 1988), landslides (Schweingruber 1988) and volcanic activity (LaMarche & Hirschboeck 1984, Yamaguchi 1985, 1986, Baillie & Munro 1988, Scuderi 1990), and (4) a variety of geophysical questions, such as possible biotic effects of rising atmospheric CO₂ (LaMarche et al. 1986, Kienast & Luxmoore 1988), isotopic variations (Pilcher 1990), large-scale global

circulation patterns (Fritts in press), solar variability, (Stockton et al. 1985) and climatic change (Briffa et al. 1990, Fritts in press).

Dendrochronological data are now being systematically collected and archived for many land areas of the world (Stockton et al. 1985), and modern and sophisticated statistical techniques (see Chapters 3, 4 and 5 in Cook & Kairiukstis 1990) are being used for their analysis. Yet many existing models of forest growth (Dixon et al. 1990, Graham et al. 1990) do not consider the information on climate growth relationships that could be obtained from dendrochronological analysis (Fritts 1990).

MODELING TREE-RING CLIMATE RELATIONSHIPS

Models are formal representations of ideas, concepts, principles or applications of a discipline. They may be simple statements and diagrams of relationships (Wilson & Howard 1968, Fritts 1976), or they may be more complex representations of entire systems involving mathematical expressions and computer simulations (Gay 1989, Dixon et al. 1990, Graham et al. 1990, Stout et al. 1990). According to Jeffers (1988), 'The advantages of formal mathematical expressions as models are: (1) they are precise and abstract; (2) they transfer information in a logical way; and (3) they act as an unambiguous medium of communication.' Our paper describes 2 mathematical models, which can be used in tandem or separately to investigate relationships or to predict and evaluate alternative outcomes involving climatic conditions governing dated tree-ring structures.

These structures include earlywood, latewood and annual ring width, cell size, cell-wall thickness and density of the wood, all of which can vary markedly from year to year. Variations in all of these structures can be related to variations of physiological processes within the trees that govern division, enlargement and differentiation of growing cells in the xylem (Wilson 1964, Wilson & Howard 1968, Kozlowski 1971, Fritts 1976, Kramer & Kozlowski 1979). The initial modeling efforts use dendroclimatological materials that have come from climate-stressed sites (Fritts 1976, Schweingruber 1988, Fritts & Guiot 1990, Vaganov 1990). Thus, we have included many dendroclimatic procedures and have emphasized relationships between growth and limiting environmental conditions that are linked to variations in macroclimate (Fritts 1976). Now we are expanding the model to include more forest processes and ecological relationships including competition and productivity of the site.

However, all simulated relationships are based upon:

(1) well-known physiological principles involving cambial growth described in a variety of works including Lyr et al. (1967), Kozlowski (1971), Running et al. (1975), Fritts (1976), and Kramer & Kozlowski (1979); (2) published data on growth rates, cell production and cell-size variations throughout the growing season (Oppenheimer 1945, Bannan 1955, Smith & Wilsie 1961, Larson 1963, Kramer 1964, Wilson 1964, Zahner et al. 1964, Whitmore & Zahner 1966, Zahner 1968, Skene 1969, Wodzicki 1971, Denne 1976, Thompson & Hinckley 1977, Ford et al. 1978, Berlyn 1982); and (3) results from our own experiments on seasonal growth and tree-ring structure (Fritts 1976, Vaganov et al. 1985, Vaganov 1990).

The model calculations begin with either monthly or daily climatic data. An empirical model, called PRECON (for PRECONditioning) uses multivariate techniques to calibrate monthly temperature, precipitation and Palmer Drought Severity indices, PDSI (Palmer 1965), with standardized annual ring measurements, such as total width, earlywood width, latewood width, maximum density and minimum density (Fritts 1976, 1982, 1990, Fritts & Swetnam 1989, Fritts & Guiot 1990). A mechanistic model, called TRACH (for the TRACHeIdogram described by Vaganov 1987, 1990), reads daily temperature and precipitation measurements for each year and uses mathematical equations to translate this information into (1) a daily water balance, (2) factors limiting cell growth, (3) daily changes in cell size, wall thickness and density and, finally, (4) cell size, wall thickness and wood density of one radial file of cells in the xylem. The programs are written in ANSI standard FORTRAN and compiled under Ryan McFarland FORTRAN 2.4 to run under DOS (Ryan McFarland Corporation, PO Box 20045, Austin, TX 78720-0045, USA). Data for graphics are written in ASCII code for input to Graph-In-The-Box Analytic, New England Software, Greenwich Office Park # 3, Greenwich, CT 06831, USA.

PRECON: STATISTICAL ASSESSMENT OF FACTORS AFFECTING CHRONOLOGIES OF ANNUAL RINGS

General description

Dendrochronologists have utilized multivariate regression models to evaluate tree-ring and climate relationships (Fritts 1976, Lofgren & Hunt 1982) such as:

$$\hat{y}_i = \sum_{k=0}^K x_{i,k} \beta_k + a + \varepsilon_i \quad (1)$$

where $x_{i,k}$ are k statistical predictors representing climatic variables for year i , which are used to estimate

y_i , a ring-width index. β_k are the regression coefficients, a is a constant and ε_i are the residuals from the regression estimate (Fritts 1976, Hughes et al. 1982, Stockton et al. 1985, Fritts & Guiot 1990).

Multivariate models enable scientists to explore a number of dimensions of a relationship simultaneously, and one of the dimensions can be time (Jeffers 1988). The general linear form of the assumed relationships and their interpretation were based on field investigations of physiological processes and direct measurements of growth (Fritts 1969a, 1976, Fritts et al. 1965, 1979). Also, more complex relationships than shown in Eq. (1) can be modeled. Response function and transfer function models developed by Fritts et al. (1971) use principal component analysis and canonical regression to help resolve colinearities among predictor variables (Fritts 1962, 1967, 1969a, 1969b, 1974, 1976, Schweingruber et al. 1978, Fritts et al. 1979, Brubaker 1980, Fritts & Gordon 1982, Guiot et al. 1982, Gray & Pilcher 1983). Statistical estimates from such models are the bases of many dendrochronological procedures and practices currently in wide use (Fritts 1976, Hughes et al. 1982, Brubaker & Cook 1983, Schweingruber 1988, Cook &

Kairiukstis 1990). More recently, Kalman filters have been introduced as a method for evaluating time variation in the growth response (Visser 1986, Van Deusen & Koretz 1988).

Data input

A variety of statistical algorithms have been assembled in PRECON. The model reads 1 or 2 tree-ring chronologies from files provided by the model (Fig. 1) or imports chronologies written in the format of the International Tree Ring Data Bank (Bauer 1990). Thus any tree-ring chronology in the world written in this standard format can be analyzed. All ring measurements have been dendrochronologically dated and the gradual trends in growth due to age and site changes have been removed to obtain a time series showing the tree-growth climatic response (Fritts 1976). The mean value of these annual responses from a sample of trees collected from a particular species and site is called a chronology (Fritts 1976).

If chronology files are selected from those provided by the model, the names and site statistics of each

OVERVIEW OF PROCEDURES IN THE EMPIRICAL MODEL

SELECT AND READ width/density measurements as standard/residual index from:

1. Two sets of North American ring-width chronologies, climate data
2. Three sets of European ring-width and density chronologies, climate data
3. International Tree-Ring Data Bank chronologies
4. Imported tree-ring and climatic data

CALCULATE correlations and stepwise multiple regression

CORRELATION MENU

1. Plot correlations, time series or scatter plots
2. Look at correlation coefficients and related statistics
3. Go to next menu

REGRESSION AND OTHER ANALYSES MENU

1. Plot regression coefficients, time series or scatter plots
2. Change the regression analysis
 - a. Arbitrarily change values of one or more coefficients
 - b. Change F-level - *changes confidence interval*
 - c. Change time interval for regression calibration - see figure 5
 - d. Introduce climatic change and recalculate growth - see figure 6
 - e. Transform variables - *assesses non-linearities*
 - f. Recalculate regression and/or exit to main program
3. Recalculate estimates without recalculating regression coefficients
4. Calculate response function - *principal component regression*
5. Use Zahner and Grier southern pine growth model
6. Calculate Kalman filter (*in process of being added*)
7. Compare or switch two time series
 - a. Estimate statistics of similarity
 - b. Switch variables - *allows for flexibility in analysis*
8. Save data, look at graphics or exit program

Fig. 1. Procedures in the empirical model read tree-ring and monthly climatic data, calibrate the growth response with variations in climate, allow examination and manipulation of the correlation, regression and response function relationships, simulate growth using a model by Zahner & Grier (1990) and analyze data with a Kalman filter. Five types of changes can be made and regressions recalculated, data sets can be exchanged for purpose of analysis and statistics of similarity can be calculated to test various hypotheses

chronology are scrolled across the screen. Default answers are supplied with each query of the model to assist the user in making reasonable choices. The chronology is selected by entering the abbreviated site name and species code shown on the screen and choosing the type of chronology. For imported data, only the file name is needed along with the input format, if the default format is not appropriate.

The model prompts for the required input data, such as the interval to be studied (up to 100 yr), the climatic variables to be read, the months to be assembled, the state code and climatic division. Monthly PDSI values as well as temperature and precipitation are available on disk for the USA; only the latter 2 variables are available for Europe. If European data are requested, the identification numbers, names and characteristics of available climatic records are scrolled across the screen. For Europe, a default climatic station is identified for each chronology, but the user can select any climatic record by entering a different station identification number.

Monthly data for 1 or 2 climatic variables can be selected from the 24 continuous months starting with the January record 1½ yr prior to growth and ending with the December record following growth. Temperature and precipitation for 14 mo starting in July of the prior year and ending with August are the default choices. In the current version, if 2 variables are chosen, the same months must be selected for both variables and a maximum of 19 continuous months (a total of 38 mo) is allowed.

Correlation menu

PRECON calculates the correlation coefficients between each monthly climatic variable and the selected chronology for the specified time interval and then runs a stepwise multiple regression analysis on the same data set (Fig. 1). The values of the correlation coefficients can be plotted (Fig. 2a) or displayed on the screen along with the maximum, minimum and standard deviations of the observations. Plots of the actual, estimated and residual time series produced by the regression also can be displayed (Fig. 3a) as well as scatter plots showing the observations of one variable plotted against the observations of 2 other variables along with 2 splines fit to the clouds of data points (Fig. 4). Other options in the correlation menu can save the data or exit to the regression menu*.

* After leaving the correlation menu, the simple correlations cannot be manipulated and the response profile of simple correlations cannot be plotted

Fig. 2. Three representations of the modeled growth response are applied to a 68 yr chronology of *Pinus ponderosa* from Walnut Canyon, Arizona, that was calibrated with monthly temperature and precipitation for Arizona Division 7 for 14 mo beginning with July and ending with August, when ring width growth was 95 % complete (Fritts 1976). (a) Simple correlation coefficients (values to ± 0.24 are significant, $p = 0.95$) which show ring width to be inversely correlated with temperature and directly correlated with precipitation for all but the last August; (b) the 9 significant stepwise multiple regression coefficients, which are the minimum number of predictor variables explaining 75 % of the variance of ring-width index; and (c) response function coefficients, obtained from regression with principal components of climate, that help resolve colinearities among the predictor data sets. 57 % of the ring-width variance is explained by climate and 21 % explained by prior growth (total 78 %). Boot-strap methods had not been implemented when this plot was generated, so the confidence level used to test the coefficients are lower than 0.95 %

Fig. 3. Time series modeled as in Fig. 2 except that temperature and PDSI values for 15 mo from July to September were used to estimate the ring-width index. (a) Using stepwise multiple regression as in Fig. 2, including 2 variables, with the estimate accounting for 64 % of the actual ring-width variance; (b) using the Zahner & Grier growth model with the estimate accounting for 57 % of the actual ring-width variance. A comparison of the residuals shows remarkable agreement between the statistical assessment and the Zahner & Grier simulation

Regression and other analysis menu

All significant stepwise regression coefficients can be plotted in the same format as the correlation coefficients allowing one to make comparisons between these 2 types of statistics (Figs. 1 & 2b). Time series and scatter plots can be created as in the correlation menu. Option 2 offers a submenu, called the change menu, which is used to change the regression equation (Fig.

1). This menu is described in the following section. Also, option 3 is usually used with the change menu, so it will be described in that section.

Option 4 performs a response function analysis (Fritts et al. 1971, Fritts 1974, Guiot et al. 1982, Fritts & Wu 1986, Cook & Kairiukstis 1990) of the selected data sets, which uses principal component regression of climatic variables along with prior growth to help resolve colinearities between the monthly temperature and precipitation data sets (Fig. 2c). A boot-strap method, described in Fritts & Guiot (1990), was recently added with the help of J. Guiot. The boot-strap method uses Monte Carlo simulation techniques to estimate the standard errors of the response function weights, and thus provides a robust significance test. This change meets some recent criticisms of the response function approach (Cook & Kairiukstis 1990, Fritts 1990) and makes it a viable alternative to stepwise regression.

Two other alternatives to stepwise multiple regression analyses can be modeled. The first (option 5; Fig. 1) is a simple growth model described for southern pines (*Pinus taeda* L., *P. echinata* Mill., *P. palustris* Mill., and *P. elliotti* Engelm.) by Zahner & Grier (1989), which uses climatic impact factors with scalars that are multiplied with monthly PDSI values to estimate ring-width index (Fig. 3b). The original Zahner & Grier model was designed only for 3 climatic zones in the eastern USA. The PRECON implementation extends the model to lower montane, upper montane, and subalpine zones from the western USA, which have progressively shorter growing seasons with increasing altitude as shown in Table 1*.

The growing season ranges from 8 mo in the south to 4 mo in the subalpine zone, and the relative importance of the monthly PDSI values in the simulation is pro-

* The addition of these 3 zones in the western USA applies the model to situations beyond those investigated by Zahner & Grier. Since their model was not designed or validated for these 3 zones, any estimates for these western climatic zones should be used with extreme caution and full acknowledgment of these limitations

Fig. 4. Scatter plots of any variable against 2 other variables can be used to identify non-linearities and to detect the presence of outliers in the data sets. The same data are used as in Fig. 2 with actual ring-width index plotted against February temperature and precipitation. Both relationships appear linear with no extreme values evident

Table 1. Relative importance of PDSI in the simulation of ring-width index, expressed as fractional percent

Climatic zone	Month							
	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
Western USA ^a								
Subalpine	0	0	0.050	0.300	0.500	0.150	0	0
Upper montane	0	0	0.100	0.300	0.400	0.180	0.020	0
Lower montane	0	0.050	0.160	0.280	0.300	0.150	0.060	0
Southeastern USA ^b								
Northern	0	0.120	0.260	0.255	0.210	0.120	0.035	0
Middle	0.040	0.170	0.230	0.210	0.170	0.110	0.060	0.010
Southern	0.085	0.180	0.190	0.175	0.150	0.115	0.075	0.030

^a Based on growing season observations for southwestern USA using data from Fritts (1976)

^b Based on growing season observations for eastern USA described by Zahner & Grier (1990)

portional to the fractional percentages associated with these months. The Zahner & Grier simulations are plotted and can be compared to other types of analysis (Fig. 3). As other modules are added to PRECON, more types of comparisons can be made.

The second alternative (option 6; Fig. 1) uses the Kalman filter (Visser 1986, Van Deusen & Koretz 1988) which allows the response to climate to vary through time. Examples were unavailable at the time of this writing, so they were not included here.

Option 7 was added so that a second data set (such as the output from the mechanistic model or another tree-ring chronology) could be entered and compared to the actual, estimated, residual or altered data sets. To facilitate comparison, the option can be used to exchange the data sets by switching their relative positions in the data array at any time in the analysis. For example, one might run the Zahner & Grier model, exchange the residuals from the estimates with the actual index data, and then run the stepwise multiple regression to determine whether factors other than PDSI are important contributors to growth. The output from the mechanistic model can be compared directly to ring-width indices using this option, and the mechanistic model results analysed as if they were actual ring-width indices.

Other options provide for viewing the plots, saving the data, writing input data for the mechanistic model and terminating the analysis.

Change menu and related options of the regression menu

The change menu, option 2 under the 'Regression and other analysis menu' (Fig. 1), provides additional options and more flexibility in the analysis. Item (a) displays the values of the partial regression coefficients along with maximum, minimum and standard deviations of the observations and allows for changing the coefficient values or removing them. By changing a

coefficient, exiting the change menu and recalculating the estimates with the altered coefficients (option 3), the coefficient sensitivity can be investigated or 'what if?' questions about the importance of particular variables can be tested.

(b) (Fig. 1) allows changing the *F*-level for entering variables into the stepwise regression. This affects the probability level and increases or decreases the number of variables entering the regression.

Item (c) changes the time interval used in subsequent calculations. It can be used to examine pollution effects by changing the interval to the time before pollution began, recalibrating the growth and climate relationship over that interval, increasing the interval to include the remainder of the tree-ring record and using option 3 to extrapolate the calibrated relationship over that time period (Fig. 5). This estimates the effect of climate on growth over the pollution period, assuming no other factor has become limiting (Cook et al. 1987). A departure of actual growth from the estimated growth (Fig. 5) over the projected period suggests that something else has changed. Also, this part of the model can be used to assess possible effects of atmospheric CO₂ enhancement, fertilizer treatments, site disturbance and fire on growth.

Item (d) can introduce a gradual climatic change for a specified time interval or a sudden change starting with a particular year. Other types of climatic change can be modeled as needed. The annual effect of the climatic change on growth is calculated as:

$$\hat{y}_i = \sum_{k=0}^K (x_{i,k} + c_i) \beta_k + a + \varepsilon_i \quad (2)$$

where y , x , β and ε are the same as in Eq. (1) and c is the specified climatic change (Fig. 6). The change can be confined to 1 or 2 continuous seasons or applied to the annual period. The difference between 'Estimated index' and 'Change on index' (Fig. 6) estimates the growth change attributed to that particular climatic change for the sampled species and site.

Fig. 5. Item 2c in the 'Regression and other analysis menu' (Fig. 1) allows calibration over one time period (1896 to 1940) and extension of the calibration into another time period (1941 to 1984) to evaluate possible pollution effects on ring-width index. Similar analyses include growth enhancement from rising atmospheric CO₂ or influences of environmental or site factors on ring-width index. Data are for *Pinus ponderosa* in the Santa Catalina Mountains, north of Tucson, Arizona, where emissions after 1940 from distant copper smelters appear to have reduced growth. This possible pollution effect had not been recognized (Graybill & Rose 1989) until the PRECON empirical model was applied to the data set

Fritts & Dean (unpubl.) applied the climatic change module to examine the hypothesis of Peterson (1988) that unusually low summer temperatures caused the prehistoric abandonment of Chaco Canyon, New Mex-

ico. It was also well known that the widths of rings in trees growing during that time period decreased. Tree-ring chronologies growing in the same region were calibrated with 20th century temperature and precipitation records and then a decrease in summer temperature was modeled. Temperature was inversely related to ring width in all cases, and ring widths were modeled to increase, not decrease in response to a decline in temperature. It was concluded that summer temperatures during the time of abandonment were higher rather than lower and that high temperatures associated with drought, not low temperatures, were responsible for abandonment.

Grissino-Mayer & Fritts (in press) applied the change module to evaluate the future growth of a relict stand of *Picea engelmannii* growing on Mount Graham, Arizona, if greenhouse warming occurs as suggested by climatic models. Rising temperatures were simulated to increase ring widths in trees on a north-facing slope but to decrease ring widths in trees on a south-facing slope, where low soil moisture rather than low temperature is more likely to be limiting.

Fig. 6b is a similar analysis of a maximum density chronology from *Pinus sylvestris*, Pyhntunturi National Park, Finland. It examines the hypothesis of Briffa et al. (1990) that a regional greenhouse warming will not be detectable from Fennoscandia tree rings until 2020. A projected change of 0.04 °C yr⁻¹ was simulated for 50 yr, and it increased maximum density by only 0.21 index units, which is only 1.29 standard deviations of the maximum density chronology. The small response is consistent with the Briffa et al. conclusions, but more than one chronology should be analyzed and other statistics examined, to make a thorough test of this hypothesis.

Item (e) (Fig. 1) can be selected to generate a variety of non-linear transformations, calculate interactions, combine several variables to obtain seasonal averages and then make new calibrations. The model solves the equations showing significant curvilinear interactions and displays 3-dimensional relationships as shown in Fig. 7.

Fig. 6. Item 2e in the 'Regression and other analysis menu' (Fig. 1) can introduce a progressive or sudden climatic change and calculate its separate effect on the chronology ring-width index. Dashed-dot lines indicate the climatic change that was modeled, dashed lines are the estimates from climatic data (Fig. 3) and the heavy solid lines are simulations with the hypothesized climatic change added to the relationship. The difference between the dashed and heavy solid lines reflect the effect of climatic change on ring-width index. (a) Same data as in Fig. 2 but with a progressive decrease in percentage of precipitation simulated for 1930 to 1950; (b) data are for maximum density of *Pinus sylvestris* from Finland with temperatures hypothesized to rise by 0.04 °C yr⁻¹ during 1820 to 1970 (see text for explanation). Ring width indices of Arizona *P. ponderosa* may be substantially reduced by relatively small deficits of annual precipitation, but maximum density indices from *P. sylvestris* in Pyhntunturi National Park, Finland, appear less responsive to a 2 °C temperature rise

Fig. 7. Significant interactions and curvilinear relationships can be modeled and plotted. The equation for each interaction was solved by varying one variable at a time over units of one standard deviation. This interaction between winter precipitation and temperature for August at the end of the growing season was found to be a significant predictor of ring width in *Picea engelmannii* growing at 3000 m on a south-facing slope of Mt. Graham. In this example, August temperature was held at -2 standard deviations (solid line) while precipitation values from -2 to $+2$ standard deviations were substituted into the equation and the resulting growth was plotted. The procedure was repeated for temperatures at -1 , 0 , $+1$ and $+2$ standard deviations (dashed and dotted lines). Low winter precipitation may be interpreted to be most growth-limiting when high August temperatures accentuate internal water stress. However, high winter moisture can also be growth-limiting through its effect on snow pack, delaying initiation of growth, shortening growing season and reducing ring width. In the latter case, soil moisture reserves are adequate from high winter precipitation, so that low rather than high temperatures in August become growth-limiting by slowing down cell division, hastening the end of the growing season and contributing to reduced ring width. Such interactions and curvilinear relationships are important for accurate appraisal of climatic change effects

TRACH: MECHANISTIC SIMULATION OF RING STRUCTURE

Transformation of initial climatic data

Fritts (1976) presents schematic diagrams of a model relating variations in precipitation and temperature to variations in plant processes affecting ring-width. The mechanistic model (Fig. 8) is an attempt to replace this model with mathematical equations that govern these relationships. The modeling work began with the tracheidogram method of tree-ring analysis described by Vaganov (1990), which is concerned with cell size variations across the rings. The first version was a computer model developed by Vaganov et al. (1985), which uses daily climatic data to reconstruct cell size variations and related histometric properties of the annual ring.

In the current version, temperature is modeled as an important limiting factor through its effect on respiration and assimilative growth processes, as well as its effects on transpiration, evaporation from the soil and cell water stress (Kramer & Kozlowski 1979). Mean daily temperature measurements are used because they approximate the integrated effect of temperature variations over the day and also are standard meteorological measurements. Daily mean temperature data are converted to degrees Celsius and are used as model input without further transformation. Degree-day calculations are used to initiate cambial activity. Maximum, minimum, day and night temperatures and degree-day calculations will be used in future versions

of the model to characterize photosynthesis, respiration, damage from frosts and other growth-controlling factors.

Water storage in the soil and its availability throughout the season also regulates cambial activity and cell growth. Only a few direct measurements of water storage are available from meteorological records, and usually they are from stations far from forest sites. Measurements of precipitation are more widely available, but they do not portray the soil water dynamics that limit processes controlling growth. Thus, precipitation is converted to a soil-water balance using temperature and humidity deficit to calculate the daily evapotranspiration losses (Fig. 8).

The water balance (W_t) for Day t is calculated as:

$$W_t = W_{t-1} + k_6 P_{t-1} - k_5 F(T_{t-1}^\circ, e_{t-1}, W_{t-1}) \quad (3)$$

where W_{t-1} = water balance on the previous day; P_{t-1} = precipitation on Day t ; k_6 = coefficient of available precipitation (the portion of total daily precipitation that enters the soil); k_5 = coefficient of water loss from evapotranspiration; and $F(T_{t-1}^\circ, e_{t-1}, W_{t-1})$ is a function that describes the water losses by evapotranspiration and depends upon temperature T_{t-1}° , air water deficit e_{t-1} , and water storage on the previous day.

The model calculations are:

$$W_t = W_{t-1} + k_6 P_{t-1} - k_5 e_{t-1} \ln(T_{t-1}^\circ/5) F(W_{t-1}) \quad (4)$$

where $F(W_{t-1})$ is the S-shaped curve approximated by a third order polynomial that represents experimental data describing the dependence of evapotranspiration on soil moisture storage as shown in Kramer & Koz-

OVERVIEW OF PROCEDURES IN THE MECHANISTIC MODEL

INPUT control parameters and daily climatic data

CALCULATE:

$$\text{Water balance } W_{t-1} + K_6 \cdot P_t - K_5 \cdot F(T_t, E_t, W_{t-1})$$

Calculate beginning of growth, daily limiting conditions

integrate effects over the season

USE TOTAL CELL PRODUCTION FROM PRECON AND LIMITING CONDITIONS TO:

1. Identify intervals of enlargement, wall thickening for each cell

2. Enlarge cell, thicken wall over allocated intervals, calculate density

PLOT CELL CHARACTERISTICS ALONG WITH VALIDATION DATA

Fig. 8. The mechanistic model reads in daily climatic data and uses mathematical equations to calculate a daily water balance to initiate and terminate the growing season and to calculate daily limiting conditions to cell size and cell-wall thickness growth. Limiting effects are integrated over the season and used to identify when and how fast each cell grows and when its wall thickens. After all cells enlarge and their walls thicken, various attributes of the simulation are plotted and validated using actual cell measurements. The water balance equation is shown and shapes of curves illustrate some of the important growth-environmental relationships (see text for explanation)

lowski (1979) (Fig. 9). Evapotranspiration rates increase from zero with maximum rates of change occurring at intermediate values. The maximum rate is attained at the upper soil moisture limit corresponding to field capacity, and no change in evapotranspiration rate occurs when soil moisture exceeds this upper limit. The values of this function are normalized so that they range from 0 to 1.

An alternative calculation is provided for cases where there is no estimate of air water deficit. K_5 is multiplied by the exponent of temperature divided by 5:

$$F(T_t^\circ, W_t) = k_5 \exp(T_t^\circ/5) F(W_{t-1}). \quad (5)$$

Fig. 9. Two growth response curves can be used to model the limiting effects of available moisture on cell enlargement and wall-thickening. The growth response varies from 0 to 1 with maximum growth at 75 mm and higher for relatively shallow soils and at 100 mm and higher for deeper loam soils. Any curve of the same general shape can be specified as input in new versions of the model

In the water balance calculation K_6 may be constant or variable. In the constant case, the proportion of the daily precipitation that is added to the soil is the same for all soil moisture conditions. In the variable case, K_6 depends upon the antecedent percentage of water in the soil (a greater proportion of precipitation enters the soil as soil moisture percentages approach zero). Fig. 10 shows the high agreement between soil moisture calculated by the model compared to the soil moisture calculated by Thornthwaite & Mather (1955, 1967) for the growing season of 1964 (see Fritts 1976).

Insolation data are rarely available for modeling work. Therefore, daylight duration and sun azimuth, which vary over the season and also depend upon latitude, are used to model systematic changes in environmental variables over the growing season.

Fig. 10. Modeled water balance for *Pinus ponderosa* in the Santa Catalina Mountains near Tucson compared to the Thornthwaite & Mather (1955) water balance. Both dry and wet periods are reproduced well

Growth-rate calculations

Temperature growth response. The temperature-dependent growth rate is modeled from experimental data summarized by Lyr et al. (1967), Fritts (1976) and Kramer & Kozlowski (1979) using 3 third-order polynomial curves with optimum responses at 12, 18 and 22 °C (Fig. 11).

The temperature response curves have the following characteristics:

- for temperatures $T_i < 5$ °C the growth response $V(T_i) = 0$,
- for temperatures 5 °C $< T_i < T_{opt}$ the growth response increases non-linearly with a gradual increase at the beginning, a rapid increase in the middle range and a gradual increase near the optimum,
- for $T_i \equiv T_{opt}$, the growth response $V(T_i) = 1.0$,
- for temperatures $T_i > T_{opt}$ the growth response decreases at an increasing rate until it reaches zero (due to the limitation of higher than optimum temperatures).

Water growth response. Growth is modeled to depend on the absolute value of soil moisture storage (expressed as mm of water contained in a 50 cm soil layer) using an S-shaped curve with field capacity at $V_{max} = 1.0$ (Fig. 9). The dependence for soil moisture is approximated by the same third-order polynomial used to estimate the water budget $F(W_{i-1})$. A different polynomial could be used if experimental data warrant it.

The soil moisture response curves have the following characteristics:

- if $W_i = 0$, the growth response $V(W_i) = 0$ (a threshold moisture, W_{min} , can also be selected so that if $W_i < W_{min}$ the growth response is zero),
- if $W_i > W_{min}$ the growth response $V(W_i)$ increases to a maximum value of 1.0 at the upper water limit, $W4$
- if $W_i > W4$, growth is unlimited so $V(W_i)$ is 1.0.

Fig. 11. Three growth response curves are used to model the limiting effects of average daily temperature on cell enlargement and wall-thickening. The growth response varies from 0 to 1 with maximum growth at 12, 18 and 22 °C. Any curve of the same general shape can be specified as input in new versions of the model

Now, a downward trend can be used to represent poorly drained conditions when $W_i > W4$ if field measurements warrant it. In the present model, the trees are assumed to be growing on well-drained sites where excessive moisture is not commonly limiting to growth.

Originally, variants with 2 different upper limits of the water growth response were available (Fig. 9). The upper limit, $W4$, was set at either 70 or 110 mm to allow for relatively loamy soils with a small or large range of available moisture. Now, the shapes of these curves can be specified by varying input variables.

Day length response. This parameter is used as an indirect representation of potential photosynthesis resulting from changes in day length, as well as the potential effects of day length on phenological behavior. The assumed growth response to day length $V(L_i)$ is linear:

$$V(L_i) = \beta (L_i - \tau) \quad (6)$$

where β and τ are empirical coefficients depending on latitude and tree species. In simulations for *Pinus sylvestris* L. from dry sites in south Siberia, we used values of day length in hours, and for *P. ponderosa* Laws. from southern Arizona we used values of day length in relative units from tables of Thornthwaite & Mather (1967). These data are now generated from the latitude of the site using physical equations.

The day-length response has the following characteristics: for the longest day in the year, June 22, $V(L_i) \equiv 1.0$; and for the equinox, September 22, $V(L_i) \equiv 0.0$ (in some cases a limiting day length of 13 rather than 12 h might be more appropriate).

Sun angle varies with latitude so the following equation was added and could be substituted for Eq. (6):

$$V(L_i) = \beta \cos \Theta (L_i - \tau) \quad (7)$$

where $\cos \Theta$ represents the highest sun angle at a given latitude for Day t . The limiting effects of day length can be scaled upward or downward by specifying a scaling factor, with 1.0 corresponding to no scale change from the above computations.

Common growth response. Finally, 3 different growth responses, $V_i(T_i)$, $V_i(W)$ and $V_i(L)$ are calculated for each day. The tree growth response is calculated in 2 ways. A multiplicative growth model is calculated as:

$$V_i = V_i(T_i) V_i(W) V_i(L). \quad (8)$$

A limited model is calculated as:

$$V_i = V_i(L) \min \{ V_i(T_i), V_i(W) \}. \quad (9)$$

The multiplicative model includes the effects of each environmental factor in the common growth response while the limited model includes the effect of only that

factor that is most limiting. These results are expressed in units of relative growth ranging from 0 to 1.0.

Transforming growth rate curve to cell-size estimates

The calculated growth-rate array is transformed into a cell-size array (called a tracheidogram) by the following procedure*:

$$D_j = a V_j + D_0 \quad (j = 1, \dots, n) \quad (10)$$

or

$$V_j = (D_j - D_0)/a$$

where D_j = cell size measured in the radial direction; V_j = relative growth rate; D_0 = initial cell size, which is the size of the cambial daughter cell after division; and a = a scaler.

At first the curve V_t is standardized for the duration of the growing period $M_2 - M_1$. M_1 and M_2 are input parameters of the program or M_1 may be estimated when the accumulation of a heat sum in degree-days starting with April 1 exceeds a specified value. Growth will not be calculated for days before the beginning date or after the end date even though environmental conditions may be favorable. The standardized tracheidogram is constructed for N cells as specified from program PRECON or entered by the user. If input from PRECON is requested, either the actual index, estimated index or index resulting from climatic change can be selected. An average radial dimension for cell size (ACS) of 20 μm (the value for *Pinus ponderosa*) is assumed unless the user enters a different value. At present an average ring width of 1000 μm is also assumed, but this parameter may also be programmed to change with the productivity of the site, tree age, crown class, stand stocking conditions or other factors affecting ring width.

Ring width (RW) is calculated as:

$$RW = I/ARW \quad (11)$$

where I = the selected ring-width index value, and ARW = the average ring width.

The cell number is calculated as:

$$N = RW/ACS - 24.5 \exp(-0.005 RW) + 1 \quad (12)$$

based on the relationship shown by Terskov et al. (1981).

The value of V , the integrated growth response, is obtained as:

$$(V_1, V_2) V = (1/N) \sum_{t=M_1}^{M_2} V_t \quad (13)$$

where the integral for V is the sum of $M_1 - M_2$, the beginning and end of the growing season portioned out to the interval of favorable growing conditions assigned to the cell. Thus, each cell in the time sequence is formed during a period of $1/N$ of the total integral. The calculations are made at time steps of 0.05 d and one cell is formed at time (t), terminating whenever the consecutive summation equals a multiple of V corresponding to the transition to the next cell.

Cell size is calculated as in Eq. (10):

$$D_j = D_0 + (RW - ND_0)/V T_j \quad (14)$$

where $D_0 \equiv 7.0 \mu\text{m}$ and T_j is the time interval of cell j growth during which

$$\sum_{t=k}^{k+T_j} V_1 t \equiv V, \quad k = M_1 + \sum_{i=1}^{j-1} T_i \quad (15)$$

and

$$\sum_{j=1}^N T_j = M_2 - M_1.$$

Cell-wall thickness calculations

Cell-wall thickness (CWT) in the radial direction is calculated using the experimental relationship noted for *Pinus sylvestris* by Vaganov et al. (1985) (Fig. 12a). If the cell sizes range between D_0 (ca 2.0 μm) and some intermediate value, D_c , CWT_j is directly correlated with cell size (D_j) as follows:

$$CWT_j = 0.25 D_j. \quad (16)$$

When cell sizes exceed D_c , CWT_j decreases with increasing D_j in the following manner:

$$CWT_j = 0.00722 \exp(-0.134 D_j (D_j)^{3.27}). \quad (17)$$

This is a negative exponential relationship based upon measurements obtained from *Pinus sylvestris* from dry and wet sites in the southern part of the Krasnoyarsk region. Since D_c is closely correlated with the number of cells in the ring ($r = 0.74$), it is evaluated using that number to obtain $CWT_{\max}$ for each yearly data set. CWT_j is calculated from Eq. (16) if $D_j \leq D_c$; otherwise it is calculated from Eq. (17).

This relationship was modified to accommodate measurements from *Pinus ponderosa* (Fig. 12b) where small thin-walled earlywood cells were often associated with mid-season drought. A similar modification also may be applied to subarctic tree-rings where 'light latewood' appears to be associated with thin-walled latewood and a cold summer climate (Filion et al. 1986). In this modification, normal latewood for $D_j \leq D_c$ has the same dependence as Eq. (16), and Eq. (17) is used to estimate the maximum CWT_j associated with D_j for *P. ponderosa*. Under drought conditions early in the

* The reverse procedure of converting cell-size measurements to growth-rate is described by Vaganov et al. (1985).

Fig. 12. Cell-wall thickness plotted against cell diameter in the radial direction. (a) For *Pinus sylvestris* with wide rings from the southern part of the Krasnoyarsk region, USSR (Vaganov et al. 1985); (b) for *P. ponderosa* with a 'false ring' in 1964 from southern Arizona (see Figs. 17 & 18); (c) theoretical description of cell-wall simulation for *P. ponderosa*, variant 1 for normal earlywood and latewood and variant 2 for *P. ponderosa* earlywood under drought conditions; and (d) simulated values for the 1964 season

season, CWT_j is less than this maximum value which is evaluated from the inverse of V_t (Eqs. 8 and 9) but using a later time period from that used to calculate CS_j . This delay in the CWT response averages 11 d for *P. ponderosa* but can be changed by the user. The delay represents the interval of time required for maturation (cell-wall thickening) to occur, and in this version of the model it is assumed to be constant over the entire growing season. This must be changed to vary the interval over the growing season. More cell-wall thickness measurements are being collected to help refine this part of the model.

The following steps are used in the calculation:

(1) Estimate the mean growth rate $\bar{V}_j(t + \delta t)$ for cell enlargement where t is the day when cell enlargement is complete and δt is the time delay;

(2) Calculate the inverse value, $1.0 - \bar{V}_j(t + \delta t)$, so that favorable conditions for cell-wall thickening are estimated when conditions are unfavorable for cell enlargement and

(3) Calculate the real CWT_r as:

$$CWT_r = CWT_{min} + \delta CWT (1 - \bar{V}_j(t + \delta t)) \quad (18)$$

where CWT_{min} is the minimal value of CWT (ca 2.0 μm) and the terms to the right represent the different between the CWT estimated from Eqs. (16) and (17) and CWT_{min} reduced in proportion to soil moisture, temperature or light conditions that are limiting. Fig. 12 shows the cell size and cell-wall thickness relationships used in the model.

Density calculations

The 2 simulated cell characteristics, CS and CWT , are then used to obtain density estimates. Three assumptions are necessary to make the calculations:

(1) The mean tangential diameter of the cells, D_T , is relatively constant;

(2) D_T is ca 30 μm ;

(3) The cell-wall thickness is the same on all sides of the cross section.

Density (optical density), DEN_j , of each cell is calculated as:

$$DEN_j = 1.0 - (D_j - 2.0 CWT_r) / (D_T - 2.0 CWT_r) / (D_T D_j) \quad (19)$$

where D_j , CWT_r and D_T are the same as defined above. The physical wood density, DEN_w , can be estimated as:

$$DEN_w = 1.5 DEN_j \quad (20)$$

where 1.5 is the density of wood substance. A wood density trace is simulated by converting the x-axis from cell number to distance from the ring boundary. The data are automatically written to files that can be read by the graphics program, plotted on the screen or sent to the printer

* This was the value obtained from 10 000 measurements of tangential diameters from *Pinus sylvestris* growing on both dry and wet sites south of Krasnoyarsk (Vaganov et al. 1985) and is reasonable for *P. ponderosa*.

Other TRACH features

Other features of the TRACH model should be noted. The model is based on a relatively small number of parameters which may be changed or selected depending upon the conditions and species to be simulated. They are:

- 3 temperature curves with different T_{opt} ;
- base-level for calculating heat-sum;
- total heat-sum to initiate growth;
- the proportion of precipitation entering the soil, K_6 , which may or may not vary with soil moisture;
- the coefficient of water loss, K_5 (multiplier for evaporation);
- initial soil moisture, W_0 ;
- 2 levels of maximum available soil moisture, W_4 , where growth is optimum;
- humidity deficit which may be read in or estimated;
- a scaled day length value with or without azimuth;
- beginning of growth which may be specified or calculated from the total heat-sum;
- end of growth;
- cell numbers and ring width estimated from index data in PRECON or specified by the user;
- average cell size to model (not needed if width and cell numbers are specified by the user); and
- smooth growth or temperature data using an arithmetic 7 d average, a one-sided (7 d) filter or a longer one-sided (12 d) filter.

Different values must be assigned to these parameters to model either limiting or enhancing environments for trees of different species or trees growing in different habitats. We selected default values to be the optimal parameters for *Pinus ponderosa* in southern Arizona. Independent water balance estimates, measured cell sizes and wall thicknesses are used to validate these results and tune the model. The means, mean squares and total mean squares of the differences between actual measurements and simulations are calculated and used in evaluating different input parameters.

Examples of TRACH model results on *Pinus sylvestris*

The first TRACH model was tested and tuned using climatic data and measurements from *Pinus sylvestris* growing in the southern Krasnoyarsk region of the USSR. All results were standardized to 30 cells to facilitate comparisons among rings of varying width. Daily climatic data from Bogard, 6 km from the trees, was used in the simulation. Analyses began with May 1, but the actual duration of the growing season was calculated as the continuous period of days for which the simulated growth rates were greater than zero. The

Fig. 13. Comparison of measured and modeled radial cell-sizes for *Pinus sylvestris* from the southern part of the Krasnoyarsk region, USSR, during different growing seasons

seasonal curves of temperature and air humidity dynamics were smoothed before analysis. The initial soil moisture was unknown, so 3 different values of initial soil moisture were used. All other conditions were the same. The initial values for the curves with the lowest root-mean-square deviation between the tracheidograms of the simulations and measurements were selected.

Fig. 13 includes the calculated and measured cell sizes from 6 rings formed during different growing seasons. The calculated data correlated well with the measured data both qualitatively and quantitatively. The simulated growing seasons began about May 15 and ended about August 15. From June 1 to July 15, 75 to 85 % of the cells in the ring were produced. Variations in cell size later in the growing seasons appeared to be related to variations in soil moisture. Small cells in the latter half of the ring were associated with simulated drought, while large cells were associated with unusually moist conditions. In general, there is a rapid increase in growth at the beginning of the season followed by a progressive decline in growth associated with the transition from earlywood to latewood.

The simulations indicated that soil moisture storage at the beginning of the season plays a dominant role in determining cell-size variations throughout the annual ring. Thus, a realistic estimate of the water balance from precipitation and temperature is an important model consideration.

Fig. 14. Modeled seasonal dynamics of (a) soil moisture storage, (b) relative growth rate for *Pinus sylvestris* and (c) cell-size variations at low and high initial soil moisture. A simple change in initial soil moisture created large cell-size differences. The simulated growing season continued for 110 d in both cases and cell numbers were converted to 30 cells by standardization (Vaganov 1990) to facilitate comparison

Fig. 14 shows the results of 2 calculations by the model made for initial conditions of high and low soil moisture. The season was cold at the beginning and warm and dry later. All precipitation and temperature conditions were the same for both simulations. The growth rate curves (Fig. 14b) were qualitatively similar for both sets of conditions with a rapid increase in growth rate early in the season, a decline in rate during mid-season and an increase in rate near the end of the season associated with rains falling during that period. However, the cell sizes along the radial direction of the simulated tree rings (Fig. 14c) were considerably different for the 2 moisture conditions. With low initial soil moisture, sizes diminished from Cell 3 through Cell 19 because low soil moisture became more limiting than low temperature beginning with Day 8 and continuing until Day 80 of the growing season when soil moisture was replenished. A 'false ring' was simulated from this combination of low and high soil moisture. With high initial soil moisture, sizes increased until Cell 12 and

then decreased until Cell 25, because early in the season growth rates were limited less and less by temperature and unlimited by moisture. Later, as soil moisture declined, growing conditions became more and more limiting. However, the change in growth associated with rainfall and increased moisture late in the season was insufficient to produce a well-defined 'false ring' structure.

Further model analyses of *Pinus sylvestris* produced qualitatively similar results with moderate variations in climatic conditions. For example, a brief but severe drought early in the growing season, associated with low initial soil moisture conditions, produced a similar tracheidogram of cell-size variation as a more prolonged drought following average initial conditions. Yet, when the spring period was dry, the maximum cell size was often observed in the first third of a ring; when the spring was cold, the maximum cell size occurred in the middle of the ring. When July was hot and dry, the largest cells were often in the first third of the ring; when July was cold and wet, the largest cells were often observed in the middle of the ring. 'False rings' made up of small cells were usually associated with severe early to mid-season drought. Warm wet summers frequently produced rings with large cells that diminished in size near the outer ring boundary as latewood was formed. The calculations also suggested that the width of the transition zone between large earlywood cells and small latewood cells was most affected by climatic variations (Vaganov et al. 1985).

Examples of TRACH model results on *Pinus ponderosa*

The most recent version of the model was tested and validated using measurements from *Pinus ponderosa* growing in the Santa Catalina Mountains near Tucson, Arizona, USA. Simulations were compared to phenological observations, dendrograph measurements and cell sizes observed on thin sections sampled from trees during and after the growing season (Figs. 15, 16 & 17). Fig. 18 summarizes the environmental regimes of the study trees for the 5 seasons that were simulated.

Figs. 12b, 12d, 17 and 19a show both measured and calculated cell sizes and wall thicknesses for *Pinus ponderosa* subjected to the 1964 early-season drought (Fig. 10). There was little precipitation in May and June. A 'false ring', evident in Figs. 16 & 17, was produced because early-summer drought was severe enough to reduce the rate of radial growth (Fig. 15), but sufficient amounts of precipitation fell early enough in the growing season for continuation of cambial activity into the summer months (Fritts 1976). Under extreme conditions or with a delay of summer rains, growth can

Fig. 15. Daily maximum and minimum dendrographic measurements of stem size and phenological observations from one *Pinus ponderosa* for 1966 made at the base (Dendrograph A), middle (Dendrograph B) and upper (Dendrograph C) positions in the main stem, were used to check the growth that was simulated. T: apical buds swelling; B: buds opening; C: cambial activity initiated; N: needles emerging from bud; L: lignified latewood cells observed; M: needles reach mature size; t: days when the whole tree was enclosed in a plastic tent to obtain detailed physiological measurements (from Fritts 1976)

cease entirely so latewood cells that would have become a 'false ring' become true latewood and the cambium remains dormant unless a second growing period is initiated and a second ring is produced.

Daily climatic data collected at the tree sites (Fritts 1976, p. 97) (Fig. 18) were used in the simulation analysis. The estimated and actual measurements (Fig. 19a) are in good agreement. The mean square of the differences between the measured and modeled values were 10.8 for cell size and 0.447 for wall thickness, which are remarkably acceptable errors for the analysis considering the dissimilarities noted between and within trees growing under the same climatic conditions.

During 1966, winter soil moisture was much higher and spring rain was absent, so soil moisture in spring steadily declined until late June when 50 mm of rain replenished some soil moisture. Bud opening was followed by the initiation of cambial activity in mid April and stems increased in size throughout May and June, but the rate of growth was reduced somewhat (Fig. 15) by the decline in soil moisture. High growth resumed after the June rain, but rates of growth decreased again as soil moisture became depleted (Fig. 18). When the summer rainy period began in mid July, growth rates rose again and remained normal until the end of the growing season. The 2 periods of growth reduction (Fig. 15) were associated with 2 troughs and peaks in both the cell size measurements and simulations (Fig. 19b), but the model placed the first trough and peak 2 to 3 cells too early. The simulations of cell size for 1966 did not agree

Fig. 16. Photograph of cell-size variations from a basal section of a *Pinus ponderosa* stem used to validate the simulation (from Fritts 1976)

Fig. 17. Numbers and wall thicknesses of cells differentiated during 1966 in the upper stem of one *Pinus ponderosa* and a diagram of observations made from microscopic sections at the end of the growing season. Less cell-size variation for that year was found at the base of the stem (see Fig. 11) (from Fritts 1976)

as well with the measurements for 1964. The mean squares of the differences between the measured and modeled values were $28.9 \mu\text{m}$ for cell size and $0.308 \mu\text{m}$ for wall thickness, but these are still acceptable values.

Fig. 20 shows the modeled cell size, cell-wall thickness and wood density plotted against the sequence of the cells within the ring for 1964. Density is largely a function of cell-size, but cell-wall thickness values are of some importance. Similar patterns were noted in the upper stem of the tree (Fig. 17) but a greater proportion of cells show a reduction in size with a more pronounced 'false ring' evident.

CONCLUSIONS AND FUTURE PROSPECTS

The empirical and mechanistic models are simple approaches compared to more elaborate models of forest processes. However, they appear to capture many of the basic processes governing ring width, cell enlargement, wall thickening and density, which are not usually considered by other models. We believe our

2 models simulate fundamental relationships as accurately as possible based upon current knowledge of the growth controlling processes and dendrochronology. We chose the most basic and simplest relationships possible in hopes that this would facilitate the task of further model development.

The empirical model, PRECON, is important as it requires no prior knowledge about the growth-climate relationships because the parameters of the model are statistically estimated. It can be applied to any tree-ring chronology where an average monthly climatic data record of sufficient length also exists. In its present form, PRECON examines the correlations between standardized tree-ring index measurements for the interval of overlap between the tree-ring data and the climatic data, estimates multiple regression and response functions, considers non-linear interactions and calculates a Kalman filter. Regressions based on one interval can be projected over another interval to evaluate possible pollution, disturbance and other environmental changes, and growth changes in response to climatic change can be examined and

Fig. 18. Three-day averages of air temperature, precipitation and soil moisture measured in the *Pinus ponderosa* study area for 1963 to 1967 along with calculated upper and lower layer water balance (Thornthwaite & Mather 1955) (from Fritts 1976)

estimated. A tree-growth model relating Palmer Drought Indices to southern pine by Zahner & Grier (1989) is also a part of the PRECON model, and different data sets can be manipulated and compared providing flexibility in the analysis.

The mechanistic model, TRACH, uses mathematical equations for the environmental-growth relationships that are species independent. Differences in input para-

meters are used to model relationships for different species and sites. Daily climatic data are transformed into estimates of cell-size, cell-wall thickness and wood density. The cell size and wall thickness simulations have been tested using data from 2 species of pine from 2 widely separated geographic areas. The density simulations have not been validated adequately by direct density measurements, but they mimic published density data.

Fig. 19. Comparison of measured versus modeled cell sizes and cell-wall thicknesses for (a) 1964 and (b) 1966 growth rings from *Pinus ponderosa* in southern Arizona (see Fig. 16)

The validation data presented in this paper demonstrate that these 2 models of tree-ring and climate relationships do simulate realistic physiological relationships and produce reasonable anatomical results. The limiting effects of different climatic factors can be assessed and simulated and a number of hypotheses about these limiting conditions can be tested. The results are instructive as to what factors are important and when these factors become growth limiting and affect cell structure. The models can be used simply to

improve our understanding of growth-environmental relationships, and they can suggest new approaches for viable calibration and climatic reconstruction work.

We are continuing to validate the models and apply them to other species and sites. We have added a cambial module to the mechanistic model which will provide a basis for calculating cell numbers, thus eliminating the need for input from PRECON (Shashkin et al. unpubl., Vaganov et al. unpubl.). However, PRECON is still important to verify the relationships in the mechanistic model and to identify areas needing improvement. PRECON also is an analytical tool in its own right and will continue to be developed in tandem with TRACH.

We are developing a photosynthetic module to handle environmental and food storage relationships that may occur before the growing season is initiated and that cannot be explained by soil moisture relationships. We plan to consider possible effects of extreme conditions, degree-days, and other climatic influences on ring structure (Kienast et al. 1987) using daily, as well as monthly, climatic data. Such relationships are thought to cause some pointer rings as described for Europe (Becker et al. 1990) and are not well modeled by using mean values of climate over an entire month.

The models describe our understanding of dendro-climatological relationships as a series of statistical parameters and mathematical equations. The parameters will change from species to species and the equations will be altered to accommodate more complications. We argue that it is important to begin constructing such models now, even though there are many complexities beyond our present understanding. The models are a beginning effort to serve as an unambiguous medium of communication, which represent the state of knowledge at the present moment as we perceive it. In this form, the relationships can be examined objectively and tested. We hope this will be a meaningful modeling effort to forest scientists as well as dendrochronologists and invite the interest and support of those in the scientific community who might wish to develop the model further and apply it to their own research.

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Fig. 20. Cell sizes, cell-wall thicknesses $\times 10$ and density variations simulated for the 1964 ring from *Pinus ponderosa* in southern Arizona

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