A COMPUTER PROGRAM FOR SIMULATING CAMBIAL ACTIVITY AND RING GROWTH

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ABSTRACT

This paper describes an interactive computer program which simulates daily cell growth and differentiation in a single radial file of tree cells. The growth processes are controlled by 22 model parameters, half of which are constants, the remainder time-dependent. The program user specifies the constants and the form of the time variations desired. The program computes daily values for the time-dependent parameters, and applies these values to the calculation of cell diameters, cell division, cell wall thickness, and ring width for each day of the growing season. Output is in tabular and graphical form. The tabular listing consists of the cell diameter at each position in the radial file, and for the xylem it also prints cell wall thickness and a relative density for each cell. The graphical output plots cell diameter, wall thickness, and relative density vs. file position. The program was designed primarily as an instructional tool and has been used for this purpose with good results. Because of its flexibility it has potential for research, and some possibilities for such use are discussed.

INTRODUCTION

Wilson and Howard (1968) have described a computer model designed to simulate cell growth and differentiation along a radius (radial file of cells) of a tree during a growing season. At the suggestion of Harold C. Fritts in the late spring of 1975, I undertook the construction of a similar model designed specifically for interactive operation on the DEC-10 computer system owned by The University of Arizona. My primary objective has been the development of the model as an instructional tool; however, it also offers considerable potential for research.

The computer program, named ARBOR, is written in FORTRAN IV for the DEC-10 computer. Conceptually, ARBOR is virtually the same as Wilson and Howard's model; it differs in some features, as described in the remainder of this paper.

Starting with a cambial initial cell and some xylem and phloem mother cells at the beginning of the growth season, ARBOR simulates the following processes day by day as the season progresses:

(1) radial growth, elongation, and division (both radially and pseudotransversely) of the cambial initial cell;
(2) radial growth and division of the mother cells;
(3) differentiation of cells into enlarging and maturing phases of growth;
(4) radial growth of cells in the enlarging phase;
(5) thickening of xylem cell walls in the maturing phase.

Following Wilson and Howard (1968), these growth processes are controlled during the growing season by specifying values for several model parameters. Since the model was developed primarily as an instructional tool, this specification process was designed to be as flexible as possible without making the program too cumbersome for general use. After careful consideration, 22 model parameters were chosen, half of which are constants, and the remainder time-dependent. For the latter, a method was devised for calculating daily values for each parameter, thus avoiding the tedious process of entering them separately. The method allows the user to specify starting and end values, various maxima and minima at specific times in the growing season, and the general shape of the time variation. Daily values are calculated using specific exponential functions whose constants are adjusted to fit the specifications.

ARBOR is designed for use by persons having no previous experience with computer usage. The program proceeds by printing instructions for the user and requesting the input data it needs (Stevens 1975).

THE MODEL PARAMETERS

Following is a list of the parameters used in ARBOR. The cell dimensions are in micrometers, and the growth rates are in micrometers per day.

A. Constants

Growing Season

1. Start date (month, day)
2. End date (month, day)

Cambial Initial Cell

3. Starting radial diameter
4. Maximum radial diameter
   This determines when the initial cell divides radially.
5. Starting length
6. Maximum length
   This determines when the initial cell may divide pseudotransversely.

Mother Cells

Xylem

7. Starting radial diameter
8. Maximum radial diameter at division

Phloem

9. Starting radial diameter
10. Maximum radial diameter at division

Maturing Xylem Cells

11. Initial wall thickness

B. Time-Dependent Parameters

For each of the following parameters, the program calculates a daily value in accordance with specifications supplied by the user, and stores these values for use as the growing season progresses.

Cambial Initial Cell

12. Daily rate of radial growth
13. Daily rate of elongation
14. Daily probability that a daughter cell resulting from periclinal division of the initial cell becomes a xylem mother cell.

Mother cells

15. Daily maximum number of xylem mother cells
16. Daily rate of radial growth of xylem mother cells
17. Daily maximum number of phloem mother cells
18. Daily rate of radial growth of phloem mother cells.

Enlarging Cells (no longer dividing)

19. Daily rate of radial growth
20. Daily maximum radial diameter
    This determines when enlarging cells stop enlarging. Xylem cells reaching this limit enter the maturing phase and begin wall thickening. Phloem cells reaching this limit pass into the mature stage.

Maturing Xylem Cells

21. Daily rate of wall thickening
22. Daily maximum wall thickness
    This determines when xylem cells pass into the mature phase.

C. Forms of Time Variation

There are two general forms of time variation available for each of the parameters listed in B. above. These are: 1) single-maximum form; 2) double-maximum form (Figure 1). For each time-dependent parameter, the user determines the form to be used and its particular shape.

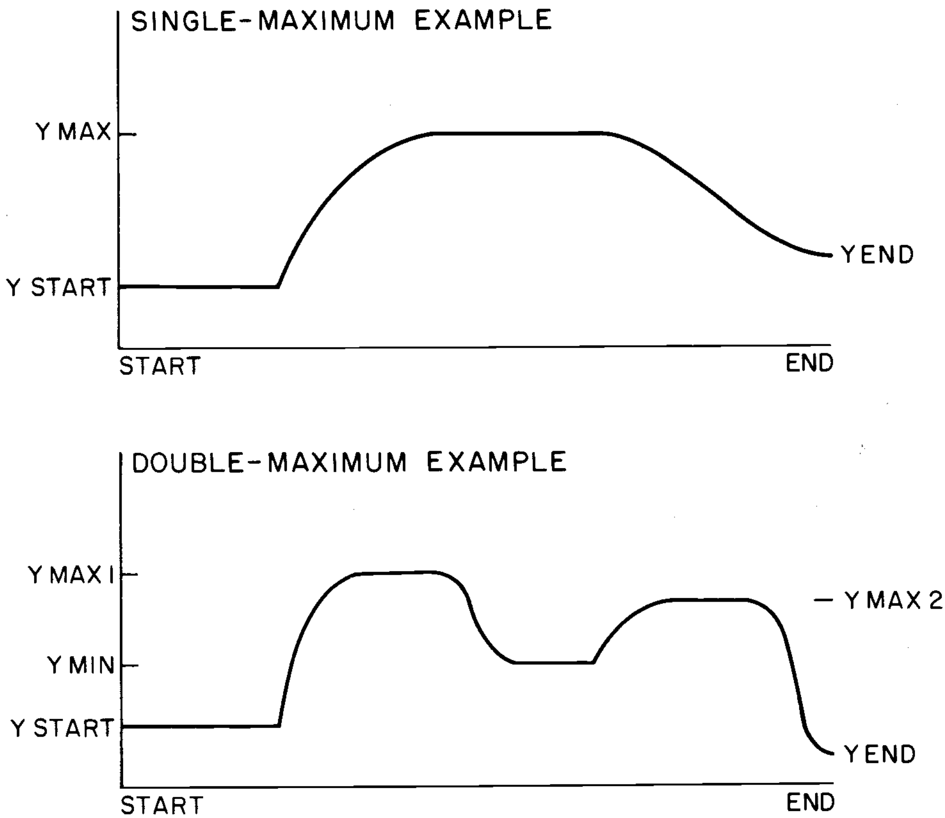

Figure 1. General forms of time variation.

The user controls the time variation for each parameter by entering the following information:

a) starting and end values for the parameter;
b) maximum and minimum values;
c) dates (month, day) at which the various maxima and minima are reached;
d) durations of constant periods, if any.

Given this information, the program computes daily values for the parameter and stores them for subsequent use. The rising and falling portions of each time curve are exponential functions chosen to provide the shapes indicated in Figure 1. By varying the input information listed in a) through d) above, the user may produce almost any type of time curve desired.

D. Spatial Variation of Mother Cell Maximum Diameter

During model development, the following situation arose: If all xylem (or phloem) mother cells had the same growth rate and maximum diameter, then ultimately they would all divide simultaneously. To avoid this apparently unrealistic case, the maximum diameter of mother cells is functionally related to the distance from the cambial initial cell. For the mother cells contiguous with the initial cell, the maximum diameter is that of the initial cell. Going away from the initial cell, the maximum diameter increases in a certain way up to the specified value at the boundary of the mother cell region. Figure 2 illustrates this for a typical case.

MODEL OPERATION

With two additions, the sequence of program operations (summarized in items (1) through (5) of the Introduction) is the same as described by Wilson and Howard (1968). The additional steps are:

a) at the end of each day, the diameters of all xylem cells outside the mother cell region are summed and the sum is defined as the ring width;

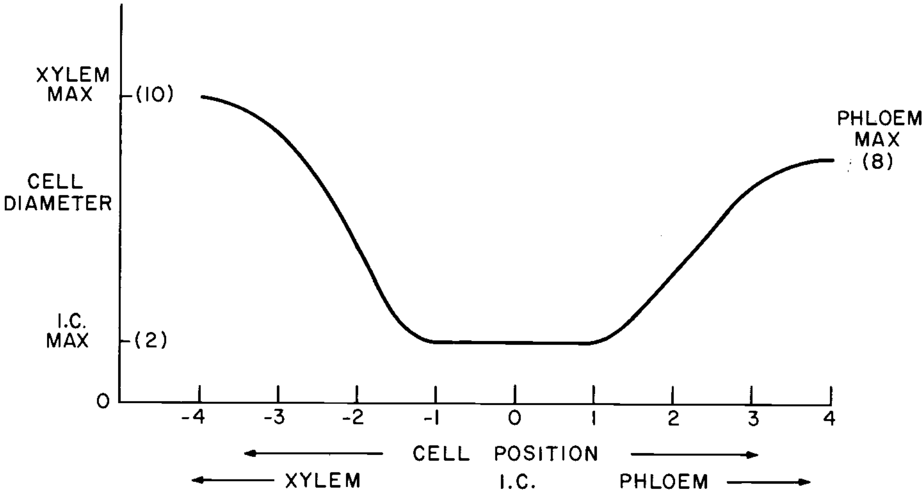

Figure 2. Variation of mother cell maximum diameter with distance from cambial initial cell.

b) a relative density is computed for each of these cells; this relative density is defined by:

$$DEN = 1 - [(D - 2T)/D]^2,$$

where D is the cell diameter and T is the cell wall thickness.

The program establishes an array of storage locations corresponding to the radial file of cells, and cell diameters are stored and moved within this array as the program proceeds. The elements of the array are assigned numbers as follows: The position of the cambial initial cell is always numbered zero. Xylem cell positions are assigned consecutive *negative* numbers going away from the initial cell, and phloem cell positions are assigned consecutive *positive* numbers. Boundaries between the various growth regions are defined as the array expands during the growing season, and these boundaries move along the array as required.

ARBOR OUTPUT

ARBOR produces two types of output: basic and expanded; the latter is optional.

A. Basic Output

This is tabular in form, and consists of the radial diameter of each cell in the file, wall thickness and relative density for each xylem cell outside the mother region, and ring width. The data are listed by file position, and the various growth regions are listed separately. Data are listed only for the following three days:

1) day zero (initial conditions);
2) the midpoint of the growing season;
3) the last day of the season.

Figure 3 is an example of the output for the last day of a typical run.

B. Expanded Output

There are three options, any or all of which may be used:

1) Intermediate day output.
   This has the same format as the basic type, but the user may obtain outputs at specified intervals during the season (every 10 days, for example).
2) Plots.
   The user may obtain lineprinter plots of any or all of:
   (a) cell diameter vs. file position;
   (b) cell wall thickness vs. position;
   (c) relative density vs. position
   Figure 4 is an example of plot type (a).
3) Daily values of the parameters.
   This output consists of tables of daily values for each of the time-dependent parameters. It also includes daily counts of the numbers of cells in each growth region, and daily ring widths.

ADDITIONAL FEATURES OF *ARBOR*

There are three features of ARBOR which should be mentioned because of their contribution to ease of use and flexibility.

A. Data Entry Options

ARBOR will accept input data from three data sources:

```
RING WIDTH:    1.58 MM.

DATE:  1 SEP   DAYS SINCE START: 153

MATURE XYLEM CELLS.

POS:  -47  -46  -45  -44  -43  -42  -41  -40  -39  -38  -37  -36  -35  -34  -33
DIA: 51.0 51.0 51.0 50.3 50.7 50.7 50.7 49.3 49.3 51.2 48.0 48.0 50.1 51.4 50.1
CWT:  2.1  2.1  2.1  2.1  2.1  2.1  2.1  2.1  2.1  2.1  2.1  2.1  2.1  2.2  2.1
DEN: 0.16 0.16 0.16 0.16 0.16 0.16 0.16 0.16 0.16 0.16 0.17 0.17 0.16 0.16 0.16

POS:  -32  -31  -30  -29  -28  -27  -26  -25  -24  -23  -22  -21  -20  -19  -18
DIA: 50.1 50.1 49.9 49.0 49.0 50.5 50.3 50.6 49.8 49.0 50.8 49.3 47.5 46.6 43.0
CWT:  2.1  2.1  2.2  2.2  2.2  2.2  2.2  2.6  2.9  2.9  2.9  4.0  5.3  5.4  5.0
DEN: 0.16 0.16 0.17 0.17 0.17 0.16 0.17 0.19 0.22 0.22 0.22 0.30 0.40 0.41 0.41

POS:  -17  -16  -15  -14  -13  -12  -11  -10   -9   -8   -7   -6
DIA: 45.0 35.2 34.5 28.2 25.3 26.9 16.5 14.1  9.9  9.4 12.1 11.5
CWT:  5.0  5.3  5.3  5.3  5.3  5.3  5.3  5.3  4.9  4.7  5.3  5.3
DEN: 0.40 0.51 0.52 0.61 0.66 0.63 0.87 0.94 1.00 1.00 0.99 0.99

MATURING XYLEM CELLS.
NONE.

ENLARGING XYLEM CELLS.
NONE.

XYLEM MOTHER CELLS.

POS:   -5   -4   -3   -2   -1
DIA: 10.1  5.6  5.6  4.4  4.4

INITIAL CELL.
DIA:  7.4   LENGTH: 1716.5

PHLOEM MOTHER CELLS.

POS:    1    2
DIA:  4.2  4.2

ENLARGING PHLOEM CELLS.
NONE.

MATURE PHLOEM CELLS.

POS:    3    4    5    6    7    8    9   10   11   12
DIA:  8.0 14.8 22.3 34.6 45.8 50.4 47.1 50.1 51.3 51.1

RING WIDTH:    1.76 MM.
```

Figure 3. Example of tabular output for the last day of the growing season.

(1) manual entry from the terminal keyboard;
(2) an existing disk file containing data generated during a previous run;
(3) a special disk file containing preset input data used for program demonstrations.

B. Storage of Parameters in a Disk File

At the end of an ARBOR run, the user is offered the option of storing all of the original input data and the computed daily values of the parameters in a special output file. This file may be used later as the input source under option (2) above, and one or more parameters may be changed for a new run.

C. Reentry Mode

This option, offered at completion of a run, allows the user to make changes in one or more parameters and rerun the program. By changing only one or two parameters at a

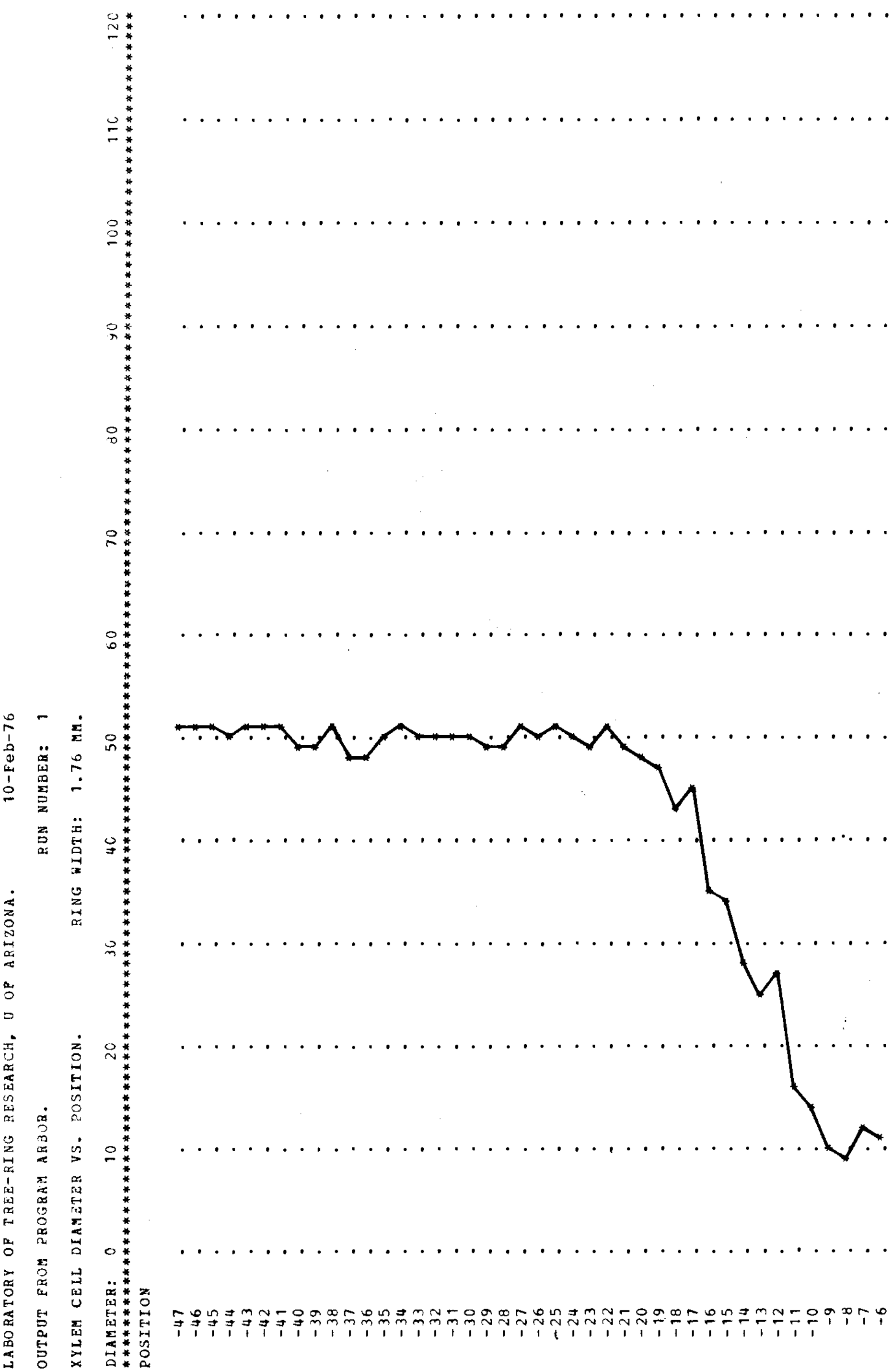

Figure 4. Sample plot of cell diameter vs. file position.

time and making successive runs, the user may quickly examine the relative importance of various parameters to the structure of a tree ring.

CONCLUSION

ARBOR made its debut during the autumn semester of 1975, when students who used it extensively reported improved understanding of factors which affect tree growth. Several students attempted to approximate the structure of real tree rings. Others attempted the simulation of the more complicated changes in cell growth which might be associated with environmental stress factors, such as midsummer drought.

While ARBOR has not yet been used for research studies, it does offer the potential. Perhaps the most exciting possibility at present would be to develop relationships between environmental factors and the model parameters, in order to assess their effects on ring structure and growth. Assuming this could be done, then the user could specify the external conditions (climatic variations, for example) and study the resulting effects on the various growth processes. Another possibility might be to devise a way of incorporating statistical response functions (Fritts 1974) into the model and then input variables of temperature and precipitation to create different ring structures and amounts of growth.

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