A Computer Model For Cambial Activity

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Abstract. This model simulates on a daily basis cell differentiation in a radial file of fusiform cells; cell division in the cambial zone, cell enlargement in the secondary phloem, and enlargement and cell wall thickening in the secondary xylem. Input variables specified for each day of the growing season include the number of mother cells, rates of enlargement and cell wall thickening, and maximum radial cell dimensions. The rules for the behaviour of cells as they pass through successive phases of differentiation are based on available data and observations. Output variables for each day of the season include the position of each cell in the radial file, all cell radial diameters, and cell wall thickness in the xylem. The daily output may be compared with actual cell measurements from trees in the field to check the model and the values for input variables. Examples are given of simulating annual ring formation in a *Pinus strobus* tree growing under good conditions and a *Pinus resinosa* tree that suffered a summer drought. The cell dimensions of these model rings are almost identical to those in the rings being simulated. The daily output of the model permits following the daily differentiation of any one cell, which cannot be done by destructive sampling of trees. Examples are given showing how cells may be followed through the phase of division to count the number of times each mother cell redivides, and to study the frequency distribution of mitoses in the cambial zone. Potential uses could be to convert environmental data into cell dimensions in an annual ring or, by summing radial files, to simulate cambial activity in whole trees.

CAMBIAL ACTIVITY is a general term that includes the production of cells by the vascular cambium and the subsequent differentiation of cells into secondary xylem and phloem elements. Although models employing modern computer techniques are commonly used as valuable research tools in engineering, economics and business (Dantzig 1963, Jones and Gray 1963, Chappelle 1966), biological models of cell developmental systems are rare (Bonner 1965).

This paper presents a model designed to simulate the daily processes of cambial activity in a conifer throughout a growing season. The model is a combination of "rules" that specify the behavior of cells in a radial file as they pass through the various phases of differentiation. These rules are based on the fund of knowledge that has accumulated about cambial activity. The daily inputs for the model are values for 14 variables that include the rate of cell division, cell enlargement and wall thickening. The daily outputs are cell sizes and cell wall thicknesses. The model was written in FORTRAN IV for operation on an IBM 7094 computer to handle the large number of computations.

Literature Review

Components of cambial activity. The basic units of cambial activity are the radial files of cambial initials and their derivatives. The present model was designed to represent cambial activity in a single radial file of fusiform cells, the long (1–4

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mm) needle-like cells that ultimately differentiate into tracheids in the xylem and sieve cells and fusiform parenchyma in the phloem. A radial file is continuous from the xylem through the cambial zone to the phloem. Some extend from the pith to the oldest phloem, but most radial files are shorter because new files are constantly being produced and old ones lost (Bailey 1923, Bannan and Bayly 1956). Adjacent files are similar so this model representing a single file can be considered representative of a population of adjacent files at one position in a tree.

Radial files of cells have a marked tangential zonation because (1) each cell, both xylem and phloem, is ultimately derived from the initial cell in the file, and (2) each of these cells passes through successive phases of division, radial enlargement, and maturation (restricted to cell wall thickening by secondary wall formation in this model) before it becomes fully differentiated (Wilson *et al.* 1966). Thus, the cells in a file are in a time and developmental sequence in both the xylem and phloem directions from the cambial initial. The further a cell is from the initial the older and more fully differentiated it is.

Derivatives of the initial cell that can still divide are called mother cells. With few exceptions, mother cells divide periclinally so that each division produces a new cell in the radial file, i.e., a cell that ultimately differentiates into mature xylem or phloem. The number of cells in the cambial zones of adjacent radial files does not vary over a period of a few days. Indeed, cell number in the cambial zone may not change even above a girdle where the rate of cell production is doubled or tripled (Wilson 1968).

When the initial cell divides periclinally, one of the daughter cells stays as the initial cell and the other begins differentiation as either a xylem or phloem mother cell (Newman 1956, Philipson and Ward 1965). The initial cell can also divide pseudotransversely to form new initials that in turn produce new radial files (Bailey 1923). Bannan (1956) has shown that a daughter initial cell elongates for a period of years after a pseudotransverse division until it reaches the approximate length of the parent cell, and then there is another pseudotransverse division. During the period of elongation all divisions of the initial cell are periclinal.

Radial enlargement of mother cells occurs rapidly between divisions (Wilson 1963), but the cells do not enlarge radially to more than 10 or 15 μ before redividing. Cells that enter the phase of enlargement do not divide and may enlarge up to 40 or 50 μ radial diameter. The final radial diameter varies according to the seasonal or experimental conditions under which enlargement takes place. The number of cells in the zone of enlargement is a function of the rate of entry of cells from the cambial zone, the rate of loss as cells farthest from the initial cell enter the phase of maturation, and the time taken for the entire phase of enlargement. The length of time for cell enlargement is a function both of the rate of enlargement and of the final radial diameter of the cell.

During the phases of division and enlargement, cells have only primary walls that remain relatively thin. Wall thickening from secondary wall formation in the xylem begins as cell enlargement stops. Final wall thickness varies throughout an annual ring, but seldom exceeds 5 μ. The factors governing the number of cells in the zone of cell wall thickening are, as in the zone of enlargement, the rate of entry and loss of cells to the zone and the time taken to form the wall. The time is a function of the rate of thickening and the final thickness (Wodzicki and Peda 1963).

Seasonal changes in cambial activity. Cell production starts in the early spring and soon achieves maximum rate. Usually the rate of production then gradually decreases until the end of the season, but in some cases there is a midseason decline

in production followed by a resurgence before the end of cambial activity in the autumn (Bannan 1955). In rapidly growing trees 1.5 to 2 xylem cells are produced per day per file (Wilson 1964, Kennedy and Farrar 1965). The total production of a fast growing tree is 100 to 200 cells in a season. More studies of phloem production and development are needed to provide the quantitative inputs used in the model. In general, approximately two phloem cells that had been previously indistinguishable from cambial zone cells enlarge and mature before mitotic activity begins in the spring, then phloem production proceeds concurrently with xylem production at about two cells per month until both xylem and phloem production cease. Annual phloem production is higher in faster growing trees, but appears to be relatively constant in comparison to annual xylem production (Bannan 1955, Grillos and Smith 1959, Wilson 1964, Alfieri and Evert 1966).

The two major components of cell production, namely, number of cells in the cambial zone and the length of the cell cycle (time between successive mitoses), appear to change somewhat independently of each other. The number of cells in the cambial zone is at a minimum (4–8) during winter dormancy. New cell production in the spring increases the number of cambial zone cells to a maximum of 10–15 in fast growing trees (less in slow growing trees) before any cells enter the phase of cell enlargement. Throughout the rest of the season cell number in the cambial zone gradually decreases back to the dormant condition. The length of the cell cycle has been estimated at 7 days in *Thuja occidentalis* (Bannan 1955) and at 10 days in *Pinus strobus* (Wilson 1964). The length of the cell cycle in *Pinus strobus*, judging by the mitotic index (percent of cambial zone cells in mitosis), is at a minimum early in the season and increases throughout the season until it is more than twice the minimum value (Wilson 1966). In *Pinus strobus* the mitotic index may double, thus doubling the rate of cell production, without any increase in the number of cambial zone cells. White spruce (*Picea glauca*) trees in Alaska that produce cells twice as fast as trees of comparable size in New England, have the same number of cells in the cambial zone, but the mitotic index is about two times higher in the Alaska trees (Gregory and Wilson 1968).

There are only two studies of the distribution of mitoses across the cambial zone and both show a peak frequency of mitoses in the center of the zone (Bannan 1955, Wilson 1964). There are no known studies of the change in distribution of mitoses throughout the growing season, but Bannan (1955) has observed that the first mitoses in the spring occur near the xylem. In addition, the ratio of phloem to xylem production is lower in the spring than in the autumn. These observations could be interpreted to suggest that the peak of cell divisions shifts from the xylem side of the cambial zone in the spring to the phloem side in the autumn.

In the dormant winter condition there are no zones of enlargement or cell-wall thickening. These zones do not develop until new derivatives enter these phases. Therefore, the zones of enlargement appear in the spring after the cambial zone has reached its maximum size and later the zone of cell wall thickening develops as some derivatives reach their final size. Mature derivatives are not produced until secondary wall formation is completed. The general trend appears to be that the zone of enlargement reaches maximum size early in the season and then gradually decreases, but the zone of wall thickening reaches maximum size towards the end of the season when the thickest walls are formed (Wodzicki 1960, 1962, Wodzicki and Peda 1963, Whitmore and Zahner 1966).

The radial diameter and cell wall thickness of a mature tracheid is determined at the time when it finishes each of these phases of differentiation.

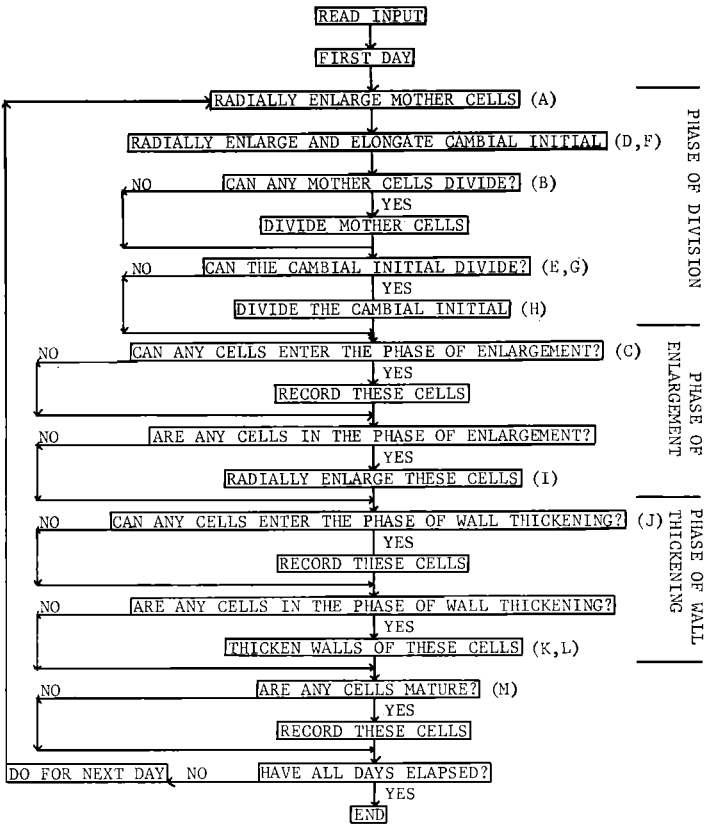

FIGURE 1. *Flow chart showing logic and sequence of operations performed by the programmed model. Letters in parentheses refer to rules and variables discussed in the text. The chart applies to either the xylem or the phloem, except that wall thickening is omitted in the phloem.*

Radial diameter is greatest in tracheids maturing early in the season and for tracheids formed during the middle of the season may decrease slowly, or stay about the same. At the end of the season tracheids enlarge very little and the last formed tracheids often have radial diameters comparable to cambial zone cells. Cell wall thickness is least in cells maturing early in the season and generally increases to a maximum in cells formed near the end of the season, but decreases again in cells maturing at the very end of the season (Wodzicki 1962).

The changes in cell radial diameter and cell wall thickness across an annual ring result in the characteristic large, thin-walled earlywood and the narrow, thick-walled latewood. In many species, however, there are transitional cells that are large radially but also have relatively thick walls. Experimental research with induced drought and controlled photoperiods suggests that the two variables cell wall thickness and cell radial diameter are independent of each other although increased wall thickness is often associated with decreased radial diameter (Wodzicki and Witkowska 1961, Larson 1962, Zahner and Oliver 1962). With proper manipulation of experimental conditions it is possible to produce tracheids with almost any combination of wall thickness and cell radial diameter.

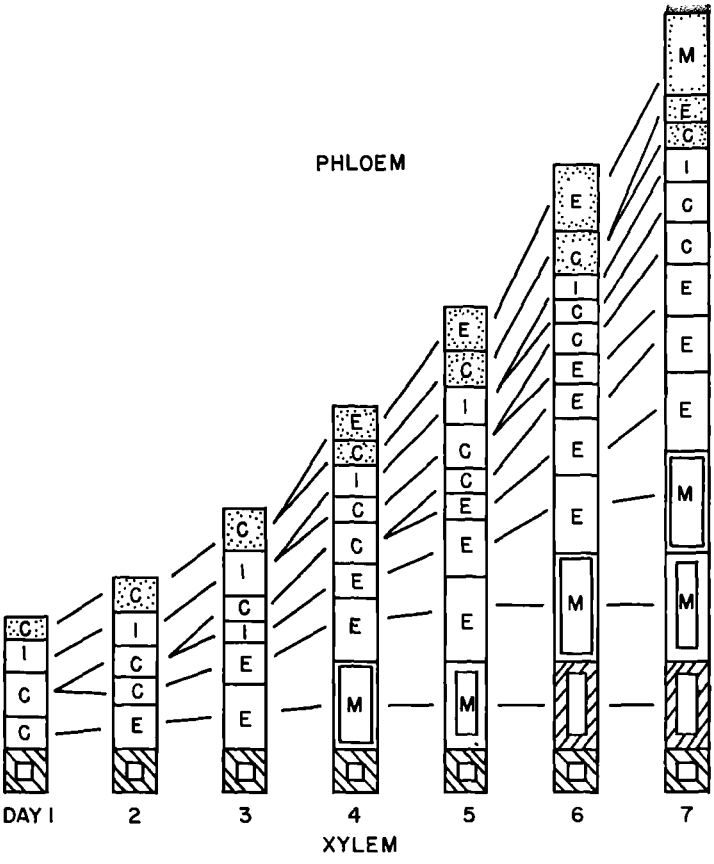

FIGURE 2. *Pictorial representation of the operation of the model. Stippled cells are phloem. Cells are lettered C for mother cells, I for initial cell, E for enlarging cells, M for maturing cells (wall thickening in the xylem). Unlettered cells are mature. This diagrammatic example assumes a constant number of phloem and xylem mother cells, constant rates of enlargement and wall thickening, and constant maximum cell dimensions.*

Rules and Operation of the Model

The basic inputs for daily operation of the model are the values for 14 variables. These variables are defined in the following section and each is italicized when first mentioned. The rules that govern the behavior of cells as they pass through the phases of differentiation are also defined. The identification letters following variables are used in the flow chart of the logic of the program (Fig. 1) to show where the variable is used. A diagrammatic illustration of how the model operates using these rules and variables is given in Figure 2. After each simulated day of development the program prints as output the radial diameters of all cells in the radial file, the length of the initial cell and xylem cell wall thicknesses. An example of this output for one day is shown in Figure 3.

Phase of division. For each xylem and phloem mother cell the *rate of radial enlargement* (*dividing cells*) (A) and the *maximum radial diameter* (*dividing cells*) (B) that a cell can attain without dividing are specified. After each dividing cell

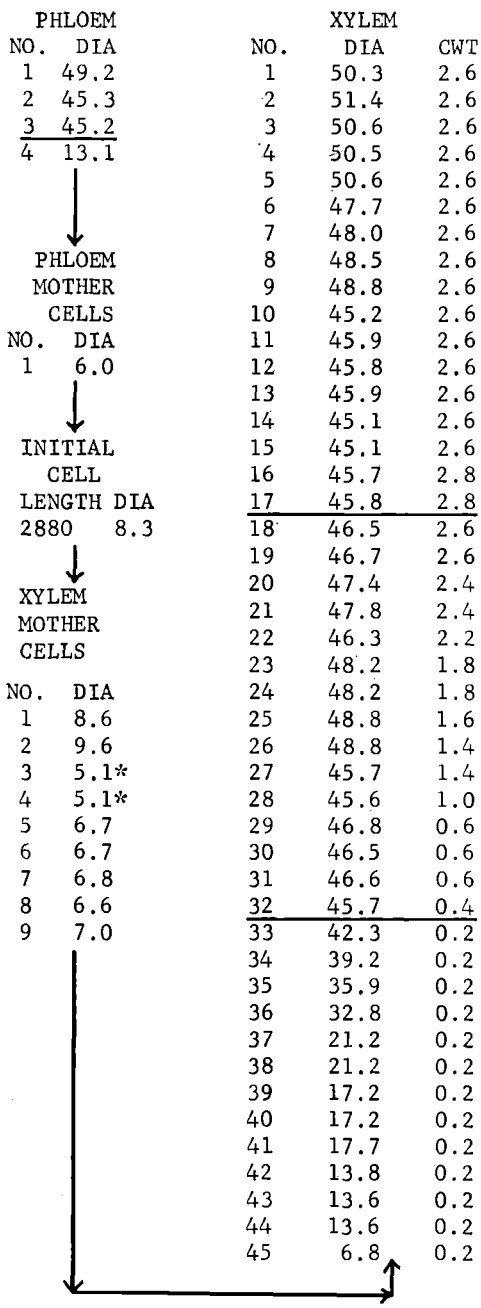

FIGURE 3. *An example of the daily output from the computer model after 40 days of simulated seasonal activity by a white pine. All cell measurements are in microns, DIA = radial diameter and CWT = cell wall thickness. The positions of the mother cells are numbered in sequence going away from the initial cell. Phloem and xylem cells are numbered in sequence as they leave the phase of differentiation. In the xylem, cells 1–17 are mature, cells 18–32 are in the phase of wall thickening, and cells 33–45 are in the phase of enlargement. In the pholem, cells 1–3 have stopped enlarging (the phase of maturation is omitted in the phloem), and cell 4 is enlarging, cells marked by (*) are daughter cells of the xylem mother cell that was in position 3 before dividing at a diameter of 10.2μ. This division caused the cell at the edge of the mother cell zone, now xylem cell 45, to enter the phase of enlargement.*

grows each day at a specified rate its radial diameter is checked to see if it equals or exceeds the maximum specified diameter. If it does, the cell automatically divides periclinally to form two cells, each one-half the radial diameter of the parent cell. The length of the cell cycle is equal to one-half the maximum radial diameter divided by the rate of radial enlargement for dividing cells.

The maximum number of xylem mother cells (C) and the *maximum number of phloem mother cells* (C) are specified. The total numbers of xylem and phloem mother cells are determined for each day after all cells have div ded. If the total number of either xy'em or phloem mother cells exceeds the maximum specified number the excess cells farthest from the cambial initial enter the phase of radial enlargement.

Initial cell. The *rate of radial enlargement* (D) and the *maximum radial diameter* (B) the initial can attain before dividing are specified as for mother cells. To determine when pseudotransverse divisions occur, the *rate of elongation* (F) and the *maximum length* (G) that the initial can reach before a pseudotransverse division occurs are specified. The initial enlarges and elongates each day. When the radial diameter is equal to or exceeds the specified maximum the initial divides. The initial divides pseudotransversely if the length equals or exceeds the specified maximum length, otherwise it divides periclinally.

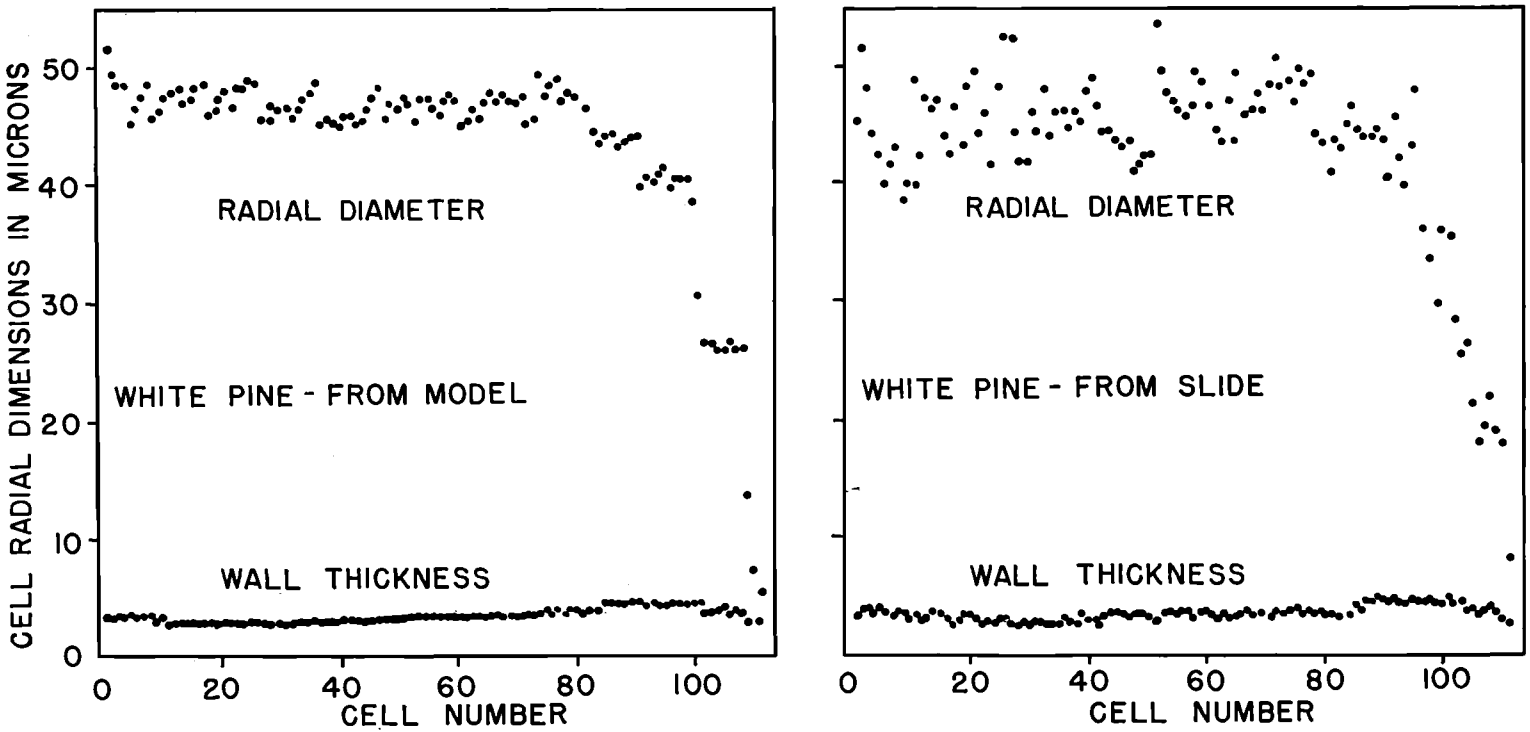

FIGURE 4. *The radial diameter and cell wall thickness of tracheids from real and model rings of white pine. Measurements for the model ring were taken directly from the output of the last day of the season after using the input in Table 1. Measurements from a microslide for the real ring are the averages of 5 adjacent radial files in transverse section.*

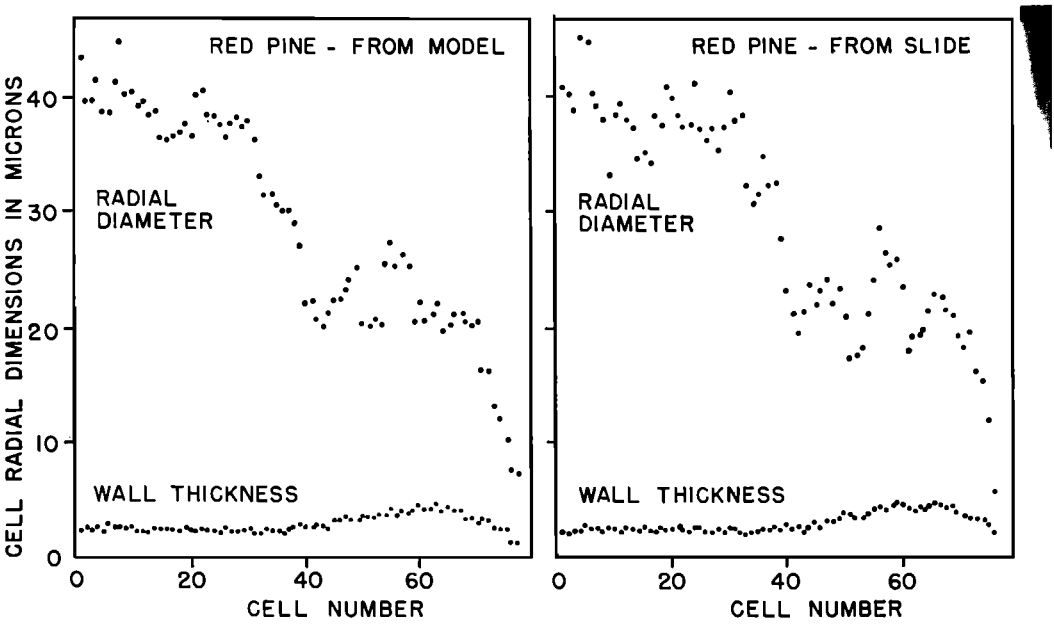

FIGURE 5. *The radial diameter and cell wall thickness of tracheids from real and model rings of red pine that passed through a mid-summer drought. Measurements for the model ring were taken directly from the output of the last day of the season after using the input from Table 2. Measurements from a microslide for the real ring are the averages of 5 adjacent radial files in transverse section.*

The *probability for a daughter cell from a periclinal division of the initial becoming a phloem mother cell* (H) is specified for each day of the season. Following each periclinal division of the initial, this probability is compared with a number selected pseudo-randomly to determine whether a xylem or phloem mother cell is formed.

Phase of enlargement. The *daily rate of enlargement* (*enlarging cells*) (I) is the same for each cell in the phase of enlargement, although it may change each day. The cells enlarge at this rate until they reach a *maximum radial diameter* (*enlarging cells*) (J). If the radial diameter is greater than or equal to the maximum diameter the cell enters the phase of cell wall thickening. *Phase of cell wall thickening*: During the phase of cell wall thickening (in the xylem only) the *primary wall thickness* (K) is constant. A *rate of cell wall thickening* (L) is specified to simulate the formation of the secondary wall. The cell wall thickens each day until a *maximum wall thickness* (M) is equalled or exceeded, then the cell becomes mature (dead in the xylem) and does not undergo further differentiation.

Examples of the Use of the Model

In this section two examples are given of annual rings that were reproduced by the model. One is a ring formed by an eastern white pine (*Pinus strobus*) under good growing conditions in Petersham, Massachusetts, the other is a ring formed by a red pine (*Pinus resinosa*) in Michigan, where the tree was subjected to a natural summer drought[1]. The similarity between the model and the "real" rings is a striking confirmation of the validity of the model (Figs. 4, 5).

[1] Many of the values used to quantify the variables for the growth of red pine were supplied by R. Zahner, University of Michigan.

TABLE 1. Values for input variables used to develop the white pine ring shown in Figure 4. Length of the cell cycle is half the maximum diameter of the mother cells (5 μ in this example) divided by the rate of enlargement for dividing cells (not given in the table). XMC = xylem mother cells, CWT = cell wall thickness.

Day No.	Dividing cells		Enlarging cells		Maturing cells	
	Max. No. XMC	Avg. length cell cycle	Rate of enl.	Max. rad. dia.	Rate CWT	Max. CWT
		(*days*)	(*μ/day*)	(*μ*)	(*μ/day*)	(*μ*)
0	5					
1–10	11	5.8	3.5	49	0.2	3.5
11–20	11	6.0	3.5	49	0.2	3.0
21–37	10	7.1	4	45	0.2	3.1
38–55	9	8.0	4	45	0.2	2.7
56–70	8	9.2	3	45	0.2	2.9
71–85	7	10.0	3	45	0.2	3.0
86–100	7	8.5	3	47	0.2	3.0
101–115	6	10.3	2.5	43	0.3	3.5
116–130	6	11.6	2.5	39	0.3	4.1
131–145	5	13.8	2	25	0.3	4.0
146–160	5	—	0.5	5	0.18	3.5

For selection of suitable values for the variables, cell number and the final size and wall thickness of each cell in the real ring can easily be measured from transverse sections. The general rates of cell production throughout the season can be estimated from successive samples from comparable trees, or they may be calculated from the measurements of diameter growth by dendrometers (Kozlowski and Peterson 1962). When the rate of cell production and the number of cells in the cambial zone are determined, the average length of the cell division cycle of cambial zone cells can easily be calculated (Wilson 1964), and the average rate of radial cell enlargement of dividing cells in the cambial zone can be computed. The distribution of rates among cambial zone cells must be estimated on the basis of the few published data. The rate of cell enlargement and the rate of cell wall thickening during cell maturation must be calculated from estimates of the rate at which cells pass through each respective phase, based on the width of each zone in relation to the rate of cell production. Usually data are available for only a few samples during a season, so values for the rest of the season must be extrapolated or interpolated. Values for the rate of elongation of the cambial initial and the probability of periclinal division of the initial forming a mother cell are essentially unknown, but may be estimated from studies reported in the literature (see section on components of cambial activity).

The model could, theoretically, use a different set of inputs for each day. In practice we used the same input for several successive days or an "interval" (Tables 1, 2). When a ring is quite homogeneous, like the earlywood of a white pine ring (Fig. 4), the intervals may be up to 15 days long and still account for most of the variations in final cell dimensions. For complex rings, like the red pine ring (Fig. 5), or where there are steep gradients in cell size as in the latewood of a white pine ring (Fig. 4), the intervals must be 5 days or less.

Another use of the model is the analysis of developmental processes that can be followed over time in the same cell. The destructive sampling inherent in studying

most aspects of cambial activity of trees in the field means that these processes must be inferred by comparing averages of sequential samples or by comparing adjacent cells in a radial file. With the model, differentiation of a given cell may be followed day-by-day from initiation to maturity. Two examples of such use of the model are (1) determining the distribution of mitotic activity across the cambial zone and (2) determining the number of divisions that each mother cell undergoes before entering the phase of enlargement. The model was run for a 50-day interval with constant input to simulate cambial activity under constant conditions.

The few data available on the frequency distribution of mitoses in the cambial zone (Bannan 1955, Wilson

TABLE 2. Values for input variables used to develop the red pine ring shown in Figures 5 and 6. Length of the cell cycle is half the maximum diameter of the mother cells (5 μ in this example) divided by the rate of enlargement for dividing cells (not given in this table). XMC = xylem mother cells, CWT = cell wall thickness.

	Dividing cells		Enlarging cells		Maturing cells	
Day No.	Max. No. XMC	Avg. length cell cycle	Rate of enl.	Max. Rad. Dia.	Rate CWT	Max. CWT
		(*days*)	(*μ/day*)	(*μ*)	(*μ/day*)	(*μ*)
0	3	—	—	—	—	—
1–5	7	6.2	5	40	.2	2
6–10	7	5.6	5	43	.3	2
11–15	9	5.0	6	39	.3	2.1
16–20	11	4.6	7	38	.4	2.1
21–25	10	6.6	6	36	.4	2.2
26–30	9	10.6	5	36	.35	2.1
31–35	8	14.3	4	36	.3	2.4
36–40	7	18.4	3	37	.3	2.2
41–45	6	20.0	2.5	31	.3	2.1
46–50	5	20.6	2.5	30	.3	2.0
51–55	4	24.0	2	28	.25	2.0
56–60	4	24.0	2	22	.2	2.4
61–65	4	24.0	2	20	.2	2.5
66–70	3	31.3	1.75	19	.2	2.6
71–75	3	31.3	1.75	20	.2	2.5
76–80	7	6.0	4	22	.2	2.5
81–85	7	5.9	4	23	.3	2.6
86–90	7	5.8	4	22	.3	2.8
91–95	6	5.4	2	19	.3	3.0
96–100	5	7.4	3	25	.25	3.2
101–105	4	10.3	2.5	20	.2	3.4
106–110	4	12.5	2	19	.2	3.6
111–115	4	14.6	2	20	.2	3.8
116–120	4	14.6	1.5	20	.2	4.0
121–125	3	13.2	1	22	.2	4.5
126–130	3	15.6	1	16	.25	4.0
131–135	3	17.8	1	12	.25	3.5
136–140	3	19.2	0.5	10	.2	3.0
141–145	3	20.8	0.5	8	.3	2.5
146–150	3	—	—	4	.2	2.5

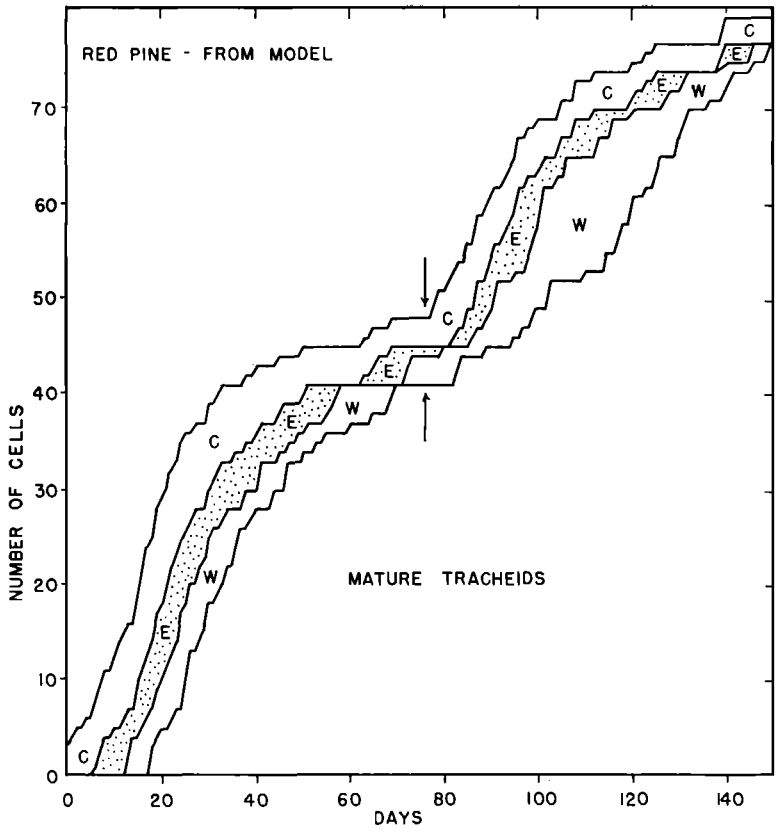

FIGURE 6. *Simulated development of a model red pine annual ring. The portion marked C is the cambial zone, the portion marked E and stippled is the enlarging zone, the portion marked W is the zone of cell wall thickening. Note that the zones of enlargement and wall thickening disappear when no new cells enter these respective phases. The arrows mark the end of a simulated mid-summer drought. The input for this ring is given in Table 2 and the final cell measurements in Figure 5. If read vertically, the graph gives the number of cells in each zone of differentiation for each day of the season. For instance, at day 40 there are two cells in the zone of wall thickening, six cells in the zone of enlargement, and seven cells in the cambial zone. If read horizontally, the graph shows how long each cell was in the phase of enlargement and cell wall thickening. For instance, cell number 50 spent two days in the phase of enlargement and six days in the phase of wall thickening.*

1964) show a peak in the middle of the cambial zone suggesting that the cells in the middle of the cambial zone divide most rapidly. The input for this example (with 1 phloem mother cell, an initial and 8 xylem mother cells) was chosen so that cells would enlarge and divide fastest when in the center of the cambial zone. On the basis of these rates the predicted number of divisions for each position from the phloem to the xylem side was 5, 7, 8.5, 9.5, 10, 10, 9.5, 8.5, 7 and 5. However, because cells change position in the cambial zone during the cell divisions cycle (Fig. 2), the number of divisions observed for each position was respectively 4, 7, 7, 7, 7, 7, 8, 5, 6 and 3. Although the input predicted a peak in frequency, the output was a plateau across most of the cambial zone. These results suggest that each radial file in a sample must have a different distribution of mitotic frequency. If all files were the same, there could be no peak in frequency

in the center of the cambial zone. In addition, this example shows that it may not be possible to interpret the observed peak of mitotic frequency as representing a point where the length of the cell division cycle is minimum and, hence, where there is a high concentration of mitotic stimulating substances.

There is a difference of opinion about the number of times that xylem mother cells redivide after being formed by the initial cell (Philipson and Ward 1965). The real problem is that redivisions cannot be counted from cross sections. The model, however, permits actual counting of the number of redivisions. Under the constant conditions used in this example 41 cells passed through the entire phase of division in the 50-day interval. Of these 41 cells, 1 redivided 2 times, 23 redivided 3 times, 15 redivided 4 times and 2 redivided 5 times. Other test runs were made using different numbers of mother cells and different rates and distributions of division. With 15 xylem mother cells, about the maximum observed in conifers, a few cells redivided 6 times. In general, the number of redivisions in these test runs was independent of the average length of the cell division cycle, but was lower when the peak rate of division was at the phloem edge of the cambial zone than when it was at the xylem edge.

Discussion

The construction and use of the model shows some of the values of the modelling technique and the special value of being able to test the output against real cell measurements. First, to construct a workable model necessitates the identification and definition of variables and an analysis of the process of cambial activity. Thus using the model is a good way to learn about the process of cambial activity. Second, the model enables quantitative values for different variables to be tested even where few experimental data are available. In this way the expected range of values for unquantified variables can be estimated. Third, the model provides information not directly obtainable from destructive sampling of trees because individual cells may be followed through differentiation.

Perhaps the most valuable characteristic of the model is that it can generate new information. Examples have been given of the data obtainable by following individual cells day-by-day. Another example is that setting up input to simulate a ring provides insight into the timing of the various processes of differentiation. It is easy to forget that a cell which leaves the phase of division may then spend a week or more in the phase of enlargement followed by an additional week or two in the phase of wall thickening. Thus, the radial size of the cell is determined by the input of one interval and its wall thickness by the input of another, as demonstrated experimentally for compression wood formation by Kennedy and Farrar (1965). For example, the sudden increase in cell division that followed relief of the drought in the red pine ring produced cells that did not reach maximum size and maturity until 12 days and 20 days, respectively, after the resurgence of cambial activity. Six cells then matured within the same 5-day interval and all had the same wall thickness. There are many similar instances where the timing of the controls that determine the final dimensions of a cell are not intuitively obvious, but can be pinpointed by studying the output of the model.

It must be remembered that similar models could be developed using closely related rules. For example, key points in cambial activity are the rules that control the time when a cell stops one phase of differentiation and starts the next. We have chosen to use rules governing, for each day, the maximum number of mother cells, maximum radial cell diameter and maximum cell wall thickness. Alternative rules could be developed that would determine the phase of differentiation of a cell by its distance

from the phloem, as suggested by Whitmore and Zahner (1966), or that specified the length of time that a cell can remain in each phase, as suggested by Wodzicki (1962). All three sets of rules could be used to produce analogous output because they are so closely related. It is not possible to ascertain by using our model which set of rules is most analogous to real cambial activity.

It is important also to remember that there are other sets of variables at other levels, such as environmental conditions and concentration of growth regulators, that may directly determine the values for variables in our model. These molecular and physical variables could be set up as subprograms to generate the values used in the model. For example, Zahner and Stage (1966) have developed a method for calculating and accumulating daily moisture deficit from rainfall data, showing that 78 percent of annual variation in cambial activity (annual basal area increment) could be accounted for by variation in the accumulated moisture deficit. Presumably the magnitude of the water deficit at any time influences the values of the variables used in the present model. It should be possible to have the daily water deficit translated into daily sets of input values so that rainfall data could be converted directly into the structure of the annual ring at a particular point in the tree.

The model could also be used to accumulate data on radial files at different positions in the tree to simulate cambial activity for the tree as a whole. The secondary xylem and phloem of a tree is composed of a large number of radial file subunits whose characteristics change with position in the tree. Use of the model in this way could provide two types of information: (1) a description of how the variables in cambial activity are affected by position in the tree, thus elucidating the mechanism of the position effect; (2) the simulation of the production of the entire annual sheath of secondary xylem and phloem from meteorological, site and positional data that in turn generate the input for files at all positions in the tree.

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