Interrelationship between mean length, rate of intrusive elongation, frequency of anticlinal divisions and survival of fusiform initials in cambium*

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The length of fusiform initials has important bearing on the length of xylem cells produced by the cambium, at least in conifers. Itself it is determined by the rates of such events in cambium as intrusive elongation, anticlinal divisions and intracambial competition for survival. It is therefore important to formulate relations between the quantities characterizing these events and the mean length of cambial cells.

Symbols and definitions

- R — radius of cambium cylinder, in mm.;
- ΔR — increment of R due to the production of xylem, mm.;
- S_r — surface of the cambium with radius R , mm.²;
- ΔS — increment of S during the production of ΔR of xylem;
- L_r — total length of the fusiform initials in the cambium with radius R , mm.;
- $L_{r+\Delta r}$ — as above but at $R+\Delta R$;
- ΔL — increment of L during the production of ΔR of xylem, mm.;
- N_r — number of fusiform initials in the cambium with radius R ;
- $N_{r+\Delta r}$ — as above but at $R+\Delta R$;
- H_r — mean length of the fusiform initials at R , mm.;
- $H_{r+\Delta r}$ — as above but at $R+\Delta R$;
- W_r — average width (tangential diameter) of the fusiform initials at R , mm.;
- $W_{r+\Delta r}$ — as above but at $R+\Delta R$;
- ΔL_e — total intrusive elongation of the fusiform initials, i.e. the sum of the increments in length of the cells due to their intrusive elongation during the production of ΔR of xylem, mm.;
- E — mean rate of intrusive elongation of a fusiform initial during the production of 1 mm. of xylem, $E = \frac{\Delta L_e}{N_r \Delta R}$, in mm.⁻¹.
- ΔL_p — total length of the partitions formed by the anticlinal divisions of pseudotransverse type in the fusiform initials during the production of ΔR of xylem, the partitions are measured along cell axis, mm.;
- ΔN_p — corresponding number of the anticlinal divisions;
- P — mean frequency of anticlinal division in a fusiform initial, i.e. mean number of anticlinal

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divisions in one cell during the production of 1 mm. of xylem, $P = \frac{\Delta N_p}{N_r \Delta R}$, no. mm.⁻¹;

ΔL_f — total length of the fusiform initials which failed during the production of ΔR of xylem, mm.;

ΔN_f — corresponding number of failed cells;

a — fraction of H_r corresponding to the mean length of one partition, $\frac{\Delta L_p}{\Delta N_p}$, formed in an anticlinal division at R $a = \frac{\Delta L_p}{\Delta N_p H_r}$;

b — fraction of H_r corresponding to the mean length of failing cell, $\frac{\Delta L_f}{\Delta N_f}$, $b = \frac{\Delta L_f}{\Delta N_f H_r}$;

GENERAL CONSIDERATIONS

The increment of total length of fusiform initials in the cambium is a sum of total elongation plus total length of the partitions formed by anticlinal divisions minus total length of failed cells:

$$\Delta L = \Delta L_e + \Delta L_p - \Delta L_f \quad 1,$$

From the definitions we have,

$$\Delta L_p = a H_r \Delta N_p, \quad \Delta L_f = b H_r \Delta N_f$$

$$\text{hence} \quad \Delta L = \Delta L_e + a H_r \Delta N_p - b H_r \Delta N_f \quad 1a.$$

On the other hand we have,

$$N_{r+\Delta r} = N_r + \Delta N_p - \Delta N_f \quad 2.$$

since every anticlinal division adds one cell and every act of failing subtracts one cell.

Introducing ΔN_f from (2) into (1a) we obtain,

$$\Delta L = \Delta L_e + a H_r \Delta N_p - b H_r (N_r + \Delta N_p - N_{r+\Delta r}) \quad 1b.$$

Total length of cells in cambium at $R + \Delta R$ is equal to the sum of the total length at R plus the increment of the length during the production of ΔR of xylem,

$$L_{r+\Delta r} = L_r + \Delta L \quad 3.$$

$$\text{but, } L_r = N_r H_r, \quad L_{r+\Delta r} = N_{r+\Delta r} H_{r+\Delta r}$$

$$\text{hence} \quad N_{r+\Delta r} H_{r+\Delta r} = N_r H_r + \Delta L \quad 3a.$$

The increment of cambium surface, ΔS , during the production of ΔR of xylem is due to the increment of total cell length and to the increment of cell width. We have then,

$$\Delta S = L_{r+\Delta r} W_{r+\Delta r} - L_r W_r$$

what can be written in a more convenient form,

$$\Delta S = \Delta L W_{r+\Delta r} + L_r (W_{r+\Delta r} - W_r)$$

hence,

$$\frac{\Delta S}{S_r} = \frac{\Delta L W_{r+\Delta r}}{L_r W_r} + \frac{W_{r+\Delta r}}{W_r} - 1 \quad 4.$$

but,

$$\frac{\Delta S}{S_r} = \frac{2\pi(R+\Delta R) - 2\pi R}{2\pi R} = \frac{\Delta R}{R}$$

hence,

$$\Delta L = N_r H_r \frac{W_r}{W_{r+\Delta r}} \left(\frac{\Delta R}{R} + 1 \right) - N_r H_r \quad 4a.$$

Introducing ΔL from (4a) and $N_{r+\Delta r}$ from (3a) into (1b) we obtain after elementary rearrangements:

$$\Delta L_e = H_r \Delta N_p (b-a) + N_r H_r \frac{W_r}{W_{r+\Delta r}} \left(\frac{\Delta R}{R} + 1 \right) \left(1 - b \frac{H_r}{H_{r+\Delta r}} \right) + N_r H_r (b-1) \quad 5.$$

This equation gives the total intrusive elongation in the considered portion of the cambium during the production of ΔR of xylem in terms of the average cell length, cell width and number of anticlinal divisions. For the given values of N_p , H_r , $H_{r+\Delta r}$, W_r , $W_{r+\Delta r}$ there is only one value of ΔL_e (R , ΔR , N_r , a and b are specified).

Introducing (5) into (1) or (1a) after rearrangements we obtain equations for total length of failed cells, ΔL_f , or number of failed cells, ΔN_f , during the production of ΔR of xylem,

$$\Delta L_f = b H_r \Delta N_p + N_r H_r b \left[1 - \frac{W_r H_r}{W_{r+\Delta r} H_{r+\Delta r}} \left(\frac{\Delta R}{R} + 1 \right) \right] \quad 6.$$

$$\Delta N_f = \Delta N_p + N_r \left[1 - \frac{W_r H_r}{W_{r+\Delta r} H_{r+\Delta r}} \left(\frac{\Delta R}{R} + 1 \right) \right] \quad 7.$$

The equation (7) shows that for the given value of ΔN_p there is only one value of ΔN_f (H_r , $H_{r+\Delta r}$, W_r , $W_{r+\Delta r}$ are specified). The number of lost cells does not depend upon intrusive elongation directly but indirectly only through $H_{r+\Delta r}$. It means that increase in ΔL_e cannot be simply compensated by increase of ΔL_f or vice versa without affecting $H_{r+\Delta r}$.

Equations (5) and (7) provide a convenient method for the estimation of ΔL_e and ΔN_f from the data about the mean cell length and the number of anticlinal divisions which can be determined more easily than ΔL_e and ΔN_f directly.

Equation (5) is in terms of total intrusive elongation and number of anticlinal divisions in a portion of cambium during the production of ΔR of xylem. It may be convenient in practice to calculate ΔL_e , however for theoretical considerations an equation in terms of frequency of anticlinal division, P , and mean rate of intrusive elongation, E , is more adequate.

Recalling the definitions of P and E we have:

$$P = \frac{\Delta N_p}{N_r \Delta R}, \quad E = \frac{\Delta L_e}{N_r \Delta R}$$

(we assume that ΔR is small, otherwise instead of N_r a mean value between N_r and $N_{r+\Delta r}$ should be used).

Introducing (5) into the definition of E we obtain,

$$E = H_r P (b - a) + \frac{H_r W_r}{\Delta R W_{r+\Delta r}} \left(\frac{\Delta R}{R} + 1 \right) \left(1 - b \frac{H_r}{H_{r+\Delta r}} \right) + \frac{H_r}{\Delta R} (b - 1) \quad 5a.$$

The mean length and width of fusiform initials may be constant in cambium during the production of xylem, i.e. $H_r = H_{r+\Delta r} \equiv H$ and $W_r = W_{r+\Delta r}$. This happens in cambium located far from the pith, i.e. when R is large. The term $\frac{\Delta R}{R}$ may be then neglected and equation (5a) reduces to

$$E = HP (b - a) \quad 5b.$$

This is the relation between the rate of intrusive elongation frequency of anticlinal division and the constant mean length of fusiform initials in an older cambium. For the number of cells failing during the production of 1 mm. of xylem we obtain in this case, from (7),

$$\Delta N_f = N_r P \quad 7b.$$

Equations (5b) and (7b) may be easily interpreted. Let us explain equation (7b) first. In cambium located far from pith and composed of cells with constant mean length and width the number of cells does not increase appraisably during the deposition of a thin layer of xylem. If anticlinal divisions occur in a certain number of cells a similar number of cells must be lost from the cambium which is just expressed by (7b). If the mean length is to be constant and equal to H then intrusive elongation must be adequately counteracted by anticlinal divisions. If during the production of 1 mm of xylem every cell divides anticlinally once, i.e. P is unity, then the rate of intrusive elongation should be such as to allow one cell of each pair to attain length H_o and the second one length bH at which length it will be lost. Since the total length of the two sister cells at the moment of their origin consists of the initial length of their mother cell, H_o , plus the length formed during the intrusive elongation of the mother cell, E , plus the length of the partition wall, aH , we have:

$$H_o + bH = H_o + E + aH$$

where H_o denotes length of a surviving cell at its origin in a pseudotransverse division, H denotes the mean cell length. The same is expressed by (5b) when $P = 1$.

Our equations contain the coefficients a and b which must be estimated for the given type of cambium before using the equations. The coefficients represent some mean values and therefore contain some errors. It may be asked if the error introduced into the calculated variable by errors in a and b is tolerable. Generally if we have a quantity A which is a function of variable x , $A = f(x)$, the error in A caused by error in x is,

$$\delta A = \pm \frac{\partial f}{\partial x} \delta x$$

and the relative error is,

$$\frac{\delta A}{A} = \pm \frac{1}{f(x)} \left| \frac{\partial f}{\partial x} \right| \delta x$$

where δA denotes the error in A due to error δx in x . Using this last formula for finding the relative error in E from (5a) due to error in b when $W_r = W_{r+\Delta r}$, we obtain,

$$\frac{\delta E}{E} = \pm \left| 1 - \frac{H_r}{E} \left(\frac{1}{R} - aP \right) \right| \frac{\delta b}{b} \quad 8.$$

For the data from the 11–12th annual ring of *Thuja* (table 1, 2)

$$\frac{\delta E}{E} = \pm 0.79 \frac{\delta b}{b}$$

what means that 10% error in b causes 8% error in E .

The relative error in E due to the error in a is

$$\frac{\delta E}{E} = \pm \frac{aH_r P}{E} \frac{\delta a}{a} \quad 9.$$

what for the data as previously gives $\pm 0.51 \frac{\delta a}{a}$.

The relative error in ΔL_f due to error in b is

$$\frac{\delta \Delta L_f}{\Delta L_f} = \pm \frac{\delta b}{b} \quad 10.$$

what means that it is the same as the relative error in b .

We can conclude that our equations are sufficiently tolerant for errors in the coefficients.

EXAMPLES OF APPLICATION

Calculations were made using the data for 3 samples of cambium (wood) of *Thuja occidentalis* presented in a previous paper (Hejnowicz and Brański 1966) and the calculated values of ΔL_e , ΔL_f and ΔN_f were compared with the respective values obtained from direct measurements. Two sets of values of the coefficients a and b were used: 1) actual values for the given sample, i.e. a and b determined from data relating to the given sample; and 2) mean values, i.e. averaged from the actual values. The calculated and measured values are listed in table 1 together with the data used in calculations. As is seen, the agreements of the calculated values with the respective measured values is fair both when actual and mean values of a and b were used.

Mean rate of intrusive elongation, E , was calculated using equation (5a). For

Table 1

Calculated and directly measured total intrusive elongation and total loss of cells in 3 portions of cambium of *Thuja occidentalis* together with the data (Hejnowicz, Brański 1966) used in calculations

Quantity		In a portion of cambium consisting of 50 cells and their derivatives during the production of the annual ring no.:		
		4	11—12	15—17
Total intrusive elongation, ΔL_e in mm.	calculated	55.4	45.8	72.2
		58.3	49.4	64.7
	measured	56.2	47.0	69.6
Total loss of cells, ΔL_f , in mm.	calculated	34.2	52.5	87.9
		29.5	60.8	87.9
	measured	39.4	53.8	93.1
Total number of lost cells, ΔN_f	calculated	30	32	42
	measured	32	32	45
Data used in calculations				
Distance from the center, R , in mm.		6.0	37.4	44.9
Increment of R , ΔR , in mm.		3.9	4.1	4.0
Number of cells	initially, N_r	50	50	50
	finally, $N_{r+\Delta r}$	69	53	53
Mean cell length in mm.,	initially, H_r	1.46	2.87	3.13
	finally, $H_{r+\Delta r}$	1.69	2.93	3.05
Number of anticlinal divisions, ΔN_p		51	35	48
Coefficient $a = \frac{\Delta L_p}{\Delta N_p H}$	actual	0.35	0.21	0.20
	average	0.25	0.25	0.25
Coefficient $b = \frac{\Delta L_f}{\Delta N_f H}$	actual	0.78	0.58	0.67
	average	0.67	0.67	0.67
Total length of pseudotransverse partitions, ΔL_p in mm.		28.1	21.3	30.1

comparison E was calculated directly from the measured ΔL_e by using the definition of E . The two sets of the values of E fit together fairly well, table 2.

The mean frequencies of anticlinal division, P , on which the calculations of E were based and which were obtained from direct measurements are shown in table 2 as well.

VARIATION OF THE MEAN LENGTH OF FUSIFORM INITIALS

It may be asked, how do intrusive elongation and anticlinal divisions influence the mean length of fusiform initials. To answer fully this question we need a function

Table 2

Frequency of anticlinal division in a fusiform initial per 1 mm. of xylem production (experimental data) and mean rate of intrusive elongation in mm. per 1 mm. of xylem production, calculated and experimental data, *Thuja occidentalis* described in table 1

	During the production of annual ring no.:		
	4	11—12	15—17
Frequency of anticlinal division, P , in no. mm. ⁻¹	0.216	0.164	0.226
Rate of intrusive elongation, E , in mm. mm. ⁻¹	calculated	0.272	0.228
	experimental	0.240	0.220
			0.310
			0.334

relating the mean length to radial distance of the cambium. Such a function may be obtained from (5a) in three steps. In the first step we put $H_{r+\Delta r} = H_r + \Delta H$, $\frac{W_{r+\Delta r}}{W_r} = 1 + \frac{W'_r}{W_r} \Delta R$, where ΔH denotes increment of the mean length occurring during the production of ΔR of xylem, W'_r denotes the derivative of W in respect to radial distance of the cambium at point R . Introducing this into (5a) after rearrangement we obtain

$$\frac{\Delta H}{\Delta R} = \frac{H^2 \left[\frac{b-1}{R} + \frac{W'}{W} (1-b) - P(b-a) \right] + HE + \Delta R \frac{W'}{W} [HE - H^2 P(b-a)]}{Hb + \Delta R \left[HP(b-a) \left(1 + \frac{W'}{W} \Delta R \right) - E \left(1 + \frac{W'}{W} \Delta R \right) + H(b-1) + \frac{W'}{W} + \frac{H}{R} \right]} \quad (11)$$

In the second step we take the limit as ΔR goes to zero. The left side of (11) becomes a derivative of H in respect to R and the right side becomes simpler because the terms containing ΔR vanish,

$$\frac{dH}{dR} = \frac{H}{b} \left[\frac{b-1}{R} + \frac{W'}{W} (1-b) - P(b-a) \right] + \frac{E}{b} \quad (11a)$$

In the third step we integrate (11a) and we obtain the demanded function in form of a general solution of (11a),

$$H_r = e^{-\int_{R_0}^R A dR} \left(H_0 + \int_{R_0}^R \frac{E}{b} e^{\int_{R_0}^x A dR} dx \right) \quad (12)$$

where $A = \frac{1-b}{bR} - \frac{W'(1-b)}{Wb} + P \frac{b-a}{b}$, H_0 is the mean cell length at R_0 as an initial condition.

For a cambium located far from the pith, i.e. when R is large, the term $\frac{b-1}{R}$ may be neglected in differential equation (11a). We can also assume that cell width is then constant, i.e. $W' = 0$. The equation (11a) reduces to,

$$\frac{dH}{dR} = \frac{E}{b} - HP \frac{b-a}{b} \quad 11b.$$

The general solution of (11b) is the same as of (11a) but $A = P \frac{b-a}{b}$. If we assume that E and P are constant when $R > R_0$, (11b) may be integrated easily and we obtain

$$H_r = \frac{H_0 - \frac{E}{P(b-a)}}{e^{\frac{P(b-a)}{b}(R-R_0)}} + \frac{E}{P(b-a)} \quad 12b.$$

As R increases the first fraction on the right side of (12b) decreases and finally vanishes, from which it follows that the mean length tends to attain a certain value determined by the second fraction, i.e. by E and P . We shall call this length as equilibrium length or in short notation H_{eq} . The H_{eq} is a value of mean length remaining in steady state in respect to E and P , i.e. the value which will not change at constant E , P and W . Hence we can put $H_{eq} \equiv H_0 = H_r$ what for cambium located far from pith and with constant mean length of the cells gives, from (12b)

$$H_e = \frac{E}{P(b-a)} \quad 13.$$

This equation is identical, of course, with the equation (5b) for constant mean length of the cells.

If the mean length is actually larger than H_{eq} it will tend to decrease, if it is smaller it will tend to increase during the production of xylem, what can be easily verified by putting H_0 larger or smaller than H_{eq} into (12b)

It is obvious that if E and P fluctuate the mean cell length will fluctuate as well except the case when the changes in E and P counteract one another. Bannan (1962, 1963, 1964 a, b) has shown for mature conifer stems that the frequency of anticlinal division rises as ring width falls below some value characteristic for the species. The rate of intrusive elongation rises in narrow rings too (Bannan 1965) but so that the ratio of E to P differs for rings of different width. Maximal mean cell length is associated with rings of about 1 mm. wide. Let us assume for a moment that there is high correlation between ring width on one hand and E and P on the other hand. Will there be equally high correlation between ring width and mean cell length? It would be so obviously if the equilibrium between H and E , P could be attained in a short time. However, if the equilibrium is attained slowly the mean length may not always show high correlation with the ring width. For instance, the length in a ring A following rings of other width than A may be different than in a ring A following rings of the same width. Thus we have a problem: what is the rate of approaching the equilibrium between H and E , P . To solve this it is convenient to introduce a concept of "halftime xylem increment" which is such an

increment of xylem during production of which approach to equilibrium with the constant values of E and P is half accomplished. Denoting the halftime increment as $\Delta R_{1/2}$ we can write,

$$H_{r+\Delta R_{1/2}} = \frac{H_r + H_e}{2} \quad 14.$$

where H_r denotes the initial length.

The concept of $\Delta R_{1/2}$ has sense for such a cambium in which H is constant if E and P are constant, i.e. for a cambium located far enough from pith. Hence, we can use equation (12b) to calculate $\Delta R_{1/2}$. Changing the notation in (12b), $H_o \rightarrow H_r$, $R - R_o \rightarrow \Delta R_{1/2}$, and introducing into (14) we have,

$$\frac{H_r - \frac{E}{P(b-a)}}{e^{\frac{P(b-a)}{b} \Delta R_{1/2}}} + \frac{E}{P(b-a)} = \frac{1}{2} \left[H_r + \frac{E}{P(b-a)} \right] \quad 14a.$$

hence
$$\Delta R_{1/2} = \frac{b}{P(b-a)} \ln 2 \quad 15.$$

We see that the halftime increment is inversely proportional to the frequency of anti-clinal division. Using the values of P , a and b for *Thuja* $\Delta R_{1/2}$ amounts to 2.4 mm. which is a comparatively large value. It means that the process of approaching equilibrium between the mean cell length and E , P is rather slow compared with the rate of annual ring formation. One year of action of a given E and P will usually not bring the mean length to equilibrium with the E and P if the latter differ from these which acted in previous year. In such a case the mean cell length during the production of a ring will be determined rather by the length at the end of the previous season and this way by E and P which were acting previously than by E and P acting actually. Since E and P are related to ring width the mean length of tracheids in a ring may show correlation with width of the previous rings which has been observed by Liang (1948).

Now we would like to consider the problem of the variation of mean cell length in young cambium when R cannot be neglected in the differential equation (11). This problem is very interesting because in nonstoried cambia the mean length of fusiform initials increase during the production of the first centimeters of xylem until a certain value is attained after which the length remains constant or fluctuates about this value (see for instance Hejnowicz and Hejnowicz 1958). What is the reason of this increase, is it due to certain systematical change of E and P during the cambium development or perhaps it reflects some equilibration process between the length and the factors determining it like E , P , R . We have seen that the mean cell length increases in an old cambium if the length is below the value of H_{eq} . One can suppose that when cambium starts its development the mean length of its cells may be much below the length in equilibrium with E and P and due to this it tends to attain this equilibrium. An expression approximating H_e in young

cambium can be obtained from (5a) by putting $H_{r+\Delta r} = H_r \equiv H_e$ and for simplicity $W_{r+\Delta r} = W_r$

We obtain,

$$H_e = \frac{E}{\frac{1-b}{R} + P(b-a)} \quad 13a.$$

We see that the H_e increases slightly when R increases, what means that the mean length cannot be constant in young cambium even if E and P are constant. From the data for the 4th annual ring of *Thuja* (table 1, 2) it follows that the mean length

Fig. 1. Comparison of the measured average length of tracheids in *Thuja* and curve of cell length H_r as function of radial distance of cambium R calculated for constant rate of intrusive elongation ($E = 0.27$), and constant frequency of anticlinal divisions ($p = 0.20$).

of fusiform initials was much below the H_e calculated from (13a); the length increased during the formation of this ring from 1.46 mm to 1.69 mm while the value of H_e was at the end 2.03 mm (E and P were similar in the two halves of the annual ring).

Let us calculate H_r from (12) making assumption that E , P and W are constant from the beginning of cambium development. A may be integrated and (12) takes the form

$$H_r = \left(\frac{R}{R_0} \right)^{\frac{b-1}{b}} e^{\frac{P}{b}(b-a)(R_0-R)} \left[H_0 + \frac{E}{b} \int_{R_0}^R \left(\frac{x}{R_0} \right)^{\frac{1-b}{b}} e^{\frac{P}{b}(b-a)(x-R_0)} dx \right] \quad 12c.$$

As an example we calculated H_r from the equation (12c) using for E , P , a and b the mean values from the data for *Thuja*, namely $E = 0.27$ mm.mm⁻¹, $P = 0.20$ no. mm⁻¹, $a = 0.25$, $b = 0.67$, $H_0 = 1.46$ mm. $R_0 = 6.0$ mm. Integration of the last term in [12c] was made graphically. The results are shown in Fig. 1. We see

that the calculated length follows a curve which fits well the mean lengths measured directly in the sample of *Thuja* wood which provided the equation (12c) with the values of E , P , a , b , H_0 . This is the same curve which we know from an ontogeny of a real cambium. Our supposition becomes a hypothesis; the increase of the mean cell length occurring in young cambium during the production of xylem maybe is an equilibration process when E and P either remain constant or each varies about the constant value characteristic for the cambium and the mean length initially is much below the respective H_e . The example considered above is not sufficient, of course, to make conclusion that the ontogenetic increase of the mean cell length in cambium is not accompanied by a systematic changes of E and P . The problem of nature of this increase needs special studies; we have pointed only on the possibility in which the increase of the length proceeds without systematic changes in E and P .

SUMMARY

The relationship between the variables mentioned in the title are formulated mathematically. Only two of them are independent. To calculate the rate of intrusive elongation, E , or the number of cells which fail during the production of ΔR of xylem we need only the mean cell length, H , and the frequency of anticlinal division, P , providing that the radius of cambium and certain two coefficients are known. The obtained equations were verified practically by calculating E and the number of lost cells for *Thuja occidentalis*. The calculated values agreed well with the values from direct measurements.

The general expression for the mean length of fusiform initials as a function of radial distance of the cambium is given. The mean length tends to attain a certain value H_e determined by E , P and R . It is shown that if the mean length is much below the respective value of H_e at small R the length will increase when R increases even if E and P remain constant, and that this increase is in close agreement with that occurring in cambium during the production of first centimeters of xylem.

If E and P vary in cambium during the production of xylem then the mean length of fusiform initials will vary too. However the actual length may be different than H_e determined by the actually acting E and P as it takes time to attain equilibrium between the mean length and E , P . The expression for the increment of xylem during the production of which this equilibrium in an old cambium is half accomplished is given. An example of calculations based on data for *Thuja* shows that the rate of approaching the equilibrium is low in comparison with the rate of formation of annual ring.

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Zależności między długością komórek, szybkością wzrostu intruzywnego, częstotliwością podziałów antyklinalnych i przeżywalnością komórek w kambium

STRESZCZENIE

Zależności między zmiennymi wymienionymi w tytule zostały sformułowane matematycznie. Tylko dwie zmienne są niezależne, w związku z czym do obliczenia szybkości wzrostu intruzywnego, E , albo ilości komórek eliminowanych z kambium w pewnym okresie czasu, potrzeba tylko danych o średnich długościach komórek, H , i o częstotliwości podziałów antyklinalnych, P , zakładając, że znany jest promień kambium i pewne dwa współczynniki. Sprawdzono użyteczność praktyczną otrzymanych równań obliczając E i ilość komórek eliminowanych na podstawie danych dla *Thuja occidentalis*. Obliczenia są łatwe i obliczone wartości zgadzają się dobrze z odpowiednimi wartościami z bezpośrednich pomiarów.

Przeciętna długość komórek inicjalnych w kambium dąży do osiągnięcia pewnej wartości H_e odpowiadającej stanowi równowagi między H a P i E . Wykazano, że jeżeli kambium rozpoczyna swój rozwój z przeciętną długością komórek która jest znacznie mniejsza niż H_e , a szybkość wzrostu intruzywnego i częstotliwość podziałów pozostają stałe, to długość ta wzrasta w czasie odkładania drewna w podobny sposób jak to się dzieje w naturze.

Jeżeli E i P w kambium ulegają wahaniom w czasie odkładania drewna to przeciętna długość komórek inicjalnych będzie się również wahać. Aktualna długość może się jednak różnić od długości zrównoważonej z E i P gdyż do osiągnięcia tej równowagi potrzeba odpowiedniego okresu czasu. Podano wyrażenie na grubość warstwy drewna w czasie odkładania której wspomniana równowaga jest osiągana w połowie. Przykład obliczenia opartego na danych dla *Thuja* pokazuje że ta połowkowa grubość jest dość duża w porównaniu z grubościami rocznych przyrostów drewna.