# Analysis of a one-dimensional model for the regulation of the size of the renewable zone in biological tissue.

S.I. Fadeev

*Institute of mathematic, Siberian department of the Russian Academy of Sciences, Novosibirsk, 630090*

S.V. Nikolaev

*Institute of cytology and genetics, Siberian department of the Russian Academy of Sciences, Novosibirsk, 630090*

V.V. Kogay

*Institute of mathematic, Siberian department of the Russian Academy of Sciences, Novosibirsk, 630090*

E. Mjolsness

*School of Information and Computer Science, and Institute for Genomics and Bioinformatics, University of California, Irvine, CA, USA.*

N.A. Kolchanov

*Institute of cytology and genetics, Siberian department of the Russian Academy of Sciences, Novosibirsk, 630090*

The results of a numerical study of a cell-oriented model of the regulation of the renewable zone in biological tissue are presented. The shoot apical meristem (SAM) that describes in a one-dimensional setting a theoretical scheme for the regulatory mechanism is provided as an example.

# 1. Introduction.

Differentiated cells make up the bulk of the cells of the adult organism. Each differentiated cell does not divide, as a rule, being specialized to perform a particular function in a particular organ tissue. However, in the adult organism there exist cells that are undifferentiated, although perhaps "predetermined". This means that their fate is, to a certain extent, predestined in the sense that they can become cells of a particular type or a restricted set of types There are stem cells that continue to divide at a definite rate. The stem cells are important for the life of the adult. In the animal tissue, they serve as sources of continuously renewable tissue (the skin, for example,) and certainly plants the stem cells of the shoot meristem (the growing tip of the shoot) provides the growth of the plant through its entire life.

According to current concepts "islets" of renewable tissue arise in a tissue during its development. The structure of the such renewable zones is as follows: one or a number of stem cells are in the zone center, these divide to create a pool of transit amplifying cells. The transit amplifying cells divide faster than the stem cells and they create the major cell bulk for the renewal process. When transit cells leave the renewable zone of the tissue they differentiate into tissue cells and cease to divide. Such a structure of the renewable zone forms a "niche" to maintain the stem cells and is maintained in the tissue for a long time. The size of the renewable zone must be regulated, depending on the organism's requirements. This is because the outflow of cells from the renewable zone depends on its size. Impairment of regulation, in the renewed zones of the epidermis, for example, causes malignant neoplasms.

In this work, a "cell-oriented" model for the structural-functional organization of the renewable zone is suggested. The shoot apical meristem (SAM) is provided as an example. The model is cell-oriented because its purpose is to describe the observed cell behavior (in the given case these are the types of the cells and the switching over from one type to another) within the framework of the minimal model [1]. The minimal model is not intended to describe real molecular-genetic systems that control cell behavior.

As indicated above, the plant retains definite groups of cells in a undifferentiated state through life. The group at the growing tip of the shoot, referred to as the shoot apical meristem (SAM), is of importance. The SAM contains stem cells that continuously divide, ultimately giving rise to all the cells of the plant. Although the

cells of the SAM are undifferentiated, they are determined with respect to the expression of certain genes, and, on this basis, the SAM is divided into compartments that are specifically positioned relative to each other in space through the entire life of the plant [2-4]. The cells that are located around the vertical axis of the meristem in the radius of 2-4 cells at the uppermost layers 3-4 (see fig.1) express, i.e. switch on-off the corresponding genes and, as a result, synthesize a protein called CLV3, belong to the central zone (CZ). Cells that express the WUS gene are located at the lower layer of the CZ cells. These cells are referred to the organizational center (OC), that is about 2-3 cells thick in the vertical direction. It is thought that the constancy of the SAM structure is required for the maintenance of the pool of the stem cells (2-4). The mechanisms that provide the constancy of the SAM structure are the subjects of both applied and basic in-depth studies. *The SAM proved to be an appropriaye candidate for developmental modeling (Mjolsness)…*

The meristem structure remains unaltered in the growing plant, but the resident cells that make up the compartments are replaced by the other cells so that the CZ cells displaced downward by the horizontally dividing above lying cells, become the OC cells, which are, in turn, displaced downward to become the cells of the rib-zone.
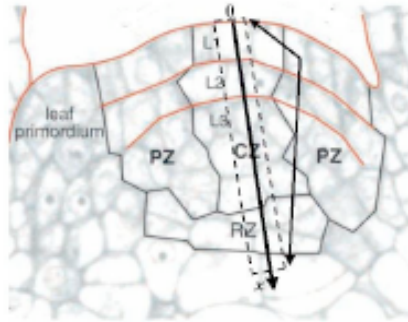
*Fig.1 Cross-section of the apical meristem shoot in  Arabidopsis T.*

Fig. 1 presents a cross-section of the shoot apical meristem of Arabidopsis T.
(adopted [2]). The external layer is denoted by L1, the second by L2; L3 is
arbitrarily called the third layer because it actually results from the cells deviding
in all the planes, it is no longer a layer, rather an accumulation (a collection) of
cells; CZ is the control zone, PZ is the peripheral zone, RZ is the rib-zone where
cells start to differentiate into the cells of the vascular system. The X axis is
pointed downwards from the shoot apex. Cells along the axis are considered as a
one-dimensional array in the proposed model.

 Here, we intend to focus attention on the stable position of the OC relative to the
upper point of the meristem in the vertical direction (position), on the possible
mechanisms of such a stabilization where the resident cells are substituting (by the
other cells, and on the regulation of the size of the renewable zone (the distance
from the meristem apex to the OC). To simplify, let us consider the vertical
column of cells on the meristem axis. Two top cells do not divide vertically and,

beginning with the third one, they make the cells flow down along the column. This allows to consider the simplest version of the one-dimensional model of the meristem structure.

**The one-demensional model for the meristem structure.**

There may be, in principle, two mechanisms that maintain the vertical compartmentalization of the meristem: first, symmetric division of the cells at the compartment boundaries with their determination in the morphogen fields and the second, asymmetric division of the cells at the boundaries [2-4]. In fact, division proceeds in all the planes in the L3 layer. This makes more likely the mechanism of the vertical structure maintenance. Furthermore, in mutants whose division orientation pattern is impaired at the early stages, seedlings with a normal structural framework are formed [5]. For this reason, a possible mechanism for cell determination controlled by positional information will be considered.

Fields of the concentrations of substances that spread over from different sources (for example, by diffusion) are the physical *carriers* of positional information. In the simplest case, the size of an assigned zone from the origin of coordinate axis may be determined by the threshold value of the concentration of the substance Y that diffuses from the origin (the activation zone W, for example). However, if the synthesis rate of the substance that "defines" the coordinate system (in the case, substance Y) changes, so the assigned zone area changes too.

In the case when, at a rather narrow range of Y concentration, a stable source of W is induced, its concentration at the origin of coordinate system may serve as a measure of its distance from the origin. The narrow zone for the W synthesis can be generated by repression of the synthesis where Y is present at high concentrations. In such a system, the W level at the origin may be interpreted as the distance from the origin to its source: the weaker the signal, the further away is the zone where it is synthesized. If the Y synthesis rate is proportional to the signal, displacement of the signal at a greater distance will produce a decrease in the synthesis rate Y and, as a consequence, the zone where the signal is synthesized will approach to the coordinate origin; an increase in the signal strength at the origin will produce an increase in Y, thereby shifting the signal source away from the origin.
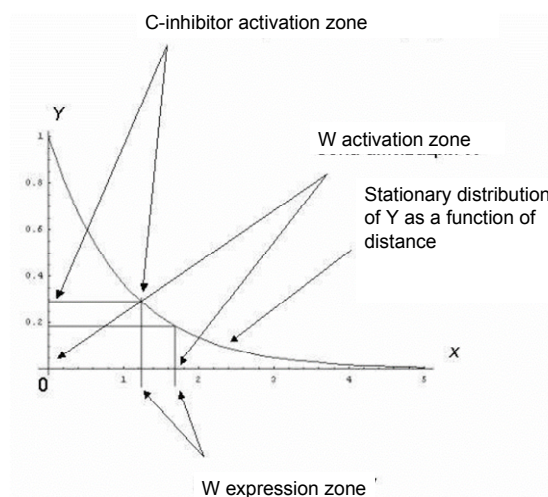


*Fig.2 represents schematically the one-dimentional model. The Y is distributed depending on the distance from the apical meristem and its threshold values at which the C and W expression is activated (enhanced).*

Fig.2 shows how the origin is related to the Y synthesis zone. The distance is plotted along the axis X in arbitrary units which corresponds to the vertical axis that passes through the center of the apical shoot. The concentration of the morphogen Y that spread from the apical shoot (from the point O) is plotted along the axis Y. As a result of diffusion of Y and of its continuous destruction (decay), a steady-state distribution (a decreasing function from x) is established. At concentration above the thresholds, Y may activate gene expression in the C and W substances. It should be noted that the activation threshold for the C is higher than that for the W gene. The assumption is made that the C substance is a repressor of the expression of the W gene. It follows that where the C gene is expressed, the W gene is repressed, and the W gene is actually expressed in the zone that is remote from the shoot apex (the axis origin).

## The equations of the model.

Let us consider an array of *n* cells between which the Y, W substances are transported with the conductance being $D_y$ and $D_w$, respectively. The reactions associated with substance synthesis may take place in the cells at a rate dependent on the presence of other substances:

$$\frac{du_k}{dt} = \frac{1}{\tau_k} g(x), \qquad x = \sum_j E_{kj} u_j + h_k.$$

where $E_{kj}$ are the <mark>regulation sensitivity coefficients</mark>. They are $> 0$ if the substance j stimulates the synthesis of the substance k., and $< 0$ if they repress it; $\tau_k$ are the coefficients inverse to the maximum expression rate. The parameters $h_k$ like $E_{ij}$ define the threhold values of the function g(x):

$$g(x) = \begin{cases} 0, & x \to -\infty \\ 1, & x \to +\infty \end{cases}$$

The sigmoid function [6] is used to describe the reaction rates in the proposed model:

$$g(x) = \frac{1}{2}\left(1 + \frac{x}{\sqrt{1+x^2}}\right).$$

It is further assumed that the substances Y and W diffuse. Y is synthesized in cell 1 and it diffuses into the other cells of the array. Its synthesis rate is dependent on the concentration of W in cell 1. Depending on the concentration of Y in the other cells the substance C may be synthesized, it does not diffuse, it <mark>decays</mark>. In these very cells, depending on the Y and C substances, the W substance may be synthesized. It diffuses throughout the cell array and, reaching the cell 1, it regulates the synthesis of the substance Y.

As a result, the model suggested for the process is stated as the Cauchy problem <mark>for an</mark> autonomous  system of equations in the following form:

$$\frac{dy_1}{dt} = -a_y y_1 + D_y(y_2 - y_1) + \frac{1}{\tau_y}g(x_1), \qquad x_1 = h_y + E_{yw}w_1,$$

$$\frac{dy_i}{dt} = -a_y y_i + D_y(y_{i-1} - 2y_i + y_{i+1}), \qquad i = 2, 3, \ldots, n-1, \tag{1}$$

$$\frac{dy_n}{dt} = -a_y y_n + D_y(y_{n-1} - y_n),$$

$$\frac{dc_i}{dt} = -a_c c_i + \frac{1}{\tau_c}g(U_i), \qquad U_i = h_c + E_{cy}y_i, \qquad i = 1, 2, \ldots, n, \tag{2}$$

$$\frac{dw_1}{dt} = -a_w w_1 + D_w(w_2 - w_1) + \frac{1}{\tau_w}g(V_1), \qquad V_1 = h_w + E_{wy}y_1 + E_{wc}c_1,$$

$$\frac{dw_i}{dt} = -a_w w_i + D_w(w_{i-1} - 2w_i + w_{i+1}) + \frac{1}{\tau_w}g(V_i), \quad V_i = h_w + E_{wy}y_i + E_{wc}c_i,$$

$$i = 2, 3, \ldots, n-1, \tag{3}$$

$$\frac{dw_n}{dt} = -a_w w_n + D_w(w_{n-1} - w_n) + \frac{1}{\tau_w}g(V_n), \qquad V_n = h_w + E_{wy}y_n + E_{wc}c_n$$

The initial conditions at t=0 are:

$$y_i = y_i^0, \qquad c_i = c_i^0, \qquad w_i = w_i^0, \qquad i = 1, 2, \ldots, n \tag{4}$$

where $y_i, c_i, w_i$ are the substance concentrations in the *i*-th cell, ay, ac, aw – are the distribution coefficients; Dy, Dw – denote the diffusion coefficients; the Ty……..

and E parameters were defined above.

Analysis of the steady-state solutions of the autonomous system demonstrated that, with a certain set of parameters, the proposed model truly describes the simple mechanism for gene expression; moreover, the model provides a stable position of the maximum concentration of the W substance in that area in space where another substance Y is at a certain concentration. If the given concentration of Y changes its position in space, the maximum concentration of W changes accordingly. It

proved that the  position of the maximum is resistant, in a rather wide range, to perturbations in the steady-state concentrations of W, i.e. this means that the model is very robust with respect to the retention ==stabilization== of the W zone positioning.

 Change in the size of the assigned zone may be due to the constant that defines the shift of the argument in the sigmoid dependency of the  synthesis rate of  W  on Y. A scheme for a regulatory mechanism underlies the considered model and, consequently, change in the constant may be interpreted as change in the steady-state level of an "external" regulator.

 Further, to describe the numerical algorithms, a vector representation of the Couchy problem will be needed. The expression will be of the following form…

$$\frac{dY}{dt} + Q_y Y = \frac{1}{\tau_y} F_y, \qquad \frac{dC}{dt} + a_c C = \frac{1}{\tau_c} F_c, \qquad \frac{dW}{dt} + Q_w W = \frac{1}{\tau_w} F_w, \tag{5}$$
$$Y = Y^0, \quad C = C^0, \quad W = W^0 \quad \text{при} \quad t = 0.$$

where Y, C, and W are the vectors with the ……. and 1,2,…, $n$, components, respectively, Y……. and W are the vectors of the initial conditions; Qy and Qw denote the three-diagonal matrices:

$$Q_y = \begin{bmatrix} a_y + D_y & -D_y & & & & \\ -D_y & a_y + 2D_y & -D_y & & & \\ \ldots & \ldots & \ldots & \ldots & \ldots & \\ & & -D_y & a_y + 2D_y & -D_y \\ & & & -D_y & a_y + D_y \end{bmatrix},$$

$$Q_w = \begin{bmatrix} a_w + D_w & -D_w & & & & \\ -D_w & a_w + 2D_w & -D_w & & & \\ \ldots & \ldots & \ldots & \ldots & \ldots & \\ & & -D_w & a_w + 2D_w & -D_w \\ & & & -D_w & a_w + D_w \end{bmatrix},$$

that are with diagonal elements prevailing and are, hence, well defined. The components of the Fy ….. and Fw vectors are sigmoid functions with the arguments indicated in (1)-(3)

$$F_y = \begin{bmatrix} g(X_1) \\ 0 \\ \ldots \\ 0 \\ 0 \end{bmatrix}, \qquad F_c = \begin{bmatrix} g(U_1) \\ g(U_2) \\ \ldots \\ g(U_{n-1}) \\ g(U_n) \end{bmatrix}, \qquad F_w = \begin{bmatrix} g(V_1) \\ g(V_2) \\ \ldots \\ g(V_{n-1}) \\ g(V_n) \end{bmatrix}.$$

## 4. Steady-State (stationary) solutions.

Let us consider a numerical definition of the stationary solutions for the autonomous system (5) by directly referring to the system of nonlinear equations (6):

$$Q_y Y = \frac{1}{\tau_y} F_y, \qquad a_c C = \frac{1}{\tau_c} F_c, \qquad Q_w W = \frac{1}{\tau_w} F_w, \tag{6}$$

It will be recalled that in (5) the first component of the W vector.

As known, the strandard solution of a system of nonlinear equations relies on Newton's method. However, the nonlinear problem has, as the rule, multiple (many) solution in the sense that the same set of parameters has a number of solutions. To detect this, recourse has been made to the method of continuation of solution with respect to parameters (7-9). The method enables to build the dependency of the solutions on the parameter with allowance made for the possible occurrence of multiple solutions in a certain variation range of the parameter The continuation method also involves Newton's iteration with the difference that, at each step of the continuation, the initial approximation is given algorithmically. This enables efficiently, after a few runs, to find the solution that correspond to the current value of the parameter.

Let us choose Ty as the parameter of the system, the rest of the parameters are all fixed. The specific form of the right hand side of the first vector equation of the system allows to take advantage of parametrization to accept W, as the system's parameter and to define the corresponding value of the $T_y$ parameter from the solution. In the given case, this allows to use the non-iteration method for the solution of the system without invoking Newton's method.

Let us consider the system (6) with the parameter p>0. Setting of p yields to the following equation:

$$\frac{1}{\tau_y} g(X_1) = p, \qquad X_1 = h_y + E_{yw} w_1. \tag{7}$$

Equation (6) then becomes a system of 3 vector linear algebraic equations whose right-hand sides depend on the p parameter. Solutions of this system may formally de written as:

$$Y(p) = pQ_y^{-1}e_1, \qquad C(p) = \frac{1}{\tau_c a_c}F_c(p), \qquad W(p) = \frac{1}{\tau_w}Q_w^{-1}F_w(p),$$

where e1 − is the first column of the identity matrix,

$$F_c(p) = \begin{bmatrix} g(U_1(p)) \\ g(U_2(p)) \\ \ldots \\ g(U_{n-1}(p)) \\ g(U_n(p)) \end{bmatrix}, \qquad F_w(p) = \begin{bmatrix} g(V_1(p)) \\ g(V_2(p)) \\ \ldots \\ g(V_{n-1}(p)) \\ g(V_n(p)) \end{bmatrix}.$$

$$U_i(p) = h_c + E_{cy}y_i(p), \qquad V_i(p) = h_w + E_{wy}y_i(p) + E_{wc}c_i(p), \qquad i = 1, 2, \ldots, n.$$

As a result, the W (p) vector, and, hence, the first component w1(p) become known. Thus the value of the Ty parameter, which corresponds to the given value of the p parameter, are estimated from:

$$\tau_y(p) = \frac{g(X_1(p))}{p}, \qquad X_1(p) = h_y + E_{yw}w_1(p). \tag{8}$$

The graph of the wi=w1 (ty) function given parametrically as w1=w1(p). Ty= will be called the diagram for the steady-state solutions of the system. Once the diagram is built, the number of steady-state solutions is defined be the number of intersections of the graph of the w1=w1(Ty) with the straight line ty=ty....where ty is the given parameter value.

Note that the sweeping method is the most powerful tool for the solution f systems of linear algebraic equations with the Qy and Qw matrices.

The stability of the steady-state solutions is defined numerically by integrating the Couchy problem (5) with the initial data in the form of the perturbed steady-state solution.

## The (semiiplicit) Halfimplicit method of integration.

To integrate the autonomous system with each constant step $\Delta$, the simplest halfimplicit scheme for the order accuracy $\Delta$ will be exploited. Let us introduce the following designations

$$t \in [t_i, t_{i+1}], \quad t_{i+1} = t_i + \Delta, \quad i = 1, 2, \ldots, \quad t_1 = 0,$$

$$Y^i \approx Y(t_i), \quad C^i \approx C(t_i), \quad W^i \approx W(t_i).$$

The autonomous system can be expressed approximately in the form of difference equations

$$\frac{Y^{i+1} - Y^i}{\Delta} + Q_y Y^{i+1} = F_y^i, \quad \frac{C^{i+1} - C^i}{\Delta} + a_c C^{i+1} = \frac{1}{\tau_c} F_c^i, \quad \frac{W^{i+1} - W^i}{\Delta} + Q_w W^{i+1} = \frac{1}{\tau_w} F_w^i,$$

Where…

$$
F_y^i = \begin{bmatrix} g(X_1^i) \\ 0 \\ \cdots \\ 0 \\ 0 \end{bmatrix}, \qquad
F_c^i = \begin{bmatrix} g(U_1^i) \\ g(U_2^i) \\ \cdots \\ g(U_{n-1}^i) \\ g(U_n) \end{bmatrix}, \qquad
F_w^i = \begin{bmatrix} g(V_1^i) \\ g(V_2^i) \\ \cdots \\ g(V_{n-1}^i) \\ g(V_n^i) \end{bmatrix},
$$

$$
X_1^i = h_c + E_{yw} w_1^i, \qquad U_j^i = h_c + E_{cy} y_j^i, \qquad V_j^i = h_w + E_{wy} y_j^i + E_{wc} c_j^i, \qquad j = 1, 2, \ldots, n.
$$

This yields the Cauchy problem for the following system of difference equations

$$
[I + \Delta Q_y] Y^{i+1} = Y^i + \frac{\Delta}{\tau_y} \Delta F_y^i, \qquad Y^1 = Y^0,
$$

$$
(1 + \Delta a_c) C^{i+1} = C^i + \frac{\Delta}{\tau_c} F_c^i, \qquad C^1 = C^0, \tag{9}
$$

$$
[I + \Delta Q_w] W^{i+1} = W^i + \frac{\Delta}{\tau_w} F_w^i, \qquad W^1 = W^0,
$$

where I is the identity matrix .

As follows from the form of difference equations (9); the Y…….. and W.. values

at $i{>}$or $= 1$ are estimated from the solution of the system of linear algebraic

equations with the ……, and….. matrices, respectively, i.e.

$$
Y^{i+1} = [I + \Delta Q_y]^{-1}(Y^i + \Delta F_y^i), \qquad C^{i+1} = \frac{1}{1 + \Delta a_c}(C^i + \frac{\Delta}{\tau_c} F_c^i),
$$

$$
W^{i+1} = [I + \Delta Q_w]^{-1}(W^i + \frac{\Delta}{\tau_w} F_w^i). \tag{10}
$$

Note that the [1+..] and […] обладают диагональным преобладанием, for this

reason the sweeping method can be used to solve the first and third systems of

linear algebraic equations.


## 6. Calculations of the steady-state solutions: examples.

Calculations for the following parameter values with n – being the number of cells are as follows:

$$
\begin{aligned}
&a_y = 0.1, &&D_y = 6, &&\tau_y = 1, &&h_y = -5, &&E_{yw} = 40 \\
&a_c = 1, &&\tau_c = 1, &&h_c = -20.5, &&E_{cy} = 20, &&&&(11) \\
&a_w = 0.75, &&D_w = 1.5, &&\tau_w = 1, &&h_w = -30, &&E_{wy} = 60, &&E_{wc} = -80.
\end{aligned}
$$

Fig.3 presents a diagram for the steady-state solutions. It follows that at Ty=1 the system (6) defines 3 steady-state solutions.
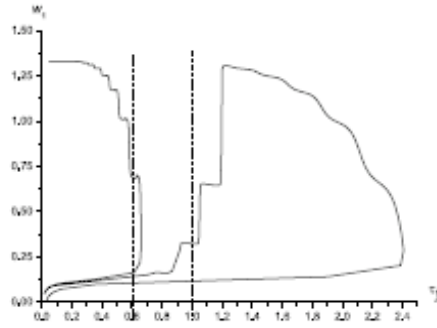


Fig.3 Diagram for steady-state solutions.
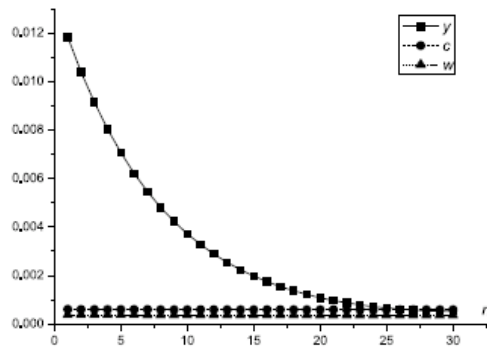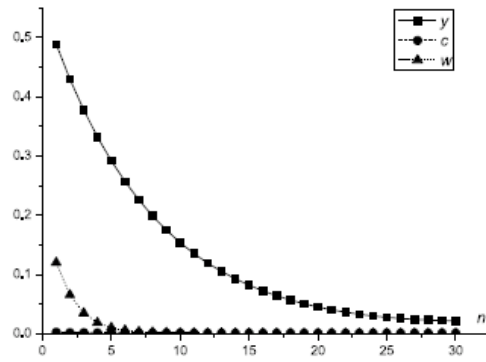
Fig.4 First steady-state solution at Ty=1.



Fig.5 Second steady-state solution at Ty=1.


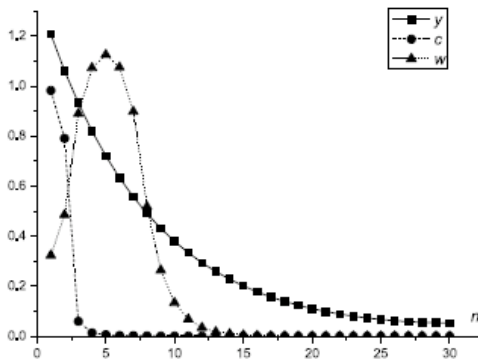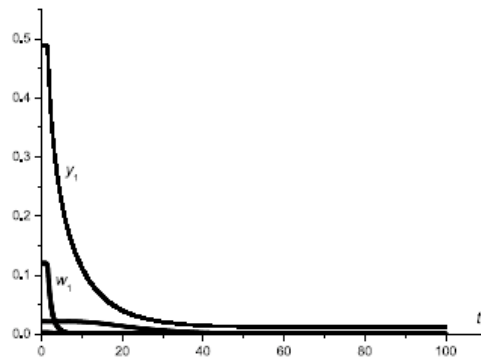
Fig.6 Third steady-state solution at Ty=1.

Fig. 7 Stability loss for the second steady-state solution
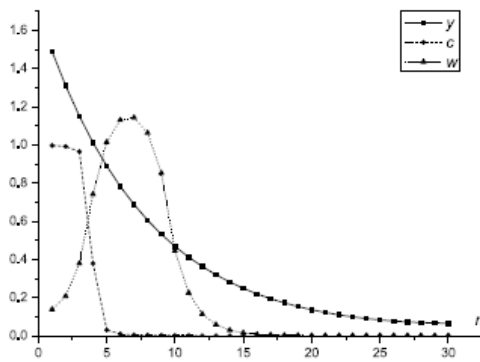


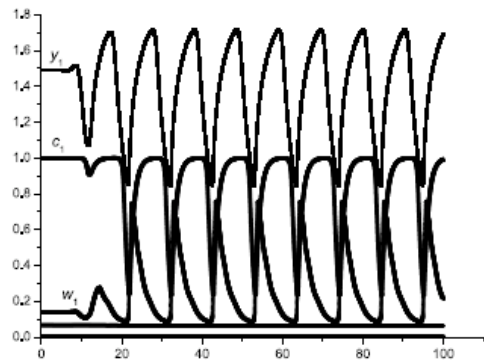Fig. 8 The third steady state solution

Fig 9 Loss of stability for the third steady-state solution

Fig. 4, 5, and 6 show how the substance concentrations are distributed in cells numbered from 1-3; fig. 4 – solution 1, fig.5 – solution 2; fig.6 – solution 3.

Stability analysis demonstrated that solutions 1 and 3 are asymptotically stable, while solution 2 is unstable. Having lost its stability, solution 2 tends to solution 1, and solution 4 to 5. After loss of its stability, solution 3 (fig. 8) passes to stable self-oscillations (fig. 9).
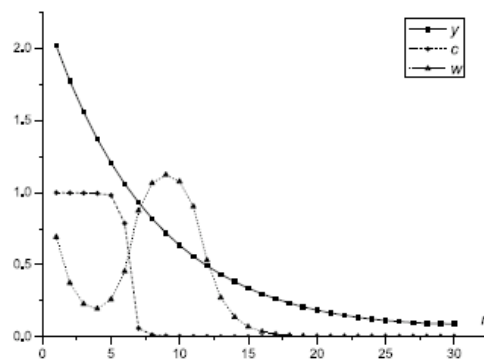


Fig.10   The fifth steady-state solution

# 7. Model for continuous distribution of substances.

The system (1)-(3) can be formally considered as the result of the discretization of the following system of equations that describe the continuous distribution of the the y(t,r), c(t,r), and w(t,r) and  substances:

$$\frac{\partial y}{\partial t} = D_y \frac{\partial^2 y}{\partial r^2} - a_y y, \qquad t > 0, \qquad r \in [0, R], \qquad R > 0, \tag{12}$$

$$\frac{\partial c}{\partial t} = -a_c c + \frac{1}{\tau_c g(U)}, \qquad U = h_c + E_{cy} y, \tag{13}$$

$$\frac{\partial w}{\partial t} = D_w \frac{\partial^2 w}{\partial r^2} - a_w w + \frac{1}{\tau_w g(V)}, \qquad V = h_w + E_{wy} y + E_{wc} c. \tag{14}$$

The $D_y$, $D_w$, $a_y$, $a_c$, $a_w$ parameters have the same sense as in the model (1)-(3). The R value is quite large. The y expression, defined by the w(t,0) value, is given by the boundary condition at the left end of the segment along $r$ :

$$D_y \frac{\partial y}{\partial r} = -\frac{1}{\tau_y} g(X), \qquad X = h_y + E_{yw} w(t, 0). \tag{15}$$

The condition is laid down at the right end of the segment along (по) $r$:

$$\frac{\partial y}{\partial r} = 0 \text{ при } r = R.$$

The boundary conditions for eq. 14 are:

$$\frac{\partial w}{\partial r} = 0 \text{ при } r = 0 \text{ и } r = R.$$

(here 'при' means 'at', and 'и' means 'and'; T.B.)

Analysis of the transitional processes requires in addition to the boundary conditions, the setting of the initial data the y,c, and w distribution at t=0.

Let us consider the boundary task on the [0,R] segment that describes the y,c, and

w distribution at t=0.

Let us consider the boundary *problem* on the [0,R] segment that describes the

steady-state distribution of substances in the form of graphs of the y(r), c(r), and

w(r) functions:

$$
\begin{aligned}
& D_y \frac{d^2 y}{dr^2} - a_y y = 0, && r \in [0, R], \\
& D_y \frac{dy}{dr} = -\frac{1}{\tau_y} g(X_1) && \text{при} \quad r = 0, \\
& \frac{\partial y}{\partial r} = 0 && \text{при} \quad r = R
\end{aligned}
\tag{16}
$$

$$
\begin{aligned}
& D_w \frac{d^2 w}{dr^2} - a_w w + \frac{1}{\tau_w} g(V) = 0, && r \in [0, R], \\
& \frac{dw}{dr} = 0 && \text{при} \quad r = 0, \\
& \frac{dw}{dr} = 0 && \text{при} \quad r = R,
\end{aligned}
\tag{17}
$$

where

$$
c = \frac{1}{\tau_c a_c} g(U), \qquad U = h_c + E_{cy} y,
$$

$$
X_1 = h_y + E_{yw} w(0), \qquad V = h_w + E_{wy} y + E_{wc} c
$$

Further use of the same designations for substance concentrations as in (1)-(3) will

not cause misunderstanding.

As above, in compliance with the idea of parameterization we will accept that in

equation:

$$\frac{1}{\tau_y}g(X_1) = p, \qquad X_1 = h_y + E_{yw}w(0), \tag{18}$$

p is predefined parameter.

The dependent on p function y(r), c(r), and p are defined from sequential solution of the linear boundary problems (16)-(17). Solution of the linear boundary with respect to y(r, p) is of the form:

$$y(r,p) = \frac{p}{\sqrt{a_y D_y}} \frac{1 + e^{-2\omega_y(R-r)}}{1 - e^{-2\omega_y R}} e^{-\omega_y r}, \qquad \omega_y = \sqrt{\frac{a_y}{D_y}}. \tag{19}$$

Therefore, it follows that:

$$c(r,p) = \frac{1}{s_c \tau_c}g(U(r,p)), \qquad U(r,p) = h_c + E_{cy}y(r,p). \tag{20}$$

Solution of the linear boundary problems with respect to w(r) can be represented in integral form using the expression of *the Green function*

$$\omega_w = \sqrt{\frac{a_w}{D_w}}, \qquad K_1(r,s) = \frac{e^{-\omega_w(r-s)}}{2\sqrt{a_w D_w}} \frac{(1 + e^{-2\omega_w(R-r)})(1 + e^{-2\omega_w s})}{1 - e^{-2\omega_w R}}, \qquad r > s,$$

$$K_2(r,s) = \frac{e^{-\omega_w(s-r)}}{2\sqrt{a_w D_w}} \frac{(1 + e^{-2\omega_w(R-s)})(1 + e^{-2\omega_w r})}{1 - e^{-2\omega_w R}}, \qquad r < s.$$

Let us introduce the following designations for convenience

$$G(r,p) = \frac{1}{\tau_w}g(V(r,p)), \qquad V(r,p) = h_w + E_{wy}y(r,p) + E_{wc}c(r,p).$$

In so doing, the solution takes the form

$$w(r,p) = \int_0^r K_1(r,s)G(s,p)ds + \int_r^R K_2(r,s)G(s,p)ds. \tag{21}$$

Therefore, we get:

$$w(0,p) = \int_0^R K_2(0,s)G(s,p)ds, \qquad K_2(0,s) = \frac{e^{-\omega_w s}}{\sqrt{a_w D_w}} \frac{1 + e^{-2\omega_w(R-s)}}{1 - e^{2\omega_w R}}.$$

Thus, the parameter value Ty(p) calculated by the following formula corresponds to the given parameter value p:

$$\tau_y(p) = \frac{g(X_1(p))}{p}, \qquad X_1(p) = h_y + E_{yw}w(0,p). \tag{22}$$

By doing so, the solution of the nonlinear boundary problem (16)-(17) is found at Ty=Ty(p).

It will be noted that, at R→∞, the solution of the boundary problem (16)-(17) is defined by formulas (18)-(22), where:

$$y(r,p) = \frac{p}{\sqrt{a_y D_y}} e^{-\omega_y r},$$

$$K_1(r,s) = \frac{e^{-\omega_w(r-s)}}{2\sqrt{a_w D_w}}(1 + e^{-2\omega_w s}), \qquad K_2(r,s) = \frac{e^{-\omega_w(s-r)}}{2\sqrt{a_w D_w}}(1 + e^{-2\omega_w r}).$$

Let us consider a discrete counterpart (analog) of the boundary problem (16)-(17). For this purpose, let us introduce an even division of the [0,R] segment into $n$-1 parts with the knots at r_i:

$$r_i = h(i - 1), \qquad h = \frac{R}{n-1}, \qquad i = 1, 2, \ldots, n.$$

Let us denote the approximate grid values of $y(r_i),\ c(r_i),\ w(r_i)$ as

$y_i,\ c_i,\ w_i$ сеточные ..... values ..... respectively.

Using the approximate differences, instead of the accurate derivatives with r:

$$\frac{\partial y}{\partial r}(r_i) \approx \frac{y_i - y_{i-1}}{h}, \qquad \frac{\partial w}{\partial r}(r_i) \approx \frac{w_i - w_{i-1}}{h},$$

$$\frac{\partial^2 y}{\partial r^2}(r_i) \approx \frac{y_{i-1} - 2y_i + y_{i+1}}{h^2}, \qquad \frac{\partial^2 w}{\partial r^2}(r_i) \approx \frac{w_{i-1} - 2w_i + w_{i+1}}{h^2},$$

we get the equation of the discrete model of the type (6):

$$\Omega_y Y = \frac{1}{h\tau_y} F_y, \qquad a_c C = \frac{1}{\tau_c} F_c, \qquad \Omega_w W = \frac{1}{\tau_w} F_w, \tag{23}$$

where Y,........ and Fw are the vectors with the same components as in (6); $\Omega$y and $\Omega$w are the threediagonal matrices dependent on the a......, and q parameters:

$$q_y = \frac{D_y}{h^2}, \qquad q_w = \frac{D_w}{h^2},$$

$$\Omega_y = \begin{bmatrix} a_y + q_y & -q_y & & & & \\ -q_y & a_y + 2q_y & -q_y & & & \\ \cdots & \cdots & \cdots & \cdots & & \cdots \\ & & & -q_y & a_y + 2q_y & -q_y \\ & & & & -q_y & a_y + q_y \end{bmatrix},$$

$$\Omega_w = \begin{bmatrix} a_w + q_w & -q_w & & & & \\ -b_w & a_w + 2q_w & -q_w & & & \\ \cdots & \cdots & \cdots & \cdots & & \cdots \\ & & & -q_w & a_w + 2q_w & -q_w \\ & & & & -q_w & a_w + q_w \end{bmatrix}.$$

Thus, the steady-state solution of the considered model formally agrees with (and actually) are solutions of the system (23) of the cell is of length h=1. It follows that, at an appropriate choice of model parameters, which a sufficiently large

number of cells, the concentration distribution in the cells y,c, and w, will be close

to the respective сеточным concentration values obtained by solving the boundary

problem (16)-(17). As an example, let us consider the solution of the boundary

problem (16)-(17) with the parameters (11) where the given R=0 instead of n Fig.

1 represents a diagram of the steady-state solution. It follows that the boundary

problem has 3 solutions at Ty=1. The diagrams in fig.3 and 11 are different. This is

because the system (6), formally representing a discrete model of the boundary

problem does not sufficiently approximate it. However, this has no real

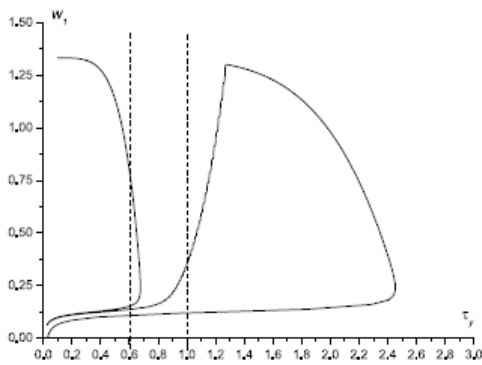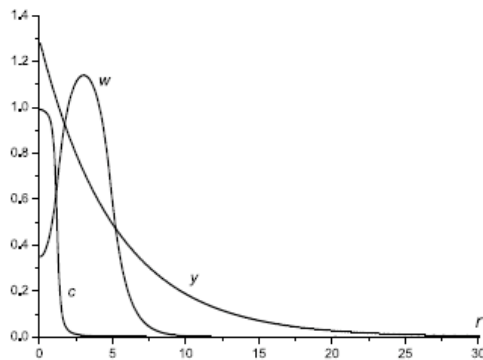consequence since the process itself is modeled by solutions of the system (6).



Fig. 11 Diagram of steady-state solutions.

Fig.12   The third steady-state solution

Fig.12 gives solution 3.

Comparison of this fig. with fig.6 makes it evident that substance concentration in the its cell is defined by the сеточные values of the boundary problem in the i-th node of the сетки, when the segment is even subdivided [0,30]into 30 parts by (по) r. The graphs represented in fig.11-12 will remain virtually the same, if the solution of the boundary problem is made on a longer segment R>30. In this case, the substance concentration will be defined by the сеточн. values of the solution of the boundary problem in the i-th node At R>30 the concentration of the substances monotonously tends to 0.

## 8. Conclusion.

The considered model demonstrates that the regulatory mechanism of the determination of the spatially distributed cells may provide a stable spatial localization of all the zone of the simulated cell ensemble. This manifests in perturbations introduced in the spatial distribution of the Y…… and W substances, which in turn, perhaps the "correct" distribution of the perturbations in the cell ensemble. The proposed mechanism produces a "correction" of these perturbations and thereby, a stabilization of the spatial localization of the zone. This is in agreement with the fact that the size and disposition of the compartments of the shoot apical meristem remains stable through the life of the plant despite the continuous perturbation caused by the environment and the other parts of the plant.

Here, emphasis is on analysis of the regulated stabilization of the size of the renewable zone. However, depending on the situations, the living organism happens to encounter, there may arise the need to retain the different sizes of the renewable zone in a particular tissue, if far no other reason than that the renewal rate of tissue depends on the size of the zone. The regulation of the zone size is possible within the framework of the model.

Change in the size of the assigned zone may by due to change in the constant that determine the shift in the argument in the sigmoid dependency of the synthesis rate W on Y. Since the considered model is a "theoretical scheme" of the regulatory mechanism, change in the constant may be interpreted as change in the steady-state level of a regulator "external" with respect to the proposed model включив? by incorporating it into the model equation.

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