Biostatics of *Arabidopsis thaliana*: 1-Dimensional Mathematical Models of the Growing Root[(*)]

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Abstract

To understand how an organism or ecosystem develops as a whole is a primary goal of systems biology. A mathematical model of an organ serves this goal by being simple and, at the same time, descriptive of the various developmental aspects, such as cell division, growth, tissue mechanics, genomics, etc., and the interplay between them. The organism of choice in this study is *Arabidopsis thaliana*, a plant that has been the object of extensive and successful research. We model mathematically two regions of the plant's root, the stele and the outermost cell layer. Using the rotational symmetry of the root, we view the longitudinal cross section of the root as a 2-dimensional region. The stele and the outer cell layer are two subregions that, in the context of our models, can be viewed as functionally independent of the rest of the root. Each subregion is then approximated, neglecting the transverse dimension, as a 1-dimensional continuum, on which our mathematical models are constructed. For the stele, our model predicts that mitotic activity decreases exponentially with the distance from the quiescent center. For the outer cell layer, we offer two continuum-mechanical models, aimed at describing the motion of the tissue and its viscoelastic properties. In the first of these models, we assume constant stiffness and obtain that a point in the tissue originally occupying position s is displaced after a time t to a new position, $s + t\,u(s)$, where u is a function well approximated by the linear form $a_0 + a_1 s$. In the second model, we assume linear displacement and find that the stiffness then varies in space, increasing toward the root tip at the rate $1/\sqrt{s}$ as $s \to 0$. This result agrees with the intuitive hypothesis that, near the tip, longitudinal strain is necessarily accompanied by tangential strain, which is hindered by the transversely oriented cellulose fibrils. The result also correlates with the expansin concentration found to decrease towards the root tip in certain plants.

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Affiliations, Credits, and Acknowledgments

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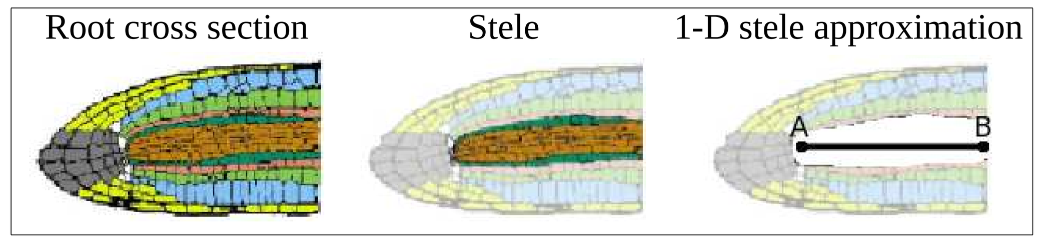
Stochastic Models of the Stele

Model Setting and Simulation Algorithm

The longitudinal cross section of the stele is approximated as a 1-dimensional continuous interval $[A, B] \subset \mathbf{R}$, as shown in the figure below.



Initially, the 1-dimensional stele cells are of roughly equal size, up to a small random perturbation. The locations of their distal (from the QC) ends are recorded as the points

$$\vec{s} = (s_1, \ldots, s_N) \tag{1}$$

in $[A, B]$, so s_j is the distal end of the j-th cell. The simulation proceeds as follows. The points (1) then move according to a velocity profile $v(s)$, which satisfies

$$v(A) = 0 \tag{2}$$

and generally alters the lengths of the cells. At every instant when a cell's size exceeds a threshold length,

$$s_j - s_{j-1} \geq \text{threshold length } d_0, \tag{3}$$

this cell divides (in this simulation, exactly in half, but this need not be the case generally). The locations of the new cells' distal ends are recorded.

The Choice of a Velocity Profile $v(s)$

We considered *a priori* the following three qualitatively different choices of $v(s)$ (here c denotes a constant),

$$v(s) = v_0 = \text{ const.}, \quad v(s) = cs, \quad v(s) = cs^2 \tag{4}$$

in the framework of the above simulation. The first of these choices is unsuitable as it does not alter cell length, hence fails to capture growth. The third choice potentially leads to discontinuous motion, contradicting intuition and observation. The second choice remains suitable, agrees with experimental data [7], and is used in the simulation.

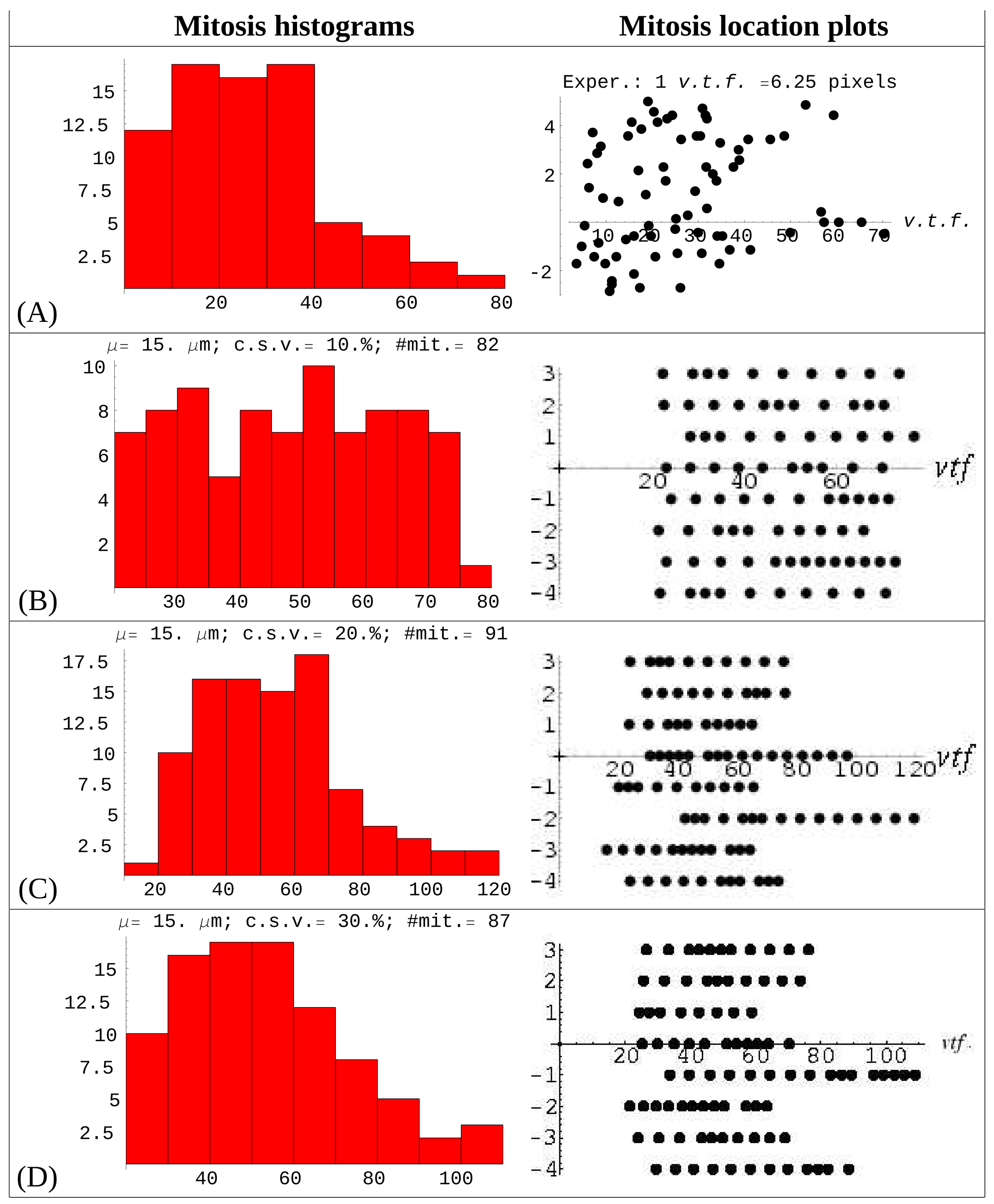
Experimental Methods and Analysis

In vivo time lapse recording of cell division in roots was performed using an automatic tracking method [3]. The experiment was run for approximately 15 hours. The obtained sequence of images was analyzed for the locations of the mitoses taking place in the observed cross section of the stele.

Simulations and Experimental Results

The following Figure shows experimental data (part (A)) juxtaposed with simulation results (parts (B-D)).

Figure Legend. Horizontal axis units: *vtf* (1 *vtf* = distance from vertex to focus in the parabola that bounds the root cross section). Panel (A): the experimentally observed 74 mitoses. Panels (B-D): a sample of simulation results, for different values of cell size variation (`c.s.v.`). Avg. cell size μ, shown above the histograms, was also varied, but only the shown value agrees with data. Tissue domain at time zero: $A = 0\ vtf,\ B = 60\ vtf$.



Panel (D) shows the best qualitative agreement with experiment. Simulations were also run for different values of the average cell size μ, but produced results in much less agreement with experiment. Thus, average cell size is a *prediction* of the present model.

1-Dimensional Steady Motion Models of the Root

A Brief on 1-Dimensional Continuum Mechanics

Consider a rod of length l and cross section A. In order to stretch or compress it lengthwise to a new length $l + \triangle l$, so as to achieve the fractional change in length

$$\epsilon = \frac{\triangle l}{l} \tag{5}$$

(negative in the case of compression), one must apply a certain force F, which depends on the required fractional stretch: $F = F(\epsilon)$. The dimensionless quantity ϵ is called, *strain*. Larger strain requires larger force. Also, the thicker the rod, the larger the force required to achieve a given strain. Thus, F is proportional to ϵA. For many materials, these proportions are linear:

$$F = Y \epsilon A, \quad \text{where the quantity } Y \text{ measures the stiffness of the material} \tag{6}$$

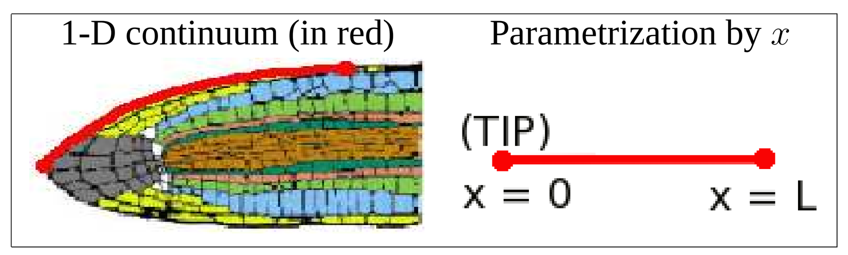
Rewrite (6) in the form

$$\frac{F}{A} = Y\epsilon \tag{7}$$

The left-hand side is called *stress*. Equation (7) describes the rod's *stress response* to a given strain ϵ. The intensity of this response is reflected by the constant Y, called *Young's modulus* [2], which characterizes the *stiffness* of the material.

Model Setting

The longitudinal cross section of the outer cell layer is regarded as a 1-dimensional continuum. It is parametrized by a variable x, which varies from 0 (the tip of the RAM) to L (some point on the RAM surface).



We consider the motion of this tissue fragment over a period of time commensurate with one cell cycle. At a time instant t during this period, a point originally in position x is displaced to a new location $x + u(t, x)$, where $u(t, x)$ is the *displacement*, to be found by solving the governing equations, below. The linear viscous effects, found small in experiments [5], have been neglected as a first approximation.

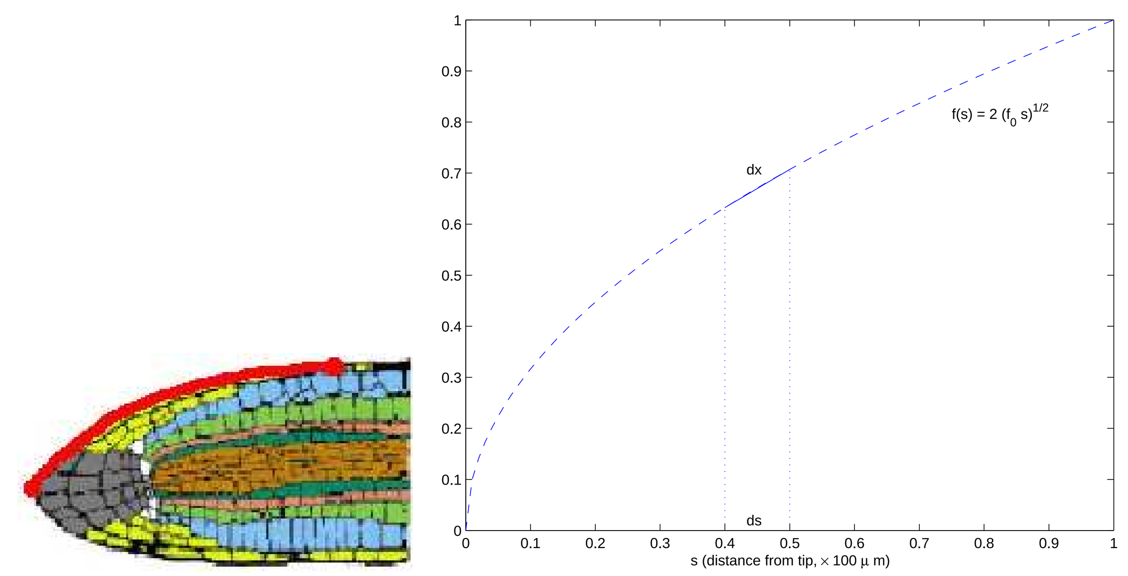
symbol	meaning	relations	steady state assumptions
$\rho(t, x)$	mass (density)		$\partial_t \rho = 0$ (so $\rho = \rho(x)$)
$u, u(t, x)$	displacement		$\partial_{tt} u = 0$
$v, v(t, x)$	velocity	$v = \partial_t u$	$v = v(x)$ (since $\partial_{tt} u = 0$)
ϵ	strain	$\epsilon = \partial_x u$	
σ	stress	$\sigma = Y\ \epsilon$ (equation (7))	$\partial_x \sigma = 0$ (so $\sigma = \sigma_0 =$ const.)

Governing Equations:

$$\left.\begin{array}{ccccc} \underbrace{\rho\, \partial_{tt} u}_{\text{mass times acceleration}} & = & \underbrace{\nabla \cdot \underline{\sigma}}_{\text{elastic forces}} & = & \partial_x \underline{\sigma} \\ \underbrace{\partial_t \rho}_{\text{rate of change in mass}} & = & \underbrace{-\nabla \cdot (\rho\, \partial_t u)}_{\text{mass transport}} & + & \underbrace{g}_{\text{source of growth}} \end{array}\right\} \tag{8}$$

BCs: By symmetry, $u|_{x=0} = 0$, so $v|_{x=0} = 0$. By data [7], $v|_{x=L} = V_L$.

The Parameter x vs. the Distance s Along the RAM Axis



Denote the distance from the tip along RAM axis by s. Then the RAM cross section is bounded by $f(s) = 2\sqrt{f_0 s}$ (principal branch), and the constant f_0 has the same units of length as s. The variable x thus parametrizes the *arc length* [4] of $f(s)$. Figure 2 of [1] suggests, to a good qualitative approximation, $f(100) = 100$, so $f_0 = 25$.

Results

The Homogeneous Case $Y =$ const.. The static governing equations and the BCs yield

$$v(x) = v(x) = v_0 + v_1 x, \qquad \text{where } v_0 = 0,\ v_1 = (V_L - v_0)/L, \tag{9}$$

which admits a linear fit $v_{aff}(s) = a_0 + a_1 s$, accurate for $v_1 =$ to 6.6%.

The Inhomogeneous Case $Y = Y(x)$. We find Y as a function of s. *Assuming* (9), one obtains $dv/ds = c =$ const., hence

$$Y(s) = \frac{\sigma_0 \sqrt{1 + (f_0/s)}}{c}, \text{ hence } \lim_{s \to 0^+} s^{1/2} Y(s) = \sigma_0 \sqrt{f_0}/c \tag{10}$$

which predicts a rapid increase in stiffness toward the RAM tip ($x \to 0^+$). This result agrees with the intuitive hypothesis that, near the tip, longitudinal strain is necessarily accompanied by tangential strain, which is hindered by the transversely oriented cellulose fibrils. The result also correlates with the expansin concentration found to decrease towards the root tip in certain plants.