Mathematical Modeling of Plant Root Growth

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The root grows longitudinally within a short (not longer than 1 cm) zone adjacent to its end. The growing part of the root consists of two zones: meristem (division zone) and elongation zone. In the meristem, which is usually much shorter than the elongation zone, the cells divide, the average cell length varying only slightly with distance from the end. After the cells have entered the elongation zone, their division stops and the cells enter the phase of growth by longitudinal elongation. At the end of the elongation zone, the cell elongation ceases and the cells enter the rest zone. The mechanisms of root growth organization, in particular, the mechanisms of the elongation zone formation remain in many respects not understood. It is natural to ask how the mechanical, including growth, characteristics of the growing tissue predetermine the observed regularities of growth deformation. The facts to be explained include the formation of a finite-length elongation zone (cessation of growth), the dependence of the elongation zone length on the intracellular pressure and the external compressive load, and the relationship between these dynamic characteristics and the average cell length.

The purpose of the present study is to construct an adequate macroscopic model of the longitudinal growth of the root in the elongation zone on the basis of clear physical principles, consider the mechanical characteristics of this process, and explain the main observed regularities within the framework of the model developed.

The root tissue can be treated as a composition of communicating intracellular volumes filled with a fluid under pressure. The absence of displacements of the cells relative to one

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another makes it possible to treat all cell walls as a united deformable framework. A general approach to modeling the biological tissues as multiphase continua that consist of solid and fluid phases was considered in [1]. Here we use one-dimensional relations that correspond to averaging over the cross-section normal to the root axis.

We introduce the coordinate system tied to the root end, with the x-axis directed upward. For the axial component of the stress tensor of the medium as a whole averaged over the cross-section σ, we assume the relation $\sigma = -p(1 - \alpha) + \alpha\sigma_1$, where α is the volume content of longitudinally oriented cell walls, σ_1 is the tensile stress in the longitudinal cell walls that acts along the x-axis, and p is the average pressure in the intracellular fluid. It is assumed that, due to slime excretion on the outer root surface in the cap region, the friction force exerted by soil can be neglected as compared with the resistance force applied to the root apex, which is only present in the boundary condition for the momentum (equilibrium) equation in the axial direction. Then the quasistatic equilibrium equation for the root tissue takes, with account for the compression force T acting on the root apex (divided by the cross-section area), the form

$$-T = -p(1 - \alpha) + \alpha\sigma_1.$$

It is well known that in the elongation zone the intracellular pressure and the thickness of the longitudinal cell walls remain almost invariable along the root axis. The mechanisms that participate in maintaining the intracellular pressure at a constant level and regulate the building of the cell walls are not considered here, and the intracellular pressure and the volume fraction of longitudinal walls are assumed to be given constants.

At large times, in parallel to the elastic tension, an inelastic deformation of the cell wall develops due to viscous material flow accompanied by the build-in of a new mass that comes from the fluid. The medium strain rate tensor is represented as the sum of two components, elastic, related to the elastic deformation of the cells,

and inelastic, associated with irreversible changes in their shape due to cell wall restructuring. We assume that above a certain stress threshold the longitudinal inelastic wall elongation rate linearly depends on the longitudinal tensile stress in the wall, whereas below this threshold there is no inelastic deformation. We thus have the following equations for the axial deformation of the longitudinal walls:

$$e = \frac{D\varepsilon^e}{Dt} + e^i, \; \varepsilon^e = \varepsilon^e(\sigma_1), \; e^i = \begin{cases} K(\sigma_1 - Y), & \sigma_1 \geq Y \\ 0 & , \quad \sigma_1 < Y \end{cases}$$

where D/Dt is the lower Oldroyd derivative, ε^e is the elastic strain in the axial direction, e and e^i are the total and inelastic strain rates, Y is the threshold stress above which inelastic deformation starts, and K is the inverse growth viscosity. The inverse growth viscosity coefficient K is assumed to depend on a structural parameter characterizing the properties of the cell wall.

We introduce an internal parameter z, which has the meaning of the relative number of effective bonds per unit solid phase volume averaged over the cross-section area. The change in the relative number of effective chemical bonds obeys the balance equation that describes the dynamics of effective bonds in a unit medium volume,

$$\frac{\partial(\varrho z)}{\partial t} + \frac{\partial(\rho v z)}{\partial x} = \rho\left(A(1-z)^\alpha - B(\sigma_1)z^\beta\right) + \theta\tilde{z}$$

where ρ is the apparent density of the longitudinal wall material, v the solid phase velocity, θ the rate of mass influx for building the cell walls, and $\tilde{z}$ is the relative number of bonds in the built-in mass. This equation describes the processes of formation of new bonds, their breakdown, and the bond influx due to the build-in of new material that comes from the fluid phase. It also takes into account the fact that longitudinal tension favors bond breakdown.

We obtain the complete description of the process of deformation of the elongation zone by supplementing the previous equations with the relationship between the solid phase velocity and the strain rate and the mass balance equation for the cell walls,

$$e = \frac{\partial v}{\partial x}, \qquad \frac{\partial \rho}{\partial t} + \frac{\partial \rho v}{\partial x} = \theta .$$

It is natural to assume that the dependence $K = K(z)$ is a nonincreasing function of the structural parameter z until it reaches a certain critical value z_c, whereas for $z > z_c$ the inelastic cell wall deformation stops and $K=0$.

We consider slow growth processes, and we can therefore assume that the elastic strain is much smaller than the growth strain. If we restrict our considerations to steady-state growth (in the coordinate system tied to the root end), then we obtain a system of two ordinary equations for v and z. As boundary conditions, we assign the equalities $v = v_0$ and $z = z_0$ at $x = l_0$, where l_0 is the coordinate corresponding to the beginning of the elongation zone. The values v_0 and z_0 are the cell velocity relative to the end and the bond density in the cells that leave the division zone. The elongation zone length l can be found from the equation $z(l + l_0) = z_c$.

The model considered makes it possible to explain the finiteness of the elongation zone length. It describes the increase in the elongation zone length with difference between the tensile stress in the cell wall and the threshold stress. This latter quantity increases with the intracellular pressure and decreases with increase in the compressive load. As can be seen from the relations that link the deformation parameters with the average cell length, the shorter elongation zone corresponds to smaller lengths of the cells as they leave this zone and their growth stops. All these facts correspond to experimental data.

References

[1] *N. N. Kizilova, S. A. Logvenkov, and A. A. Stein.* Mathematical modeling of transport-growth processes in multiphase biological continua. Fluid Dynamics. Vol. 47. No. 1, pp. 1–9. 2012.