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The Feasibility of Utilizing a Mathematical Model in Studying Nonlinear Transport Processes in Living Systems

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Abstract. On the basis of proportionality between flow and its conjugated force a mathematical model for volume, current and osmotic flows was designed and a method for the experimental measurement of flows, the transbarrier (trans-segmental) potential and the rate of flow was devised.

The results obtained experimentally as well as using the mathematical model indicate that the plant root is differentiated not only according to localization, but also according to the conductivity, permeability and selectivity of these tissues.

Thermal, diffusional, osmotic, electrical and other flows are proportional to their conjugated forces. Electromotive voltage produces a flow of charge and volume flow connected with it; the non-conjugated flow of electrical charge underlies hydrostatic pressure.

Proportionality between a flow and the force underlying the flow, is taken to be linear but linearity in these relationships is satisfied only for sufficiently slow processes as occur when the system is in a state close to equilibrium (KATCHALSKY and CURRAN 1967, MICHALOV *et al.* 1976, MICHALOV and PALČÁKOVÁ 1979). Processes, and hence flows, in living systems do not proceed linearly and thus the applied linearity is unrealistic. Therefore, equations of flow cannot have the character of linear equations. The so-called Onsager coefficients, expressing conductance and filtration properties of the barrier, can similarly not be reciprocal, since their magnitude depends on the magnitude of the acting force and on the corresponding flow produced by that force as well as on the length of the transport path and the time during which flow proceeds.

MATERIAL AND METHODS

The linking between flows and forces described in the introduction was applied here to examining substance and current flows in maize roots. For experimental study use was made of roots of the 1st, 2nd, 3rd, 4th, 5th and 6th nodes of a 165-day-old plant (Fig. 1). The individual quantities required for estimating volume, current and osmotic flows were determined from concentration c_1, the change of electric voltage (ΔE) produced by hydrostatic pressure (ΔP), the barrier area (S) through which flows took place, the

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amount of flowing solution (ΔV), the time (t) in which flow took place, the ohmic resistance (R), the rate v(t) of volume flows and the change of hydrostatic pressure (ΔP), using the method illustrated in Fig. 1. From these experimental quantities all three flows through the root segments in time were estimated and calculated from the following expressions (1) and (2):
Volume flow:

$$J_V = L_{PP} \frac{dP}{dl} v(t) + L_{PE} \frac{dE}{dc} \frac{dc}{dt} + L_{PD} RT \frac{dc}{dl} v(t)$$

Current flow:

$$I = L_{EP} \frac{dP}{dl} v(t) + L_{EE} \frac{dE}{dc} \frac{dc}{dt} + L_{ED} RT \frac{dc}{dl} v(t) \qquad (1)$$

Osmotic flow:

$$J_D = L_{DP} \frac{dP}{dl} v(t) + L_{DE} \frac{dE}{dc} \frac{dc}{dt} + L_{DD} RT \frac{dc}{dl} v(t)$$

where v(t) is the flow rate, R the gas constant, T absolute temperature, (dc/dt) the change of concentration (c) in time (t), (dc/dl) the change of concentration over the length of the transport path, P the hydrostatic pressure.

The coefficients L_{PP}, L_{PE}, L_{PD}, L_{EP}, L_{EE}, L_{ED}, L_{DP}, L_{DE} and L_{DD} in equations (1) are variable quantities describing the physical properties of the

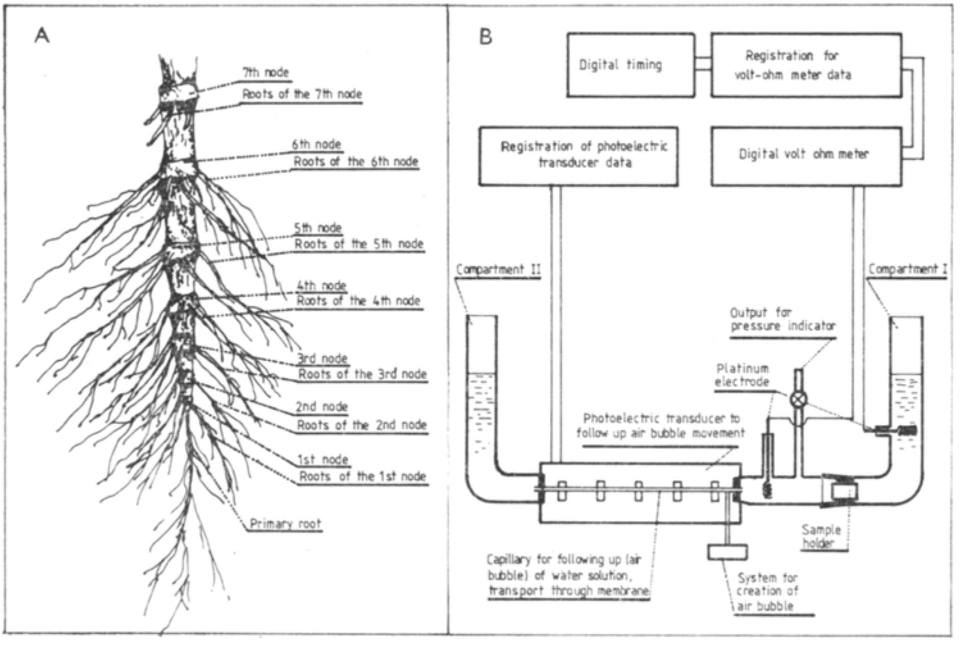

Fig. 1. The object of study and the scheme of the experimental method. — A: Vertical differentiation of the root of *Zea mays*. B: Electroosmotic measurement system.

barrier (KATCHALSKY and CURRAN 1976). They may be determined from experimental data with the help of the relations:

$$L_{PP} = (J_V/\Delta P),\ L_{PE} = (\Delta P/\Delta E),\ L_{PD} = (\Delta P/\Delta\pi),\ L_{EP} = (\Delta E/R\Delta P),$$
$$L_{EE} = (1/R),\ L_{ED} = (I/\Delta\pi),\ L_{DP} = (\Delta\pi/\Delta P),\ L_{DE} = (J_D - C)/K$$
$$\text{and } L_{DD} = (J_D/\Delta\pi) \tag{2}$$

where

$$C = (dP/dl)\, L_{DP} \,.\, v(t) + (dc/dl)\,(dl/dt)\, dt \,.\, L_{ED}RT,$$
$$J_D = -D(\partial c/\partial l),\ K = (dE/dc)\,(dc/dt),\ J_V = (\Delta V/\Delta t),$$
$$D = -(d^2/4t)\,(l/\ln(c_2/c_1)),\ (dc/dl) = (c_1 - c_2)/D,$$
$$dP/dl = (J_V/L_{PP}\, v(t)),\ dE/dc = (RT/zF)\,(c_1/c_2) \text{ and}$$
$$dc/dt = -DS(\partial c/\partial l).$$

The ultrafiltration in the barrier (the root segments) is characterized by the coefficients L_{PE}, L_{PD}, L_{EP}, L_{ED}, L_{DP} and L_{DE} while the coefficients L_{PP}, L_{EE} and L_{DD} characterize the mechanical, electrical and osmotic aspects of filtration (KATCHALSKY and CURRAN 1967, MICHALOV 1984). Osmotic pressure was determined from the approximate relation

$$\pi = -(RT/V \ln k(V_1/V_2), \text{ where } k = (\varrho_{water}/\varrho_{solution}), \tag{3}$$

V_1 being the volume amount of solution before the segment, V_2 the volume amount of solution behind the segment, V the mean volume amount of the solution within the system and ϱ the specific mass of water or solution. For the case of small concentrations use was made of the relations:

$$\pi = RT\,.\,c,\quad c_2 = c_1 \exp(zFE/RT) \text{ and } \pi_2 = \pi_1(c_2/c_1)\,. \tag{4}$$

The mathematical model (1), together with relations (2), (3) and (4) allows to study hydraulic (L_{PP}), electrical (L_{EE}) and osmotic (L_{DD}) conductivity as well as the filtration and osmotic capabilities of the barrier (the root).

RESULTS AND DISCUSSION

With the passage of time all three flows decline, stabilizing at definite values and differing in terms of root type as to size and dependence on time. Volume and osmotic flow reach their highest values in roots of the 6th node, the current flow in roots of the 3rd and 2nd nodes. Both flows proceed most quickly through the root tissues of the 1st node, the current flow through roots of the 3rd node (Fig. 2).

The conductivity and permeability of root tissues are better characterized by the time dependences of coefficients $L_{PP}, \ldots, L_{DD}$ (Figs. 3 and 4). The highest hydraulic conductivity appears to be exhibited by roots of the 2nd node, the lowest by roots of the 4th node. In roots of the other nodes this ability lies between that of roots of the 2nd and 4th node. Osmotic conductivity (L_{DD}) shows intrinsically the same behaviour as hydraulic conductivity (L_{PP}), only its values are negative and the sequence of magnitudes is different. Hydraulic-osmotic ultrafiltration (L_{PD}), brought about by the action of hydrostatic and osmotic pressure, has a similar character of time variation as mechanical filtration (L_{PP}), with the exception of roots of the 1st node, in which it increases with time. It is lowest with roots of the 6th node. Osmotic -hydraulic ultrafiltration L_{DP} grows with time to negative values in all nodal roots. The greatest negative values are reached by roots of the 2nd and 6th nodes. In case of roots of the 1st node it practically does not change.

Electrical conductivity L_{EE} increases very slightly with the passage of time, except of roots of the 3rd node where it acquires great values. In roots of the 6th node it practically does not change. The greatest hydraulic-electrical ultrafiltration capabilities (expressed by coefficient L_{PE}) are exhibited by roots of the 1st node but its variation in time is reversed with respect to that of the other roots. It may be supposed that the ineffectiveness of the action of hydrostatic pressure in root tissues is supplanted by electric voltage. The electro-hydraulic ultrafiltration capacity (L_{EP}) exhibits, in contrast to L_{PE}, a reverse feature: it increases with time to negative values, attaining highest values in roots of the 3rd node. Electroosmotic ultrafiltration (L_{ED}) does not change practically in time, except in the roots of the 3rd node. It reaches lowest values in roots of the 5th and 6th node. The time dependence of osmotic-electrical ultrafiltration (L_{DE}) changes very slightly in roots of the 1st, 3rd, 4th and 6th nodes. In roots of the 2nd and 5th nodes, however, it grows from large negative to large positive values.

It is characteristic of all ultrafiltrations in which osmotic pressure plays a primary role that time dependences decline and their values mostly vary in the negative domain. This fact is due to the exponential drop of osmotic pressure in the compartment before segment I and to the rise of osmotic pressure in the compartment behind segment II. While hydrostatic pressure

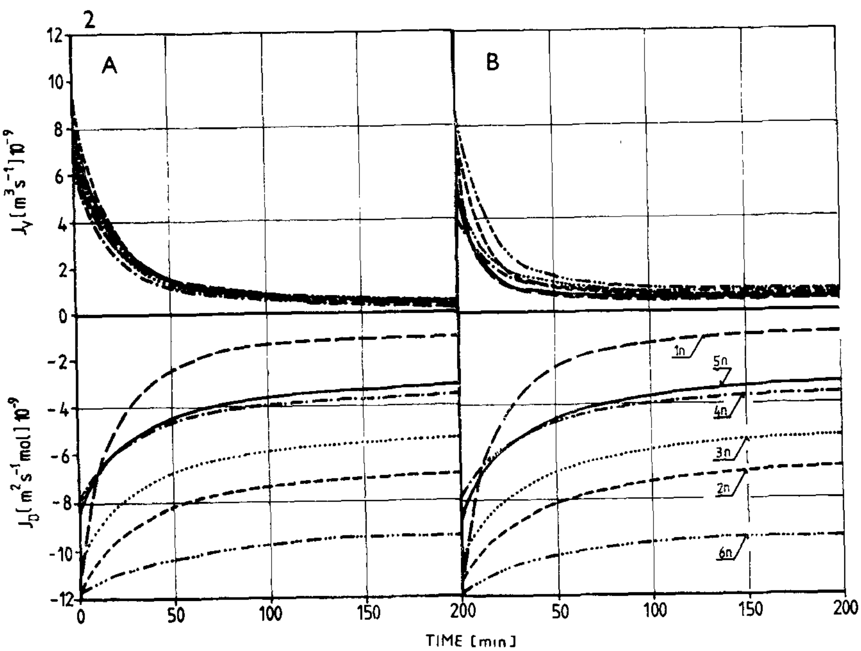

Fig. 2. Dependence of flows, potential and ohmic resistance on time. Volume (J_V) and osmotic (J_D) flows determined experimentally (A) and by the mathematical model (B). The electrical potentials (C), the current flows (D) determined experimentally and the calculated ohmic resistance (E). The roots are distinguished by the form of the curves. 1n — roots of the 1st node,..., 6n — roots of the 6th node.

decreases with time, change in pressure over the length of flow of the segment rises with time, thus giving evidence of the existence of resistance of the medium through which osmotic flow proceeds. This is in agreement with the fact that conductive paths of root tissues offer resistance to the liquid.

It may be seen from what has been said that root tissues of the 1st node have a higher hydraulic than electrical conductivity. Tissues of these roots do not offer resistance to water flow. This is apparent from the fact that concentration changes quickly with time, though it does not change practically with the length of the pathway, and this is also borne out by the time behaviour of the measured osmotic resistance (R) that drops with time quickly

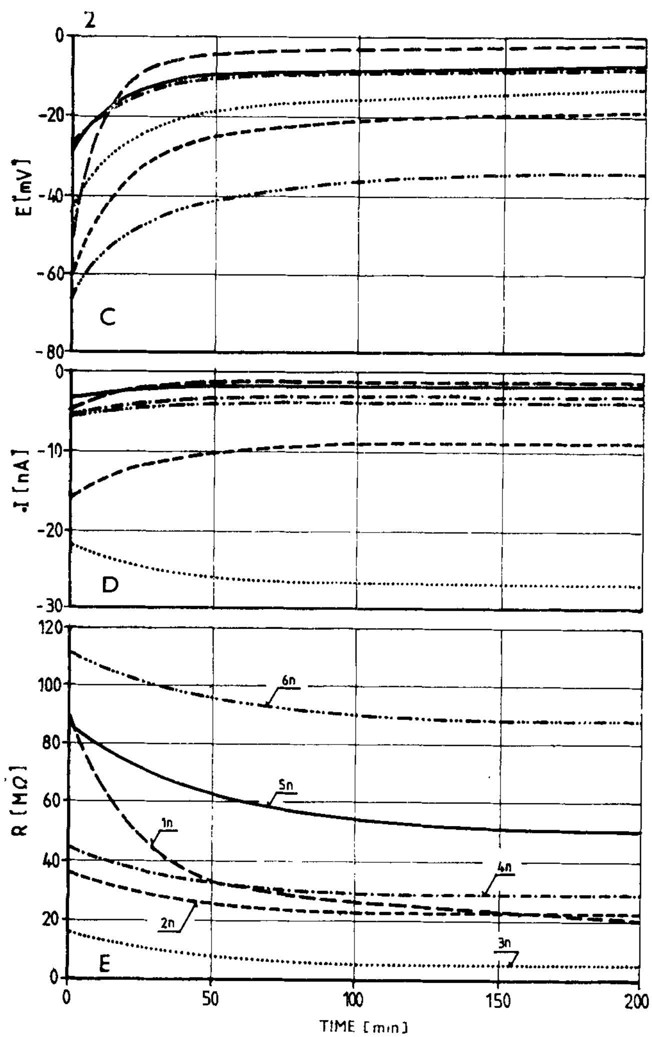

Fig. 2. (continued). See opposite side for caption.

from the initial, very high, values. For the roots of the 5th and 6th nodes it may be seen that the measured resistance is very high, exhibiting a slight decline with time in the case of roots of the 6th node. Roots of the 3rd node have the lowest ohmic resistance and similarly a slight decline from maximal values into the steady state. A peculiarity is the change of ion flow in roots of the 3rd node, its course being reverse to that of the other roots; it rises with time and exhibits relatively high values. In terms of this fact as well as according to the results obtained on electrical conductivity L_{EE}, the roots of the 3rd node are electrically most conductive.

Osmotic pressure, estimated according to relations (3) and (4), has the highest values in compartment I in the case of roots of the 3rd node, dropping

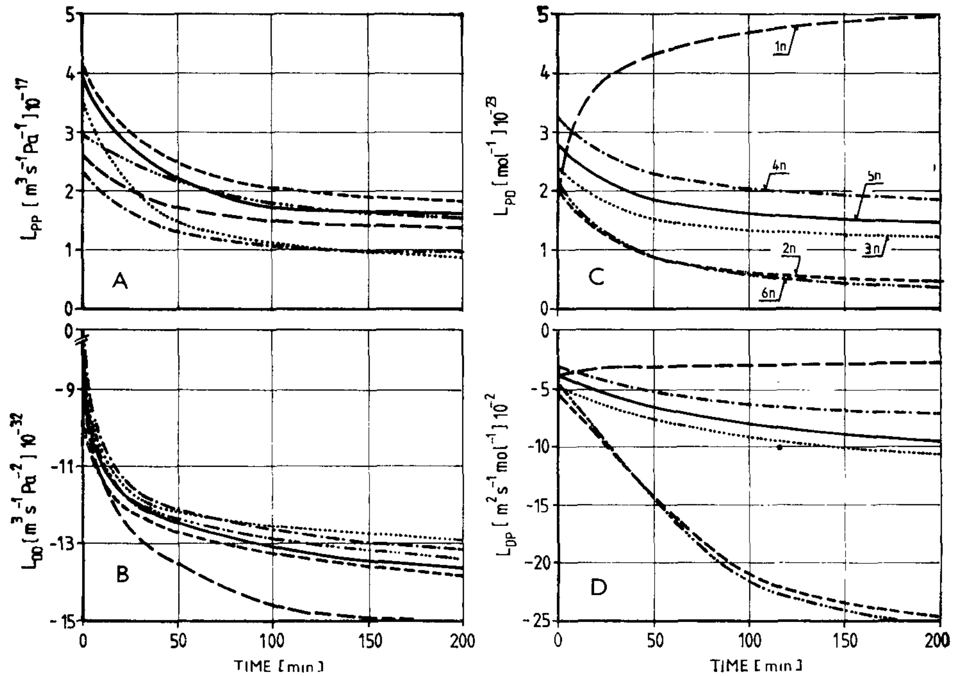

Fig. 3. Dependences of the hydraulic (A) and osmotic (B) conductivity, the hydro-osmotic (C) and the osmo-hydraulic (D) ultrafiltration on time. The roots are distinguished and denoted as in Fig. 2.

most quickly in roots of the 2nd node. In contrast, osmotic pressure π_2 in compartment II is highest in roots of the 1st node and its rate of increase is similarly greatest in these roots (Fig. 5). This agrees with the electrica, voltage showing the greatest drop in these roots, getting stabilized at the lowest value. Similarly, electrical resistance declines sharply in these roots. Current flow is lowest in these roots and hydraulic conductivity alters very slightly with time as compared with roots of the 3rd or 4th node. Similarlyl volume flow declines rapidly, stabilizing at the lowest value. Similar features are exhibited by osmotic flow, the only difference being that its values have the reverse sign.

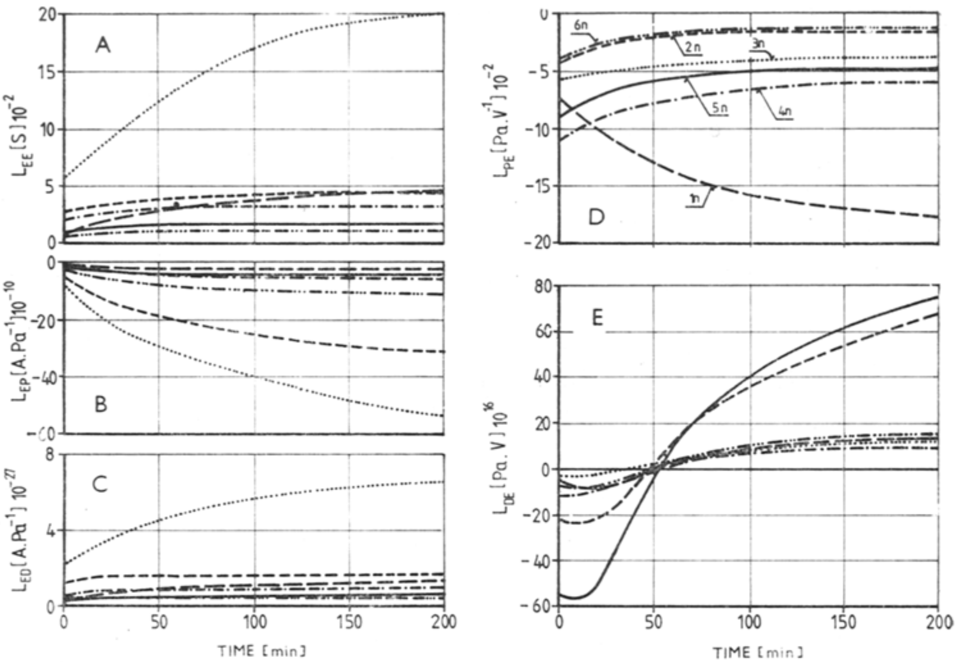

Fig. 4. Dependences of electrical conductivity (A), the electro-hydraulic (B), the electro-osmotic (C), the hydro-electric (D) and the osmo-electric (E) ultrafiltration on time. The roots are distinguished and denoted as in Fig. 2.

On the whole, it may be said that roots of the 6th node have the highest osmotic capabilities that change only slightly with time. It appears that, in terms of the identified markers, roots of the 2nd node take a major share in the process of transporting substances through the root system. They are followed by roots of the 3rd, 4th and 5th nodes. Roots of the 1st node appear to provide for conducting very fast flows brought about by pressure forces.

The selective abilities of the root tissue are also confirmed by the results of examining the permeability properties of these tissues. This may be graphically seen in Fig. 6 where permeability increases in the positive direction by the effect of hydrostatic pressure and in the negative direction by the effect of osmotic pressure. This corresponds to the fact that both pressures produce a change in solution concentrations at both sides of the segment and the permeabilities depend in the last instance on the size of the electrical field of the ohmic resistance of the root segment which is smallest in the roots of the 3rd node. It follows from this that permeability, too, is largest in these roots. These findings are also borne out by the reflexion coefficient (Fig. 6A) showing that the highest selectivity growth in dependence on time is exhibited by roots of the 1st node. Following them are the roots of the 4th node and some selectivity is exhibited by roots of the 2nd and 6th nodes. In conclusion it may be said that all roots exhibit selective properties, this being in full agreement with the fact that the plant is capable of regulating ion uptake from the surroundings, the differentiation of the individual roots following not only localization, but also the uptake function.

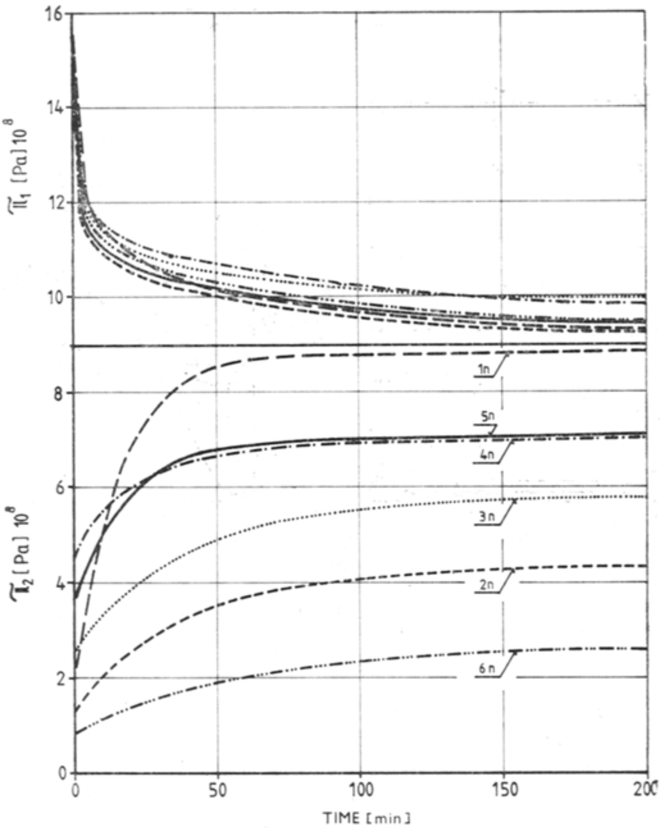

Fig. 5. Dependences of osmotic pressure π_1 (in compartment I) and π_2 (in compartment II) on time. The roots are distinguished and denoted as in Fig. 2.

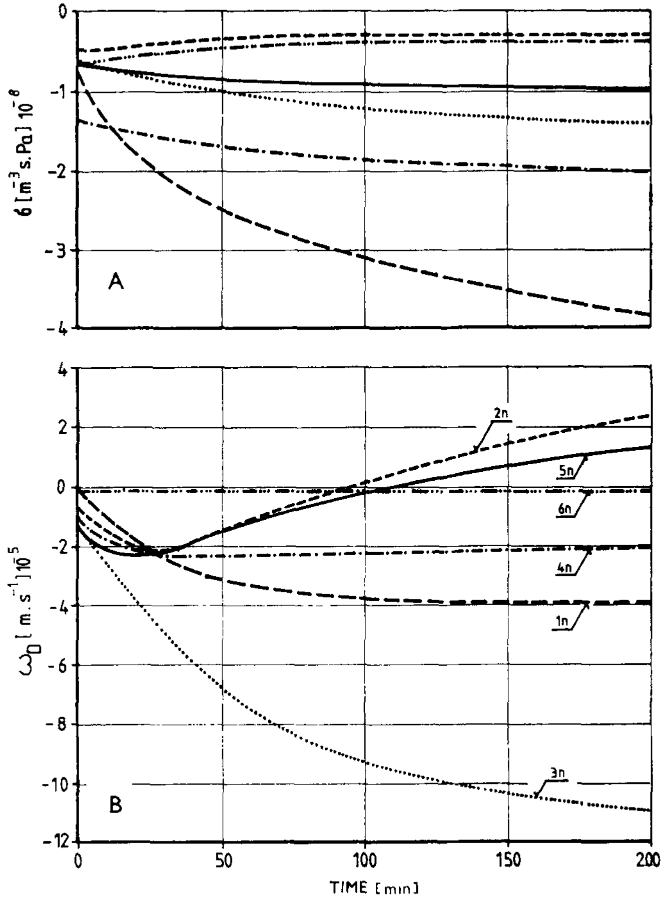

Fig. 6. Dependences of the reflexion coefficient (A) and the permeability coefficient (B) on time The roots are distinguished and denoted as in Fig. 2.

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