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DEHYDRATION EFFECT ON THE INTERNAL CELL PRESSURE

The dependence of the turgor pressure on the water content in a cellular structure is studied experimentally. The turgor pressure is found to decrease as the water content in a cell diminished. The experimental result is analyzed in the framework of a two-component cell model. The cell wall deformation is demonstrated to make a main contribution to the turgor pressure, so that a drop of the turgor pressure is a consequence of the stress relaxation in the cell wall.

K e y w o r d s: deformation, stress relaxation, cell, turgor pressure.

1. Introduction

The biological cellular structures are known (see, e.g., works [1, 2]) to undergo the action of an excess internal pressure (relative to the atmospheric one) called the turgor pressure. One of the ways of its measurement was proposed in work [3], where it was shown that the turgor pressure can be considered equal to the shear modulus of the cellular structure. Using this method, we study the influence of the cellular structure dehydration on the turgor pressure aiming at elucidating the physical mechanism of this phenomenon. To our knowledge, this issue has not been analyzed earlier in the literature from such a viewpoint.

2. Experimental Part

Specimens to be studied were cut out in the form of strips from the parenchymal tissue of sugar beet. The specimen volume V_s, mass M_s, and shear modulus G_s were determined. The latter was measured on a torsion pendulum following the known technique (see, e.g., work [4]). The specimens were held at the temperature $T = 313$ K for various time intervals; afterward, their mass $M(t_j)$ and shear modulus $G_1(t_j)$ were determined once more. As the holding time t increased, those quantities decreased with respect to their reference values M_s and G_s, as is illustrated in Figs. 1 and 2, where the experimental dependences of the quantities M and G_1 on the time t are depicted.

Let us introduce the notation $\Delta M = M_s - M$ for the measured mass difference, p_s for the turgor pressure in the freshly cut-out specimens, and p for the turgor pressure in the aged ones. In work [3], it was shown that the turgor pressure in cellular structures equals their shear modulus G_1. Basing on this result and the data shown in Figs. 1 and 2, we plotted the dependence $p(\Delta M)$ exhibited in Fig. 3.

The reduction of the specimen mass in this experiment can take place only owing to the water evaporation from the specimen. In other words, ΔM is the mass of water lost by the specimen during the time interval t. Accordingly, the dependence of p on ΔM in Fig. 3 illustrates how the turgor pressure changes at the cell dehydration, i.e. the loss of water by the cellular structure.

3. Discussion of Experimental Results

It is known that, in order to analyze experimental results, the corresponding model of the examined structure has to be used. Below, we describe a model of cellular structure that was used in this work.

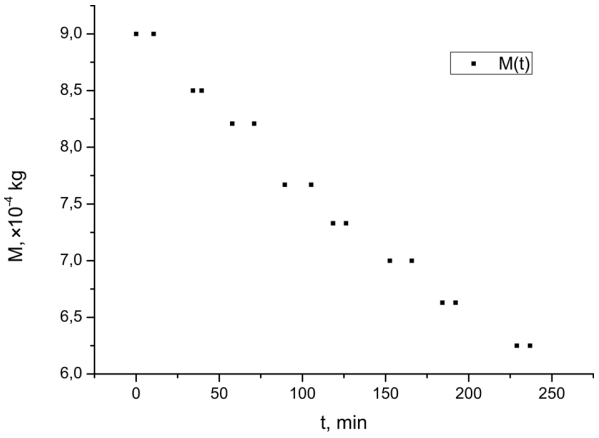

Fig. 1. Dependence of the specimen mass on the holding time

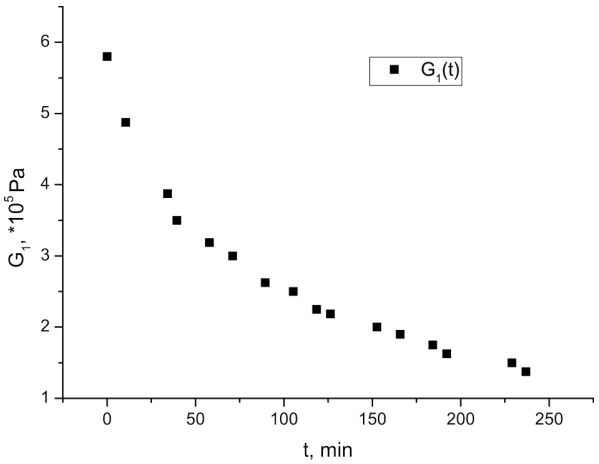

Fig. 2. Dependence of the specimen shear modulus on the holding time

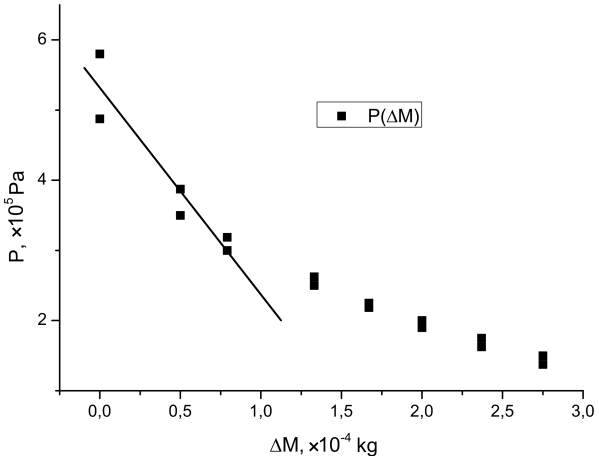

Fig. 3. Dependence of the turgor pressure on the specimen mass change owing to the water evaporation

By c, we denote the water concentration in the cell. While considering the cellular structure as a continuum, the cell can be regarded as an infinitesimal volume $d\mathbf{x}$ around the point $\mathbf{x}$ adopted as the cell center of inertia. Then the quantity $c(\mathbf{x})$ is the water concentration in this cell. Since the analysis is carried out in the continual approximation, the function $c(\mathbf{x})$ is continuous, i.e. we deal with the concentration field $c(\mathbf{x})$.

It is clear that, in the course of evaporation, water redistributes, generally speaking, non-uniformly over the specimen: there emerges the concentration gradient, ∇c, directed from the specimen middle point toward its boundaries, where the evaporation process itself takes place. However, we will not take this fact into account in further calculations and will carry out them in the mean-field approximation. The essence of this approximation is known (see, e.g., work [5]) to consist in the substitution of the actual field by its average value. In our case, this approximation means that, instead of the field $c(\mathbf{x})$, we assume that $c = \langle c \rangle = \text{const}$, i.e. the water concentration in all cells is identical,

$$\langle c \rangle = \int\limits_{V_s} \frac{c(\mathbf{x})d\mathbf{x}}{V_s}.$$

In principle, such a situation can be rather close to the real one, namely, when the diffusion rate of water molecules considerably exceeds the evaporation rate. Let us assume that just this case is realized in our experiment.

Now, when the mean-field approximation is adopted and, as a result, all cells are supposed to be under identical conditions, we can make calculations for any separate cell, rather than for the whole cellular structure. In our further speculations, the internal cell structure does not play any substantial role. Therefore, the medium filling the internal volume of a cell is considered as an aqueous solution; formally, we suppose that only one substance is dissolved in water. The number of molecules of this substance in a cell will be denoted as n. Another structural element, a cellulose wall that surrounds the cell interior, plays a considerable role in our calculations. Hence, the cell model which we are going to use is two-component: a cellulose wall (shell) and a solution contained in this shell.

As was already mentioned, the cell is internally under the action of the excess turgor pressure. Which are the reasons for this pressure to emerge? In the literature (see, e.g., work [1]), the osmotic pressure is recognized as a crucial factor responsible for this phenomenon. Below, it will be denoted by p''. In our case, the well-known formula [6] for it looks like

$$p'' = \frac{k_b T n}{v}, \tag{1}$$

where v is the volume of a cell, k_b the Boltzmann constant, and T the temperature. Which is the dependence of p'' on ΔM? If q is the number of cells in the system, then $V = qv$ is the volume of the system, and formula (1) can be rewritten in the form

$$p'' = \frac{k_b T q n}{V}. \tag{2}$$

Let ρ denote the water density. Then, the variation of the volume owing to the water evaporation equals $\Delta M/\rho$, and formula (2) reads

$$p'' = \frac{k_b T q n}{V_s \left(1 - \frac{\Delta M}{\rho V_s}\right)} \approx \frac{k_b T q n}{V_s}\left(1 + \frac{\Delta M}{\rho V_s}\right). \tag{3}$$

From whence, one can see that the growth of ΔM gives rise to an increase in the pressure, which contradicts experimental data (Fig. 3) and makes us find a different reason responsible for the reduction of the turgor pressure, when the cell losses its water. The initial point of our search for the resolution of this contradiction is the fact that the increase in the cell volume is accompanied by the emergence of stresses in the cell wall. These are the stretching stresses that are directed tangentially to the wall plane (below, they will be denoted as σ). The action of stresses results in the appearance of a counteraction from the solution filling the cellulose shell on the cell wall. This counteraction manifests itself as a pressure, with which the solution acts on the shell. We denote this pressure by p'. Let the cell be a sphere. In the absence of a pressure, let it have the radius a_0 and the wall thickness h_0. In our notations, the well-known formula (of the Laplace type) [7] looks like

$$p' = \frac{2\sigma h_0}{a_0}. \tag{4}$$

Now, let us add some water to the solution that occupies a spherical cavity with radius a_0. Let the sphere radius grow up to a_1, if the shell is absent, or to a, if the shell is present. Hence, when water is added, the boundary of the sphere filled by a solution shifts by $a_1 - a$, and the shell by $a - a_0$ along the radius. The corresponding relative deformations amount to $\frac{a_1 - a}{a_1}$ and $\frac{a - a_0}{a_0}$, which satisfy the formulas

$$p' = 3K\frac{a_1 - a}{a_1}, \tag{5}$$

$$\sigma = E\frac{a - a_0}{a_0}, \tag{6}$$

where K is the compression modulus of the solution, and E the effective stretching modulus of the wall [8]. Substituting Eqs. (5) and (6) into Eq. (6), we obtain

$$\frac{3K}{a_1}(a_1 - a) = \frac{2h_0}{a_0}\frac{E}{a_0}(a - a_0). \tag{7}$$

From whence, we have

$$a = \frac{3K + E\frac{2h_0}{a_0}}{\frac{3K}{a_1} + \frac{2h_0}{a_0}\frac{E}{a_0}}. \tag{8}$$

Then

$$\frac{a_1 - a}{a_1} = \frac{E}{3K}\frac{2h_0}{a_0}\frac{a_1 - a_0}{a_0}. \tag{9}$$

Substituting formula (9) into Eq. (5), we obtain

$$p' = E\frac{2h_0}{a_0}\frac{a_1 - a_0}{a_0}. \tag{10}$$

Let the mass of water added to the cell amount to m_1. The corresponding change of the volume equals

$$\frac{m_1}{\rho} = \frac{4\pi}{3}(a_1^3 - a_0^3) \approx \frac{4\pi}{3}3a_0^2(a_1 - a_0). \tag{11}$$

Substituting Eq. (11) into Eq. (10), we obtain

$$p' = E\frac{2h_0}{3a_0}\frac{m_1}{\rho\frac{4\pi}{3}a_0^3}. \tag{12}$$

Multiplying the denominator and the numerator on the right-hand side by q, we have

$$p' = E\frac{2h_0}{3a_0}\frac{\Delta M}{\rho V_1} \tag{13}$$

where ΔM is the water mass increment in the whole system, and V_1 the corresponding volume of the system. The turgor pressure is the sum

$$p = p' + p''. \tag{14}$$

Substituting Eqs. (13) and (3) into Eq. (14), we obtain

$$p = p_s - \left[E\frac{2h_0}{3a_0} - \frac{k_bTqn}{V_s}\right]\frac{\Delta M}{\rho V_s}. \tag{15}$$

The theoretical dependence (15) describes the initial section of the experimental dependence $p(\Delta M)$. In Fig. 3, it is shown by the solid line. While analyzing Fig. 3, one can get convinced first of all that the proposed mechanism correctly describes the behavior of the turgor pressure, when the cellular structure losses water. This figure also allows one to understand the origin of a turgor pressure drop. The mechanism consists in the relaxation of stretching stresses in the cellulose wall, which results in a reduction of the turgor pressure. This is the key result of the work.

A comparison of formula (15) with experimental data allows some numerical estimations concerning the examined cellular structure to be made. As one can see from Fig. 3, the initial section of the dependence $p(\Delta M)$ is linear. According to the experimental values, the slope coefficient amounts to $\frac{\Delta p}{\Delta M} = 2.89 \times 10^9$ Pa/kg. In turn, the order of magnitude of the quantity $\left[E\frac{2h_0}{3a_0} - \frac{k_bTqn}{V_s}\right]\frac{1}{\rho V_s}$ equals 10^9 Pa/kg. Literature data and our experimental results testify that the turgor pressure has an order of a few atmospheres and, under certain conditions, can reach about ten atmospheres. Taking into account that the quantity ρV_s has an order of 10^{-4} kg and the quantity $\frac{h_0}{a_0} \sim 10^{-3}$, we obtain $E \sim 10^8$ Pa for the effective elastic modulus of a cellulose wall. Cellulose belongs to the class of rigid polymers. Its elastic modulus along the orientation direction amounts to 10^{11} Pa. The estimate obtained for E testifies that cellulose chains are arranged chaotically in the wall plane. This is another result of our experiment.

4. Conclusions

1. Dehydration of a cellular structure results in a substantial drop of the turgor pressure: the evaporation of water with a mass of several percent of the total system mass induces a drop of the turgor pressure by several atmospheres.

2. The drop of the turgor pressure at the cell dehydration is caused by the relaxation of stretching stresses in the cellulose shell of the cell.

3. The cellulose chains are arranged chaotically in the wall plane.

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ВПЛИВ ЗНЕВОДНЕННЯ
НА ВНУТРІШНІЙ ТИСК У КЛІТИНАХ

Р е з ю м е

Метою даної роботи є вивчення впливу внутрішнього, так званого тургорного, тиску та його залежності від вмісту води в клітинах. Як відомо, цей тиск зумовлений осмотичними тисками по обидва боки плазматичних мембран клітин, а також їхніми пружними властивостями. Експериментально досліджено залежність тургорного тиску від кількості води в клітинній структурі. Встановлено, що величина тургорного тиску зменшується зі зменшенням кількості води в клітині. Результат експерименту аналізується на основі двокомпонентної моделі клітини. Показано, що основний внесок у значення величини тургорного тиску спричинений деформацією оболонки клітини, і, відповідно, падіння тургорного тиску є наслідком релаксації напружень в оболонці.