

The Problem of Water Exchange by Living Cells in the Light of Mechanistic Transport Equations

M. Kargol^{1*}, G. Suchanek¹, M. Przystalski², J. Siedlecki³, A. Kargol⁴

¹Institute of Physics, Świętokrzyska Academy, Świętokrzyska 15, 25-406 Kielce, Poland;

²Clinic of Otolaryngology, School of Medicine, Chałubińskiego 2, 50-308 Wrocław, Poland;

³County Hospital, Grunwaldzka 45, 25-736 Kielce, Poland;

⁴Department of Physics, Loyola University, New Orleans, LA 70118, USA

Received: September 8, 2004

Accepted: February 10, 2005

Abstract

Each living cell must, while performing its life functions, constantly exchange water with its surroundings. This occurs through the cell membrane. In the present paper, we have made an attempt to explain the biophysical basis of this water exchange, realized under stationary conditions, i. e. at constant cell volume. For the investigation, the mechanistic equations for membrane transport have been applied. It has been demonstrated that each living cell which subsists under stationary conditions is capable of water absorption and simultaneous water removal to its surroundings. Water absorption is osmosis-driven, while water removal is driven by the mechanical pressure difference (the turgor pressure). These are new, and very significant, research results. This stationary water exchange cannot be explained on the basis of thermodynamic transport equations.

Keywords: cell, cell membrane, surroundings, water exchange, exchange mechanisms

Introduction

Each living cell, in order to perform its life functions, must constantly exchange water and solutes with its surroundings. To be precise, it must absorb water (and substances dissolved therein), as well as removing it together with the waste products of metabolism. This exchange occurs across the cell membrane, and with its active participation. The present work is concerned with the biophysical basis of this exchange, pertaining to water only.

In general, it may be said that there are many biophysical mechanisms of generating water exchange between the cell and its surroundings, and these are determined by different driving factors, as follows from the literature [1,4-6,8,10-12,18,20-27,29]. However, fundamental factors are (as is generally acknowledged) the pressure differ-

ences which occur on the cell membrane, i. e. the mechanical pressure difference ΔP and the resultant osmotic pressure difference $\Delta \Pi$. Thus, restricting ourselves to those two factors (while modelling the cell and its surroundings), we can describe the exchange of water, using both the thermodynamic Kedem-Katchalsky (K-K) equations [18,19] and the mechanistic equations of transport, recently derived by A. Kargol and M. Kargol in the works [13-17].

At this juncture, it must be remembered that in the equations of the K-K formalism, one is not concerned with the internal (microscopic) structure of the membrane. However, in practical research situations, one has to deal, almost exclusively, with porous membranes. A membrane can be regarded as homogeneous when its individual pores have the same linear dimensions (i. e. equal cross-section radii). It is to be stressed here that cell membranes contain pores (water channels) of varying linear dimensions, and for that reason these membranes

*Corresponding author; e-mail: kargol@pu.kielce.pl

are not homogeneous in terms of transport. By the channels of these membranes, we mean for instance water pores formed by transport proteins (e. g. barrels) [3, 23, 28], water pores created by antibiotics [28] or water pores formed by porin proteins (aquaporins) [2, 3, 7, 23]. The K-K equations, when applied to heterogeneous membranes, appear ambiguous for interpretation, which is what follows from the papers [17, 19, 22].

Under the circumstances, in the present paper, we shall use the mechanistic transport equations, which are valid both for porous homogeneous and heterogeneous membranes. It should be stressed here that those equations have been derived by way of mechanistic considerations based on the model of a typical heterogeneous membrane which has the statistical number of N pores of varying linear dimensions [13-17]. Moreover, these equations are wholly transparent from the physical view point, which is more than can be said for the K-K equations.

Water exchange by a living cell can occur under non-stationary conditions (i. e. at inconstant cell volume) as well as under stationary conditions, when the cell volume remains constant. Obviously, the non-stationary water exchange is osmosis-driven and followed with cell volume increase. On the other hand, water removal may occur both osmotically and hydromechanically (driven by the turgor pressure) and is connected with cell volume decrease.

Stationary water exchange is considerably more difficult to explain. Hence, that exchange is the subject of our present considerations, whereby we will show that under stationary conditions the cell is able to absorb water osmotically and remove it hydromechanically at the same time, due to turgor pressure. This original research result is the main achievement of the present work. This result is not possible to be observed on the basis of the thermodynamic transport equations [18,19], which is easily demonstrable. The K-K equations lend themselves well only to non-stationary water exchange, i. e. at inconstant cell volume.

Mechanistic Transport Equations. Illustration of Their Functioning

It will be convenient to present the mechanistic membrane transport equations using the membrane system shown in Fig. 1, which served as a basis for their derivation. In this system, a porous membrane M separates two compartments A and B , filled with solutions of the same solute at different concentrations C_1 and C_2 ($C_2 > C_1$). The solutions are diluted, well stirred (with the stirrers m, m), and under different mechanical pressures P_1 and P_2 ($P_2 > P_1$). Thus, on membrane M , there occurs the mechanical pressure difference $\Delta P = P_2 - P_1$, as well as the osmotic pressure difference

$$\Delta \Pi = RT(C_2 - C_1) \tag{1}$$

where R – gas constant and T – temperature.

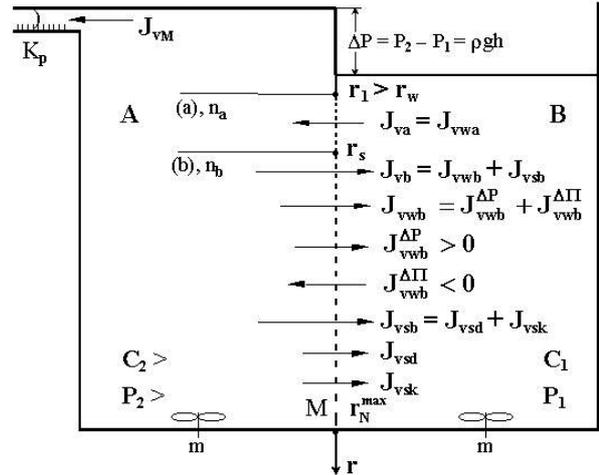


Fig. 1. Membrane system (M – membrane; A, B – compartments; m, m – stirrers; Kp – capillary; P_1, P_2 – mechanical pressures; C_1, C_2 – concentrations; (a) and (b) – parts of membrane with pores n_a and n_b ; $J_{va}, J_{vwa}, J_{vb}, J_{vwb}, J_{vsb}, J_{vsd}, J_{vsk}$ – fluxes).

Let us assume that the membrane has the statistical number of pores N permeable to the solvent (water). Let the pores vary in their linear dimensions, i. e. cross-section radii. It is also reasonable to assume that in typical porous membranes (cell membranes included), the pores are arranged randomly. However, to facilitate our considerations, let us assume that the pores are arranged in one direction of the membrane, starting from the smallest pores $r_1 > r_w$ (r_w being water molecule radius) and ending with the largest r_N^{max} .

For such a membrane, it is easy to select such a solute (s) of molecular radius r_s for which a certain number of small enough pores (in the range $[r_1; r < r_s]$) will constitute an impermeable barrier. The remaining pores, in the number $n_b = N - n_a$, will be permeable to the molecules of that solute. It is convenient to express that situation using the reflection coefficient $\sigma_M = \sigma$, which is the measure of membrane selectivity. Its name was taken from the K-K formalism [18,19]. We shall explain that parameter below. Now let us note that the membrane can be divided into part (a) with n_a pores to which the reflection coefficient $\sigma_a = 1$ can be assigned, and part (b) with pores n_b , and hence – the reflection coefficient $\sigma_b = 0$.

On the basis of the above conditions concerning the membrane system in Fig. 1, the following mechanistic equations for substance membrane transport have recently been derived by A. Kargol and M. Kargol in the works [13-17]:

$$J_{vm} = L_p \Delta P - L_p \sigma \Delta \Pi \tag{2}$$

$$j_{sm} = \omega_d \Delta \Pi + (1 - \sigma) \bar{C} L_p \Delta P \tag{3}$$

where $J_{vm} = J_{va} + J_{vb}$ – volume flow; j_{sm} – solute flow; L_p – filtration coefficient; σ – reflection coefficient; ω_d – solute diffusion coefficient; and $\bar{C} = 0.5(C_1 + C_2)$ – mean concentration.

Eq. (3) can be transformed to:

$$J_{vsM} = \omega_d \bar{V}_s \Delta \Pi + (1 - \sigma) \bar{C} \bar{V}_s L_p \Delta P \quad (4)$$

where $J_{vsM} = j_{sM} \bar{V}_s$ – solute volume flow. It can also be written as

$$J_{vsM} = J_{vsd} + J_{vsk} \quad (5)$$

where

$$J_{vsd} = \omega_d \bar{V}_s \Delta \Pi \quad (6)$$

is the solute diffusion volume flow, whereas

$$J_{vsk} = (1 - \sigma) \bar{C} \bar{V}_s L_p \Delta P \quad (7)$$

is the solute convection volume flow.

It should be explained here that the L_p coefficient is given by the formula:

$$L_p = L_{pa} + L_{pb} \quad (8)$$

where L_{pa} is the filtration coefficient of n_a membrane pores (not permeable to the solute), whereas L_{pb} is the filtration coefficient of n_b membrane pores (permeable to the solute).

In turn, the reflection coefficient $\sigma_M = \sigma$ is defined as

$$\sigma = \frac{L_{pa}}{L_{pa} + L_{pb}} = \frac{L_{pa}}{L_p} \quad (9)$$

Based on formulae (8) and (9), we immediately obtain

$$L_{pa} = \sigma L_p \quad (10)$$

and

$$L_{pb} = (1 - \sigma) L_p \quad (11)$$

The last transport parameter, i. e. the coefficient ω_d , is given by the formula [13-17]:

$$\omega_d = \bar{C} L_{pb} = (1 - \sigma) \bar{C} L_p \quad (12)$$

That formula is a correlation between the three permeability coefficients, i. e. L_p , σ and ω_d . The respective parameters are, according to Eqs. (2) and (3), given by the expressions:

$$L_p = \left(\frac{J_{vM}}{\Delta P} \right)_{\Delta \Pi = 0} \quad (13)$$

$$\sigma = \left(\frac{\Delta P}{\Delta \Pi} \right)_{J_{vM} = 0} \quad (14)$$

and

$$\omega_d = \left(\frac{j_{sd}}{\Delta \Pi} \right)_{\Delta P = 0} \quad (15)$$

It should be added here that, in view of definition (9), the membrane M as a whole will be non-selective (permeable) for the given solute (s) if $L_{pa} = 0$. Its reflection coefficient will be $\sigma = 0$. However, taking a solute (s) for which $L_{pb} = 0$, we obtain that $\sigma = 1$. Under the circumstances, the membrane is semi-permeable.

For a given membrane, such a solute can be selected for which $L_{pa} > 0$ and $L_{pb} > 0$. In such a case the reflection coefficient will be contained in the interval $0 < \sigma < 1$, so the membrane will be selective.

We can now present an illustration of the functioning of the mechanistic transport equations (2) and (3). To do so, let us refer the equation to the respective parts (a and b) of the membrane M of the system shown in Fig. 1. By so doing, for part (a) we immediately obtain that

$$J_{va} = J_{vva} = L_{pa} \Delta P - L_{pa} \Delta \Pi \quad \left(\text{because } \sigma_a = \frac{L_{pa}}{L_p} = 1 \right) \quad (16)$$

and

$$j_{vsa} = 0 \quad (\text{because } \sigma_a = 1 \text{ then } \omega_{da} = 0) \quad (17)$$

where J_{vva} is solvent volume flow. Then, if the equations are referred to part (b), i. e. to n_b pores of the membrane, a markedly complicated situation is obtained. On the basis of Eq. (2) for the pores, we obtain

$$J_{vb} = L_{pb} \Delta P \quad (18)$$

since $\sigma_b = 0$.

However, on part (b) of the membrane the differences of pressure $\Delta \Pi$ and ΔP also occur. Thus flow J_{vb} has two components [13-17]:

$$J_{vb} = J_{vwb} = J_{vbs} \quad (19)$$

where J_{vwb} is the water (w) volume flow and J_{vbs} is the solute (s) volume flow.

It should be noted here that the flow J_{vwb} is the net flow of the flows $J_{vwb}^{\Delta P}$ and $J_{vwb}^{\Delta \Pi}$, which is expressed by

$$J_{vwb} = J_{vwb}^{\Delta P} - J_{vwb}^{\Delta \Pi} \quad (20)$$

where $J_{vwb}^{\Delta P}$ is the volume water flow driven by the pressure difference ΔP and $J_{vwb}^{\Delta \Pi}$ is the volume diffusion water flow driven by the pressure difference $\Delta \Pi$. These flows satisfy the relations $J_{vwb}^{\Delta P} > 0$ and $J_{vwb}^{\Delta \Pi} < 0$. On the other hand, the flow J_{vbs} is given by formula (5), i. e.:

$$J_{vsM} = J_{vsd} + J_{vsk} \quad (21)$$

since $J_{vbs} = J_{vsM}$.

Biophysical Basis of Stationary Water Exchange by a Model Living Cell

Cell Membrane as an Heterogeneous Porous Structure

The cell membrane is, in general, a very complicated structure, and it performs a series of fundamental functions which are necessary for the cell's life activities [3, 10, 24, 25, 28]. One of the functions is the transport of water and various solutes (both electrolytes and non-electrolytes). The importance of the transport properties of the cell membrane follows from the fact that each cell, in order to live, has to absorb water and some solutes from its surroundings, as well as removing water and unwanted products of metabolism [1, 3, 10, 21, 25, 28]. This exchange goes on, mediated and affected by the cell membrane.

Cell membranes have special channels (pores) permeable to water. By these pores, we mean water pores, formed by transport proteins (barrels) [3, 23, 28], water pores created by antibiotics [28] or water pores formed by porin proteins (aquaporins) [2, 3, 7, 23, 28]. We also believe that ion channels of large enough linear dimensions (when open) can also function in that way [3, 6, 9, 27, 28]. Based on the literature [2, 3, 6, 7, 9, 23, 27, 28], one can assume that the pores (channels) of the cell membrane, permeable to water, have varying linear dimensions. If so, then it is reasonable to treat such a membrane as a heterogeneous porous structure. All the N pores of such a structure can be arranged in a line which begins with smallest pores $r_1 > r_w$ (where r_w is the radius of water molecules) and ends with largest r_N^{\max} :

$$r_1 < r_2 \dots < r_s < \dots < r_N^{\max} \quad (22)$$

In the cell cytoplasm, it is easy to find such a solute (s) of molecular radius r_s for which a certain number n_a of pores (in the range $r_1: r < r_s$) will be impermeable to that solute. But the remaining pores (in the number of $n_b = N - n_a$) will be permeable to that substance. According to the idea of the mechanistic formalism for membrane transport [13-17], n_a pores can be assigned the reflection coefficient $\sigma_a=1$, while $n_b=N-n_a$ pores – the reflection coefficient $\sigma_b=0$. In the situation presented, the substance (s) will be osmotically active only with respect to n_a pores. Thus, in their vicinity, the osmotic transport of water will be generated, whereas – through n_b pores – a flow of water, together with some solutes contained therein, may be generated hydromechanically (due to the mechanical pressure difference). It can be added here that through each of the N pores there may occur transport of solutes of linear molecular dimensions (pore radius r_s') smaller than the linear dimensions of a given pore. Consequently, the situation appears highly complex. However, in the scope of the present work, we shall limit our considerations to transport of water and one (let us say, selected) solute (s).

The Model of a Cell and Its Medium. The Cell's Turgor Pressure

In order to discuss the problem of water transport by a living cell, let us consider the model system shown schematically in Fig. 2. In that system, the studied cell is in a water solution, which is thus its medium. For convenience, we shall assume that the entire cell membrane (with N pores of varying linear dimensions) is represented by an equivalent membrane M mounted in the right wall of the cell. In that membrane, all the pores have been arranged in such a way that the smallest of them ($r_1 > r_w$) are placed at the top, and the largest r_N^{\max} – at the bottom. Let us also assume that there is an active volume flow J_{vs}^A permeating into the cell of a certain selected solute (s). Let the radius r_s of this substance come from the range $r_1 < r_s < r_N^{\max}$.

In the situation presented, let L_p , σ and ω_d denote the filtration coefficient, reflection coefficient (from the interval $0 < \sigma < 1$) and solute (s) diffusion permeability coefficient of the membrane M , respectively (in accordance with the idea of the mechanistic formalism for membrane transport). The membrane M can also be divided into parts (a) and (b), which contain n_a pores impermeable to the solute (s), and $n_b = N - n_a$ pores permeable to molecules of the solute, respectively. We can also assign to those parts the filtration coefficients L_{pa} and L_{pb} , and reflection coefficients $\sigma_a=1$, and $\sigma_b=0$, respectively [13-17].

Because of the occurrence of the flow J_{vs}^A , we can assume that the concentration C_{si} of substance (s) in the cell is greater than concentration C_{so} of the substance in the medium ($C_{si} > C_{so}$). So, on membrane M , there will occur the concentration difference $\Delta C_s = C_{si} - C_{so}$, and thus – an osmotic pressure difference $\Delta \Pi_s = RT (C_{si} -$

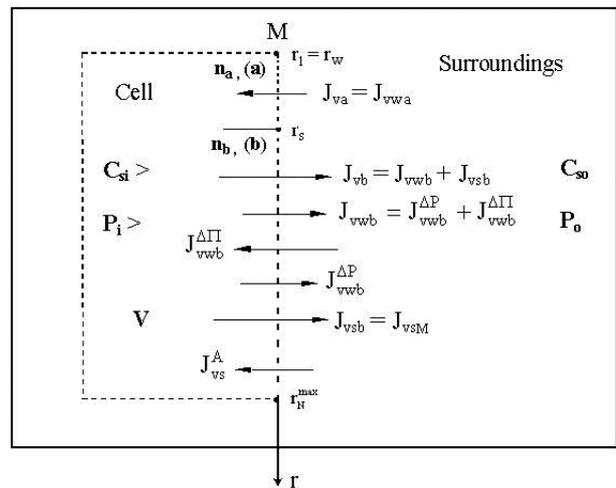


Fig. 2. Model system of the living cell and its surroundings (M – cell membrane; C_{si} , C_{so} – concentrations; P_i , P_o – mechanical pressures; r_w , r_s – radii of water (w) and solute molecules (s); r_N^{\max} – radius of largest pores; V – cell volume; $J_{va} = J_{vwa}$, $J_{vb} = J_{vwb} + J_{vsb}$, $J_{vwb}^{\Delta \Pi}$, $J_{vwb}^{\Delta P}$, $J_{vsb} = J_{vsbM}$, J_{vs}^A – fluxes).

C_{so}). Water will flow into the cell due to the pressure difference $\Delta\Pi_s$ causing a rise in mechanical pressure P_i inside the cell. Under stationary conditions, that pressure will be constant and higher than the pressure P_o outside ($P_i > P_o$). Thus, under stationary conditions, there will occur a constant osmotic pressure difference ($\Delta\Pi_s = \text{const.}$) and a constant mechanical pressure difference ($\Delta P = P_i - P_o = \text{const.}$). The cell volume will also be constant ($V = \text{const.}$). We postulate here that, under such conditions, the cell constantly absorbs and removes water. Our ultimate task is to find appropriate equations that will describe the volume flow of the water absorbed and removed by the cell.

However, first, we have to resolve the problem of the cell's turgor pressure and find an appropriate formula to describe it. With this in mind, let us note that under stationary conditions of the system (cell – medium) the resultant volume flow J_v^t satisfies the relation:

$$J_v^t = J_{vM} + J_{vs}^A = 0 \quad (23)$$

Hence, using Eq. (2), we find:

$$\Delta P = \sigma \Delta \Pi_s - \frac{J_{vs}^A}{L_p} \quad (24)$$

where $\Delta \Pi_s = RT (C_{si} - C_{so})$ and $\Delta P = P_i - P_o$, the pressure inside cell being treated as turgor pressure.

It should be added here that, under stationary conditions, the resultant solute volume flow will equal zero, which is written as

$$J_{vs}^t = J_{vsM} + J_{vs}^A = 0 \quad (25)$$

Now, taking into account formulae (3) and (12), we may write:

$$-J_{vs}^A = J_{vsM} = (1-\sigma)\bar{C}\bar{V}_s L_p \Delta \Pi_s + (1-\sigma)\bar{C}\bar{V}_s L_p \Delta P \quad (26)$$

Substituting this expression into (24), we obtain the sought formula for the cell's turgor pressure:

$$\Delta P = \bar{\sigma} \Delta \Pi_s \quad (27)$$

where

$$\bar{\sigma} = \frac{\sigma + (1-\sigma)\bar{C}\bar{V}_s}{1 - (1-\sigma)\bar{C}\bar{V}_s} \quad (28)$$

Water Absorption by the Cell

The studied cell (see Fig. 2) can absorb water osmotically within part (a) of the membrane M, as that part contains n_a pores which are impermeable to the substance (s). Its reflection coefficient $\sigma_a = 1$. The volume flow J_{vwa} of the absorbed water is given by the formula (16), i. e.:

$$J_{va} = J_{vwa} = L_{pa} \Delta P - L_{pa} \Delta \Pi_s$$

Presently, taking into account the formulae (10) and (27), we find:

$$J_{vwa} = L_p \sigma (\bar{\sigma} - 1) \Delta \Pi_s = L_p \sigma (\bar{\sigma} - 1) RT (C_{si} - C_{so}) \quad (29)$$

This is the sought formula for the flow J_{vwa} of the water absorbed by the cell from its medium. Based on that expression, we have calculated the values of the flow for membranes of three sample cells, i. e. *nitella translucens*, *human red blood cell* and *dog red blood cell* [18, 26]. The above was done with the use of the data given in Table 1. The results obtained are presented in Column VIII of the table. The values of the flows are relatively high. This indicates that the cell must constantly absorb large amounts of water to perform its life functions. We believe the values found here are close to the biological reality.

Water Removal by the Cell

In order to consider water removal by the studied model cell (under stationary conditions), let us take into account the volume flow J_{vb} which permeates across part (b) of the membrane M (Fig. 2). The reflection coefficient of that part is $\sigma_b = 0$. The flow J_{vb} is given by the formula (18). With the use of the formula (11), it can be transformed to:

$$J_{vb} = (1-\sigma) L_p \Delta P \quad (30)$$

Now, taking into account (19), we obtain:

$$(1-\sigma) L_p \Delta P = J_{vwb} + J_{vsM} \quad (31)$$

Hence, using Eqs. (4) and (27), we find the sought expression for the flow J_{vwb} of the water removed by the cell. It takes the form:

$$J_{vwb} = (1-\sigma) \left[(1-\bar{C}\bar{V}_s) \bar{\sigma} - \bar{C}\bar{V}_s \right] L_p RT (C_{si} - C_{so}) \quad (32)$$

Using the above expression and the data from Table 1, we have calculated the flow J_{vwb} for the following cell membranes: *nitella translucens*, *human red blood cells* and *dog red blood cells*. The results of the calculations are presented in Column IX of Table 1. The obtained flows of water removed from the cell (see Column VIII of Table 1) are equal to flows J_{vwa} of the water absorbed by the cell. That fact testifies to the reliability of our research endeavours. The main result is the finding that under stationary conditions each living cell is capable of absorbing and removing considerable quantities of water at the same time.

Table 1. Numerical data and results of calculations.

No	Membrane	Solute (s)	$L_p \times 10^{12}$ [m ³ /N·s]	σ	$\bar{V}_s \times 10^3$ [m ³ /mol]	Source	$J_{vwa} \times 10^8$ [m/s]	$J_{vwb} \times 10^8$ [m/s]
I	II	III	IV	V	VI	VII	VIII	IX
1	Nitella translucens	Izopropanolol	1.1	0.4	0.076	[18]	-6.50	6.50
2	Human red blood cell	Ethylene glicol	0.92	0.63	0.056	[18]	-5.29	5.29
3	Dog red blood cell	Urea	1.95	0.38	0.042	[26]	-11.37	11.37
Other data: $C_{si} = 150$ [mol/m ³], $C_{so} = 50$ [mol/m ³], $\bar{C} = 100$ [mol/m ³], $R = 8.3$ [N·m/mol·K], $T = 300$ [K]								

Final Remarks

Each living cell, while performing its life functions, has to constantly exchange water and various dissolved substances with its surroundings. To be precise, it has to absorb water and some necessary solutes, as well as removing the water together with unwanted metabolites. This water exchange is obvious from the biophysical point of view in the case of non-stationary cell operation (i. e. at inconstant cell volume) [5, 6, 12, 18, 19, 22, 27, 29].

However, the explanation of such an exchange under stationary conditions (at $V = \text{const.}$) has been problematic until now. In the present work, the problems have been resolved. Namely, we have shown that (on the basis of the mechanistic equations for membrane transport [13-16]) each cell is able to permanently exchange water with its surroundings under stationary conditions. The cell can absorb water osmotically (due to osmotic pressure difference) and simultaneously remove it hydromechanically, owing to the mechanical pressure difference (in other words due to the cell's turgor pressure). We believe that this original research result is very important and opens far-reaching research possibilities, especially concerning the influence of environmental conditions on the functioning of single living cells as well as multi-cell organisms. It is not possible to observe this research result on the basis of the K-K equations, which is easy to demonstrate by means of pertinent considerations.

References

1. ACKERMAN E. Biophysical Science. Prentice-Hall, Inc. Englewood Cliffs, New Jersey, pp. 362, **1962**.
2. AGREE P., BROWN D. NIELSEN S. Aquaporin water channels: unanswered questions and unresolved controversies. *Current Opinion in Cell Biology* **17**, 472, **1995**.
3. ALBERTS B., BRAY D., JOHNSON A., LEWIS J., RAFF M., ROBERTS K., WALTER P. *Essential Cell Biology*. Garland Publishing, Inc. New York and London, pp. 347, **1998**.
4. BRAHM J. Diffusional water permeability of human erythrocytes and their ghosts. *J. Gen. Physiol.* **79**, 791, **1982**.
5. WOLF M. B. A simulation study of the anomalous osmotic behaviour of red cells. *J. Theor. Biol.* **83**, 687, **1980**.
6. CROZIER P. S., ROWLEY R. L. Molecular dynamics simulation of continuous current flow through a model biological membrane channel. *Physical Review Letters* **86**, 2467, **2001**.
7. CURRY M. R., SCHACHAR-HILL B. and HILL A. E. Single water channels of aquaporin-1 do not obey the Kedem-Katchalsky equations. *J. Membrane Biol.* **181**, 115, **2001**.
8. DISALVO A., SIDDIQI F. A. and TI TIEN H. Membrane transport with emphasis on water and nonelectrolytes in experimental lipid bilayers and biomembranes. (Benga, G., Ed.), *Water Transport in Biological Membranes* **1**, 41, **1989**.
9. GENNIS R. B. *Biomembranes. Molecular Structure and Function*. Springer-Verlag, New York, Berlin, Heidelberg, London, Tokyo, pp. 235, **1989**.
10. GLASER R. *Einführung in die Biophysik*. Veb Gustav Fischer Verlag, Jena, pp. 185-249, 59, **1971**.
11. HERTEL A., STEUDLE E. The function water channels in *chara*: The temperature dependence of water and solute flows provides evidence for composite transport and for a slippage of small organic solutes across water channels. *Planta*, **202**, 324, **1997**.
12. HOUSE C. L. *Water transport in cells and tissues*. Edward Arnold (Publishers) LTD, pp. 36, **1974**.
13. KARGOL A. A mechanistic model of transport processes in porous membranes generated by osmotic and hydrostatic pressure. *J. Membr. Sci.* **191**, 61, **2001**.
14. KARGOL M., KARGOL A. Mechanistic formalism for membrane transport generated by osmotic and mechanical pressure. *Gen. Physiol. Biophys.* **22**, 51, **2003**.
15. KARGOL M., KARGOL A. A. Mechanistic equations for membrane substance transport and their identity with Kedem-Katchalsky equations. *Biophysical Chemistry* **103**, 117, **2002**.
16. KARGOL M., KARGOL A. A. Membrane transport generated by the osmotic and hydrostatic pressure. Correlation relation for parameters L_p , σ and ω . *J. Biol. Phys.* **26**, 307, **2000**.
17. KARGOL M. Mechanistic approach to membrane mass transport processes. *Cellular and Molecular Biol. Letters* **7**, 982, **2002**.
18. KATCHALSKY A., CURRAN, P. F. *Nonequilibrium Thermodynamics in Biophysics*, Harvard University Press, Cambridge, Massachusetts, pp. 113-131, **1965**.

19. KEDEM O., KATCHALSKY A. Thermodynamics analysis of the permeability of biological membranes to non-electrolytes, *Biochim. Biophys. Acta* **27**, 229, **1958**.
20. LEVITT D. G. A new theory of transport for cell membrane pores. *Biochim. Biophys. Acta* **373**, 115, **1974**.
21. MENGEL K. and KIRKBY E. A. Principles of Plant Nutrition. International Potash Institute, Werblanfen – Bern (Switzerland). 151, **1980**.
22. MILGRAM J. H., SOLOMON A. K. Membrane permeability equations and their solutions for red cells. *J. Membr. Biol.* **34**, 103, **1977**.
23. NAŁĘCZ K. A. Transport of water through biological membranes. *Postępy Biochemii.* **42**, 161, **1996**.
24. PRZESTALSKI S. Biological Membranes. PWN “Wiedza Powszechna”, Warszawa. pp. 5, **1983**.
25. SALISBURY F. B., ROSS C. Plant Physiology. Wadsworth Publishing Company, Inc. Belmont, California. pp. 14, **1969**.
26. SHA’AFI R. J. and GARY-BOBO C. M. Water and non-electrolytes permeability in mammalian red cell membranes. (Butler, J. A. V. and Noble, D., Eds.), *Progress in Biophysics and Molecular Biology*, Pergamon Press, Oxford and New York. **26**, 106, **1973**.
27. SIEBENS A. W. Cellular volume control. In: *Physiology and Patho-physiology*, Ed. by Seldin, D. W. and Glebisch, G., Raven Press, New York. pp. 91, **1985**.
28. STRYER L. *Biochemistry*. PWN, Warszawa. 115, **2000**.
29. WEINSTEIN A. M. Analysis of volume regulation in an epithelial cell model. *Bulletin of Mathematical Biology.* **54**, 537, **1992**.