ON THE THEORETICAL INTERPRETATION OF TURGOR PRESSURE

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(WITH ONE FIGURE)

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In a recent publication, **Burström** (**5**) has endeavored to "evaluate the physical meaning of the turgor pressure of a living cell." Modifications have been suggested in the schematic representation of osmotic quantities with change in volume of the cell, from that originally proposed by **Thoday** (**7**) and modified by **Höfler** (**6**). He has included a curve representing the influences of solute in the external medium bathing the cell, approximately paralleling the curve representing the influence of solute in the internal medium. The net effect of the osmotic influences (at any particular volume of the internal medium) related only to the solute differences of the internal and external media, is thus satisfactorily represented. A similar inclusion was made by **Broyer** (**1**), but represented in a different manner, *viz.*, a line approximately paralleling the curve usually representing the influence of an internal hydrostatic pressure. In the latter, the loci of the curves allow a more ready summation of the scalars representing influences causing water to tend to move in similar directions (inward or outward) through the cytoplasmic membrane of the cell.

It is usually recognized that, under conditions of osmotic disequilibrium such that a net influx or efflux specific free energy (**1**) exists, a finite but infinitesimal difference obtains between the internal hydrostatic pressure (turgor pressure in the usual sense) and the wall pressure. This is caused by the net movement of water across the interposed differentially permeable membrane separating the internal and external media, and attended by a corresponding change in the volume of the internal phase. There is a progressive infinitesimal, correlated change in each of the factors with time, concomitant with water movement, tending to approach osmotic dynamic equilibrium as a limit. Attended by metabolism and growth, there is a continuous shifting of the equilibrium determined by current environmental factors within limits imposed by the genetic potentialities of the organism.

Burström has defined turgor pressure in a sense quite distinct from the common usage, *viz.*, "turgor pressure equals the difference in osmotic values of cell sap and external solution." He regards turgor pressure to be an actual, instantaneously and fully effective pressure "acting from inside on the cell wall," i.e., "the expanding power of the cell content," at any particular time. He visualizes turgor pressure and wall pressure to be "of fundamentally different physical origin, and each may attain any value independent of the other." (See figure 1) He suggested (using his symbols and wording[1]) that

$$T = O - E \tag{1}$$

and

$$O = S + W \tag{2}$$

are two independent relationships among the osmotic quantities. He combined these equations, solving for $T - W$ (by substituting $S + W$ from equation 2, for O in equation 1), and obtained the relation

$$T - W = S - E. \tag{3}$$

"These two formulas (1 and 2)[2] are independent of each other. If the cell is not at equilibrium, $S \gtrless E$ and $T \gtrless W$. It also follows that under all circumstances $T - W = S - E$. That means that if a cell is absorbing water owing to a difference in suction $(S - E)$ there must also exist an excess of turgor pressure over the wall pressure $(T - W)$. T equals W only if the cell is at equilibrium with the external solution."

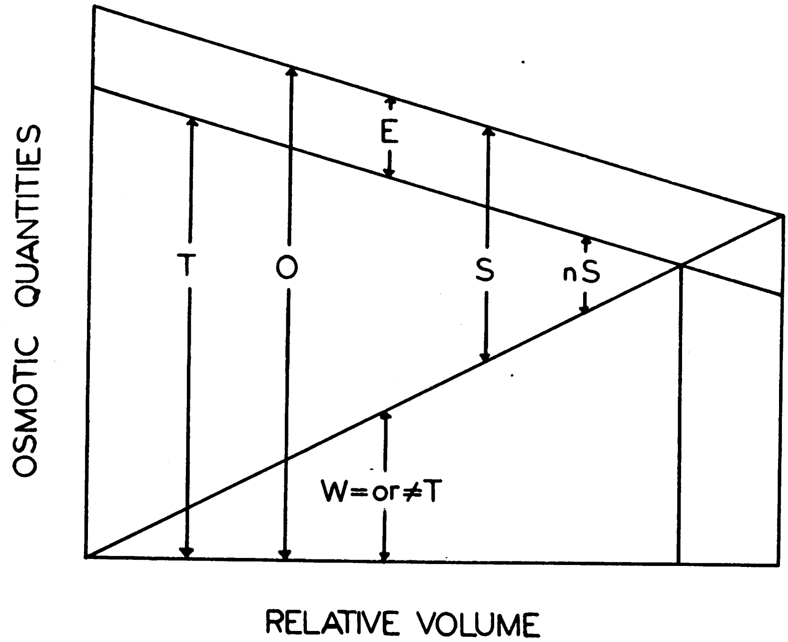

FIG. 1. Diagrammatic relationship among various osmotic quantities and the relative volume of the internal phase of a cell osmometer. In the usual osmotic diagram $T \simeq W$. The de Vries-Burström concept visualizes T to be disjunct from W, as represented otherwise above.

DE VRIES (**9**) may have had a concept similar in part at least to that suggested by Burström, *viz.*, ". . . der Zellsaft muss bei der Aufnahme von

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[1] Here "T is the turgor pressure, O is the osmotic value of the cell sap, E is the osmotic value (or "suction") of the external medium, W is the wall pressure, and S is the suction of the entire cell."

[2] Author's insert.

Wasser den Widerstand der elastisch gedehnten Zellhaut überwinden, und die wasseranziehende Kraft des ganzen Gewebes ist also gleich der Turgorkraft seiner Zellsäfte, vermindert mit der elastischen Spannkraft der Zellhäute.''—page 544. (See equation 5.)[3] He also stated, ''Die Wasser anziehende Kraft des turgescenten Gewebes ist nun zwar nicht dieselbe die des in seinen Zellen enthaltenen Zellsaftes, sondern um so viel geringer als der elastischen Spannkraft der Protoplaste und der Zellhäute entspricht. . . .'' —page 437 (equation 2 or 4).

Assuming the usual concept of turgor, the single equational expression (equations 2 or 4, or 6) including all necessary internal and external influences of an osmotic system (compare (1) equation 4a and 8), would seem to indicate the osmotic relations quite satisfactorily of itself. Herein, turgor pressure (or better, hydrostatic pressure) and wall pressure are often substituted one for the other because of their generally recognized approximate equality under all conditions. Burström proposes that ''turgor pressure is not caused by a net diffusion of water, nor by an increase in volume and a hydrostatic pressure (compare 4, pg. 24)[2] as in an osmometer, but only by the (net)[2] diffusion pressure (restricted to effects caused by a difference of solution concentration in the two media bathing the interposed membrane)[2] of the water molecules.'' This latter viewpoint, and the combination of equations 1 and 2 leads to a concept which is quite thought prompting. Here, as with the strict definition of osmotic pressure (1, pg. 5), an osmotic pressure difference can be realized at any instant of time—the biological and physical systems considered to be similar. Assuming acceptance of the defi-

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[3] Detailed comparative analysis might be as follows:

I. Burström's equations, including E in equation 1 and omitting the same in equation 2, S representing the suction of the cell;

$T = O - E$ (1)

$O = S + W$, and (2)

substituting $S + W$ from equation 2, for O in equation 1,

$T = S + W - E$, or

$T - W = S - E$ (3)

II. Alternative equations, where the external medium is water (i.e., omitting E in both equations), nS representing the net suction by the cell;

$T = O$ (1a)

$O = nS + W$, and (4)

substituting $nS + W$ from equation 4 for O in equation 1a,

$T = nS + W$; (5)

or, where the external medium is a solution (i.e., including an E in both equations), nS representing the net suction by the cell;

$T = O - E$ (1)

$O = nS + W + E$, and (6)

substituting $nS + W + E$ from equation 6 for O in equation 1,

$T = nS + W + E - E$, or

$T = nS + W$ (5)

If the alternative analysis may be assumed to represent the viewpoint of de Vries, then, the net water absorbing ''force'' of the cell relative to the external medium (nS) would be involved here rather than the suction of the cell *per se* (S) as used by URSPRUNG (**8**) and BURSTRÖM (**4, 5**).

nition of turgor as a resultant "rigidity in living cells, caused by pressure of the water contents against the elastic cell membrane," it might appear unwise however, to redefine turgor pressure as the net osmotic value (net osmotic specific free energy related only to the presence of solute in the internal and external media), equal to such an osmotic pressure difference. Under practical conditions, rigidity change, involving finite time, is usually conceived as associated with a net movement of water and corresponding change of volume of the inner phase. Therefore, it seems questionable whether any advantage accrues from grouping any certain limited number of factors causing water to tend to move in a particular direction other than, for example, the sum of the influx intensities (**1**),[4] at any particular time.

It is difficult to reconcile Burström's postulate that "turgor pressure must decrease when a cell absorbs water and the wall pressure increases," with the usual viewpoint. Further, under conditions appropriate to his concept, it might be interpreted that complete "turgor" expansion or contraction should be realized merely in the time necessary for membrane (including the wall) stretching or shrinking, since the "pressure" here would be fully effective at any condition of non- or dynamic equilibrium and independent of water movement as a causal factor. The alternative usual concept of turgor pressure, in accord with experimental observation, requires an extended measurable time for approach toward full realization of the turgor potentialities, accompanied by a progressive movement of water. Here, the time involved is that necessary for the net migration of water across the membrane and that required for the concurrent stretching or shrinking of the limiting surface.

Burström suggested that the osmotic diagrams of Höfler and Tamiya[5] are valid only at water equilibrium. This scheme, first proposed by Thoday and generally used, seems to be acceptable for all situations where all factors (E, etc., also) are included (compare (**1**) fig. 3 and equation 4a).

A detailed analysis of common ideas on the movement of materials into plants has been presented (**1, 2, 3**).[4] A discussion of some experimental observations on the water relations of roots will be reported elsewhere.

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[4] At the suggestion of others, it would be wise for dimensional accuracy, to recognize all flux specific free energies as practically measurable translational energy intensities (here volumed) rather than "action capacities."

[5] Referred to by Burström. Actually, Tamiya's representation of turgor pressure, based on experimental data of Stow with *Nitella,* follows that theoretically suggested first by Höfler, compare BROYER (**1**).

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