ON THE THEORY OF OSMOTIC WATER MOVEMENT ¹

PETER M. RAY

DEPARTMENT OF BOTANY, UNIVERSITY OF MICHIGAN, ANN ARBOR

In explaining osmotic movement of water, it is customary in plant physiology to regard water movement between cells as taking place along gradients of diffusion pressure deficit or suction force. Efforts to describe water movement quantitatively are based on the assumption that the rate of water movement between two cells should be proportional to the difference between the diffusion pressure deficits (or suction forces) of the two cells. The purpose of this paper is to consider some aspects of the theory of osmotic water movement which arise out of this elementary rate problem, and indicate some fundamental difficulties in the concepts currently in use. First we shall examine critically the meaning of the concepts "suction force" and "diffusion pressure deficit". Then their applicability as parameters of osmotic water movement will be considered. Finally, the value of rate measurements in indicating the mechanism of osmosis will be reviewed, and a hypothesis concerning the mechanism of osmotic flow will be presented.

Suction Force. The suction force of an osmotic unit such as a cell, is defined (1, 54) in two distinct ways. First, it is taken to be equal to the osmotic potential of that solution which, at atmospheric pressure, would be in osmotic equilibrium with the unit in its existing state. By osmotic potential (Π, atm)² we mean the pressure which would have to be applied to a solution to maintain osmotic equilibrium between it and pure water, through an ideal semipermeable membrane. The term "osmotic potential" is used for this potential pressure, commonly called "osmotic pressure", to minimize confusion between it and actual existing hydrostatic pressure, designated P (atm).

Second, the suction force (S) of an osmotic unit is stated (1, 54) to have the value

\[ S = Π - P \]  

I

Π and P refer to osmotic potential and pressure within the osmotic unit. This equation usually is not accurately justified, so that the student is obliged to accept on faith that S defined by equation I has the same value as when defined by the equilibrium criterion first mentioned. The meaning of equation I can be seen by comparing its transposed form

\[ P_1 = Π_1 - S_1 \]  

II

with the demonstrable fact that the pressure required to maintain osmotic equilibrium between two solutions must be equal to the difference in their osmotic potentials,

\[ P_1 = Π_1 - Π_2 \]  

III

(This relationship is readily derived from the basic equation for osmotic equilibrium, equation IV, to be discussed below.) It is thus seen that S₁ must have the same value as Π₂, the external solution which would be in equilibrium with osmotic unit Π₁ and pressure P₁. Equation I is, therefore, consistent with the experimental definition of S first mentioned; it defines a state of the osmotic unit useful in predicting whether or not equilibrium can obtain between it and any second unit.

From equation II it is readily shown, in a manner similar to that used above for an external solution, that any two osmotic units can be in equilibrium if and only if they have the same value of S.

Diffusion pressure deficit is widely accepted as having the same meaning and quantitative value as suction force. A different concept is involved, however, which must now be examined.

Diffusion Pressure. Osmosis is commonly held by plant physiologists to be a diffusion process, which may explain why the terms to be discussed are so popular. Diffusion pressure deficit is defined as follows:

"Diffusion pressure deficit of water . . . . is the amount by which its diffusion pressure is less than that of pure water at the same temperature and under atmospheric pressure" (34).

Diffusion pressure is a hypothetical quantity which is supposed to govern the rate of diffusion out of a solution. The quantitative basis of diffusion pressure, according to modern usage throughout plant physiology, is the same parameters as are used to define S. This is shown, for example, by the statement, "The osmotic pressure is an index indicating quantitatively the amount by which diffusion pressure of water in the solution is less than that of pure water at the

⁠¹ Received November 25, 1959.

⁡ An appendix defining all mathematical symbols used here, appears at the end of the paper.
same temperature and under atmospheric pressure” (34).

A consequence of basic considerations in thermodynamics, which may be found in any modern treatise of the subject, is that the pressure \( (\Pi_1) \) required to maintain ideal osmotic equilibrium between two solutions is given by

\[
P_1 = \frac{RT}{V} \ln \frac{\rho_2}{\rho_1} \quad \text{IV}
\]

where \( \rho_1 \) and \( \rho_2 \) are the partial vapor pressures\(^a\) of the solvent in solutions 1 and 2, and the positive pressure \( P_1 \) is applied to solution 1; \( V \) is the partial molar volume of the solvent. When solution 2 is pure solvent, then \( P_1 \) is equal to the osmotic potential \( (\Pi_1) \) of solution 1, as is well known. Since the partial vapor pressure of solvent approaches zero as its concentration tends to zero, it follows that the osmotic potential of a solution increases without limit as the solvent concentration approaches zero as a limit. That this must be so, can be seen by considering, for example, a sample of pure glycerol separated from water by a membrane permeable only to water. To maintain equilibrium, it would be necessary to increase the diffusion rate of water out of the glycerol until it equalled the rate of diffusion of water into the glycerol; but pure glycerol would contain no water at all, so it would be impossible to maintain equilibrium by any pressure.

The diffusion pressure of pure water must be the difference between the diffusion pressures of water and of a solution containing no water at all, in other words it must be equal to the diffusion pressure deficit of a solution containing no water, or to its osmotic potential if it is at atmospheric pressure. It follows from what has been said above that the diffusion pressure of pure water must be infinitely large; this has been remarked by Crafts, Currier, and Stocking (12). The diffusion pressure deficit of a solution (the difference between diffusion pressures of pure water and of water in the solution) is hence the difference between an infinitely large quantity and some other quantity, and therefore can have no numerical value. It is not possible to obviate this difficulty in the fashion, which seems to have been accepted almost throughout plant physiology, of setting the diffusion pressure of pure water equal to zero (12), as this amounts to setting infinity equal to a finite number. Diffusion pressure deficit is self-contradictory because the definition of this quantity in terms of diffusion pressures, and of osmotic potential and hydrostatic pressure (equation I), is not consistent. In other words, there cannot be a diffusion pressure which can be defined by the statements quoted above, and if there is no such quantity as diffusion pressure, there cannot be a diffusion pressure deficit. The concept is simply not valid.

The idea of diffusion pressure as explaining osmosis was originated by Haldane (20), whose theoretical work is cited as the basis for introducing the concept of diffusion pressure into plant physiology (33). It is important to note that in Haldane’s theory of osmosis, the diffusion pressure difference between a solution and pure solvent was explicitly not equal to the osmotic potential of the solution, and so was not identical to the diffusion pressure deficit as defined by more recent authors (equation I). The concepts of diffusion pressure are, consequently, also not the same. Thus in modern usage diffusion pressure deficit is not only self-contradictory, but it conflicts with the justification for assuming that a diffusion pressure governs osmosis.

Haldane’s theory of diffusion pressure and osmosis is inconsistent with equation IV, and therefore is thermodynamically unsound. Hence it would be fruitless to attempt to rescue the concept of diffusion pressure deficit by giving up equation I and substituting Haldane’s definition. Neither his nor the modern concept of diffusion pressure appears to have any physical meaning, and neither concept is any longer in use outside of plant physiology. It seems inevitable that the use of diffusion pressure and diffusion pressure deficit in plant physiology will have to be abandoned.

Suction force does not contain the contradictions just discussed, as it involves no concept analogous to diffusion pressure, but is simply tied consistently to equation I and to the state of osmotic equilibrium between a cell and a solution, as indicated above. The term (not the concept) has been justly criticized (34). In the remainder of this paper we shall employ the generalized term “water deficit” \( (S) \), defined by equation I, for this equilibrium parameter. Since \( \Pi \) and \( P \) in equation I are linearly connected with differences in the chemical potential of the solvent, \( S \) is linearly related to thermodynamic description of an osmotic system, as presented, for example, by Broyer (5). \( S \) can be used just as exactly as chemical potential in dealing with osmotic equilibrium through semipermeable membranes, as long as active transport of water is not involved.

**Water Movement Rates.** Since water deficit \( (S) \) correctly defines states of osmotic equilibrium, it should predict correctly the direction of water movement in systems not at equilibrium. The assumption that the rate of water movement between two osmotic units is proportional to the water deficit difference,

\[
\nu = K_o A (S_2 - S_1) = K_o A [ (\Pi_2 - \Pi_1)^+ - (P_2 - P_1)]^-
\]

has little more than an intuitive basis in the plant physiological literature, even though it was formulated as early as 1921 by Ursprung and Blum (55). There is some evidence that water movement in or into plant tissues may follow equation \( V \) (3, 4, 6, 47), although not all of the results are in close agreement with it.

\(^a\) Or fugacities, for solvents whose vapor does not behave as an ideal gas. For the original derivation, see (15).
and none cover a wide range of rates. Equation V has been supported by making an analogy between osmotic potential and electrical potential, to which current is proportional (3, 19, 23, 24). Water movement is then thought of as determined by a potential drop divided by a resistance to movement. This led to the attractive idea that in steady water flow through the plant, when total flow in each tissue of the conducting system must be the same, the potential drop in each tissue must be proportional to the resistance of that tissue,

\[ \nu = \frac{S_2 - S_1}{r_{21}} = \frac{S_3 - S_2}{r_{52}} = \frac{S_4 - S_8}{r_{48}} \]  

VI

which was suggested by Huber (24) and Gradmann (19) and was formulated by van den Honert (23). However, rates are not proportional to differences in potential with most other processes than electric current, for example, reaction rates and chemical potentials. The analogy provides no satisfying or reliable basis for belief in the principle embodied in equations V and VI.

In the literature of zoophysiology, equation V is known as "Starling's hypothesis" for movement of water between capillaries and tissue fluids. (40). A certain amount of quantitative support for it has been obtained in recent years. It has been derived theoretically using thermodynamics of irreversible processes (50), but this derivation rests on an assumption about rate proportionality which may have only limited application (13). Equation V has been derived for a diffusion process upon thermodynamic (7) and kinetic (29) grounds; in these cases it arises as an approximation.

That equation V cannot be true in general, for rates of osmotic water movement can be seen by the following example. Consider, as shown in figure 1, an osmotic system composed of pure glycerol separated from pure water by an air space, which acts as an osmotic membrane because water vaporizes into it but glycerol does not. The osmotic potential, and therefore water deficit, of pure glycerol is, as brought out above, infinitely large, but it is evident that the rate of transfer of water from the pure water into the glycerol will have a finite value; it will be equal to the rate at which water evaporates from the water surface and diffuses through the air into the glycerol. This rate will be dependent upon temperature and the cross section and length of the air space, and is determined by diffusion parameters which are not proportional to the (infinite) water deficit difference.

If osmotic movement of water through a membrane is regarded as a diffusion process, as it commonly is in plant physiology, then the above considerations will apply also to glycerol and water separated by a semipermeable membrane; the rate of diffusion of water through the membrane cannot be proportional to the water deficit difference, which is infinite. Before examining the relationship which would be expected between diffusion and rate of osmotic water movement, we shall first consider one aspect of water movement in plants for which equation VI is clearly unacceptable.

**Transpiration.** Equation IV is applicable to states of equilibrium between liquid water at pressure \( P_1 \) and water vapor at partial pressure \( p_2 \), if \( p_1 \) is the vapor pressure of liquid water at atmospheric pressure. The equilibrium pressure \( P_1 \) is the pressure which would have to be applied to make the vapor pressure of water \( p_2 \) at the same temperature. By analogy with equation I, \(-P_1\) has been called the diffusion pressure deficit or suction force of water vapor (\( S' \)) at partial pressure \( p_2 \). In conceiving of water movement in plants as involving successive potential drops, Gradmann (19) was led to assume that the rate of transpiration should be proportional to the suction force difference between leaf cells and aerial water vapor. More recent authors (2, 23, 45) have included transpiration as the last term in equation VI, where \( S_4 \) becomes the suction force of the air, and \( r_{48} \) the transpiration resistance. It can be seen from equation IV that this means that the rate of water loss by a plant should be logarithmically dependent upon the water vapor pressure difference between the leaves and the atmosphere, whereas in fact it is nearly linearly dependent upon the vapor pressure difference (30). The expectation of proportionality between \( S' \) difference and transpiration rate is a clear example of confusion between rate and equilibrium parameters, which has serious consequences*. It would mean, for example, that transpiration rate

---

* This error is related to the cause of failure of the "diffusion pressure deficit" concept. In the vapor phase, diffusion pressure deficit as used by plant physiologists (\( S' \)) is clearly not equal to the difference in diffusion pressures [partial pressures, see (34)], so the term is obviously erroneous.
would increase without limit into perfectly dry air, whereas in fact it should never be more than about twice the rate found in air of 50 percent relative humidity (other conditions constant).

There is another factor involved in transpiration rates which S' difference cannot cope with, and which is particularly significant at high relative humidities where S' and diffusion gradients are nearly proportional. This is that in sunlight, the temperature of the leaf can be higher than that of the surrounding air, increasing the internal water vapor pressure of the leaf and therefore the diffusion gradient outward; this effect is much larger than the small effect (proportional to absolute temperature) on S' of the leaf, hence it is possible with nearly the same S' difference to have quite widely different transpiration rates.

Therefore, transpiration cannot correctly be included in equation VI. A kinetically reasonable expression for transpiration rate must be based on diffusion coefficients and water vapor pressures (48) not on S'. Suction force of the air is useful only in evaluating states of equilibrium, that is, of zero transpiration.

**Osmosis as a Diffusion Process.** Regardless of whether or not a net movement of water is occurring, diffusion takes place continually across a membrane permeable to water, in the sense that water molecules are constantly moving through it in both directions. If osmotic water movement across a membrane is due to diffusion, it must represent the difference between diffusional movement of water molecules in one direction and in the other. A simple way of evaluating the molecular flux in one direction is to imagine diffusion from water or a solution into pure solute, as with the glycerol example considered above. We shall start with evaporation of solvent from a solution, which is proportional to the partial vapor pressure of the solvent and hence, for an ideal solution, proportional to the mole fraction (X) of solvent in the solution, according to Raoult's Law. Diffusion of solvent across a membrane into pure solute is an analogous phenomenon, and for an ideal solution the rate of outward diffusion (d) should be proportional to solvent mole fraction (X) and membrane area (A), and inversely proportional to membrane thickness (l), which constitutes the length of the diffusion path

\[ d = \frac{k_d A}{l} X \]

where \( k_d \) is a diffusion coefficient. We wish to know how the rate of outward diffusion will depend upon both X and any hydrostatic pressure (P) which may be applied. One way of evaluating this (there are others, stricter but more lengthy) is with an osmotic system like that shown in figure 2, in which solution 2 of composition \( X_2 \) at atmospheric pressure, is separated by a semipermeable membrane from solution 1 of composition \( X_1 \), to which a hydrostatic pressure \( P_1 \) is applied so as to maintain equilibrium. As is usual in discussions of osmosis, it will be assumed that to maintain equilibrium, P has to be adjusted until the rate of outward diffusion of water molecules from solution 1 is equal to the rate of outward diffusion from solution 2. This latter rate is given by equation VII. The required pressure is given by equation IV, which can be written

\[ P_1 = \frac{RT}{V} \ln \frac{X_2}{X_1} \]

for an ideal solution. Incorporating equation VII for the solution at atmospheric pressure,

\[ P_1 = \frac{RT}{V} \ln \left( \frac{l \cdot d}{k_d A X_1} \right) \]

then

\[ d_1 = \frac{k_d A}{l} \left( X_1 e^{P_1 \over RT} - X_2 e^{P_2 \over RT} \right) \]

The difference between diffusional fluxes in forward and reverse directions across a membrane separating any solutions 1 and 2 is then

\[ \nu_{1 \rightarrow 2} = d_1 = \frac{k_d A}{l} \left( X_1 e^{P_1 \over RT} - X_2 e^{P_2 \over RT} \right) \]

This is the basic equation for osmotic diffusion of water. A similar equation was derived, by a more detailed argument, by Laidler and Shuler (29). We may modify it, for the relatively low pressures involved in most plant cells, by expanding \( e^a \) as the series \( 1 + a + a^2/2! + \ldots \), and neglect terms from \( a^2 \) on, because \( P V / RT \) will be a number considerably less than one. Then

\[ \nu_{1 \rightarrow 2} = \frac{k_d A}{l} \left( X_1 + \frac{P_1 V X_1}{RT} - X_2 + \frac{P_2 V X_2}{RT} \right) \]

We shall now transform this equation by adding and subtracting one within the brackets, then multiplying and dividing by \( V / RT \). We get

\[ \nu_{1 \rightarrow 2} = \frac{k_d A}{lRT} \left( \frac{RT}{V} \right) \left( 1 - \frac{X_2}{X_1} \right) \left( 1 - \frac{X_1}{X_2} \right) \]

Here the quantities \( (1 - X) / V \) are, for dilute solutions, approximately equal to the volume molar solute concentrations \( c \), and the resulting terms \( cRT \) ap-
proximate the osmotic potentials \( \Pi \) of the two solutions, according to the well-known van't Hoff relationship. Also, if the solutions are dilute, \( X_1 \) and \( X_2 \) will be very close to one, so we may take the coefficients of the P terms as equal to one. This leads to

\[
\nu_{\text{diff}} = \frac{k_d AV}{\beta RT} \left[ (\Pi_2 - \Pi_1) - (P_2 - P_1) \right]
\]

XIV

It can thus be seen how equation V arises as an approximation, good only for dilute solutions and low pressures, of the more general expression for diffusion of water across membranes (equation XI). Actually, the difference between equation V and XI will be of minor quantitative importance under ordinary conditions, but it is not likely to remain so under conditions of low water content or high moisture stress, such as in seeds or desert plants. Moreover, it is important to recognize that in principle, the parameters of osmotic equilibrium (S) and osmosis rate are divergent.

**Comparison of Diffusion and Osmosis.** By comparing equation XIV with equation V it can be seen that if osmosis is, as assumed, a diffusion process, then for any given membrane at a particular temperature, the osmotic permeability \( (K_o) \) should be related to the water diffusion permeability \( (K_d) \) by the factor \( \nu_{\text{diff}} / V/RT \), which has a value of about 7.5 \( \times 10^{-4} \) atm\(^{-1}\) in the physiological range of temperature.

Diffusion permeability to water has been measured for several plant cells or tissues using isotopically labelled water (DHO or THO). In most of the cases the simplest comparison of diffusion with osmotic permeability can be made in terms of the half-times for diffusion exchange \( (t_{\text{half}}) \) and osmotic exchange \( (t_{\text{osm}}) \) of water when the cell or tissue is transferred from one situation to another. Philip (42, 43) showed that for a cell or tissue of any particular geometry, and under certain assumptions, these half-times are related to the respective permeability coefficients as follows:

\[
t_{\text{half}} = \frac{k_o (\epsilon + \Pi_o)}{k_d} \]

XV

Here \( \epsilon \) is the elastic modulus of the cell wall (atm) and \( \Pi_o \) the osmotic potential at zero turgor pressure. Accordingly, we shall compute the ratio of permeability coefficients from the formula

\[
k_o/k_d = t_{\text{half}} / t_{\text{osm}} (\epsilon + \Pi_o).
\]

Five available cases will be examined.

A. Ordin and Bonner (36) found \( t_{\text{half}} \) values of 8 to 9 minutes for diffusion of deuterium-labelled water into and out of Avena coleoptile sections 5 mm long. They also determined \( t_{\text{osm}} \) for osmotic equilibration, by following the change in length when a section was transferred into or out of 0.4 M mannitol, and found a value of about eight minutes. From their data (35) \( (\epsilon + \Pi_o) \) can be estimated as 150 atm. From these figures \( K_o/K_d = 7 \times 10^{-4} \) atm\(^{-1}\).

B. Wartiovaara (51), who was the first to use labelled water to study water permeability of a plant cell, determined the course of outward diffusion of DHO from individual cells of the alga *Tolypellopsis stelligera* (= *Nitellopsis obtusa*). He found half-times of approximately 0.7 minutes, corrected for build-up of external DHO concentration. The osmotic permeability of similar cells of *Tolypellopsis* was determined by Palva (39), using a density-gradient method, with half-times of about 2.0 minutes. From his data \( \epsilon \) is found to have a value of about 75 atm; \( \Pi_o \) is not given but can be taken as about eight atm from data of Collander (9). Then \( K_o/K_d = 4 \times 10^{-4} \) atm\(^{-1}\).

C. Collander (11) determined the permeability of single cells of *Nitella mucronata* to DHO, and reported a permeability coefficient \( (K_o) \) of 6.33 \( \times 10^{-4} \) cm sec\(^{-1}\). He also (10) found half-times of 5 to 8 seconds for osmotic exchange of water when cells of this alga were transferred between water and 0.2 M solutions of sucrose or urea. \( \Pi_o \) for the cells is given as about seven atm (10), but it is not possible to deduce \( \epsilon \) from the data. Information on Nitella given by Tamiya (52) indicates \( \epsilon = 32 \) atm over the range of turgor changes involved in Collander’s experiments. We may calculate an osmotic permeability coefficient \( (K_o) \) from the relation, which is given by Philip (41),

\[
t_{\text{osm}} = \frac{0.693 V_o}{AK_o(\epsilon + \Pi_o)} = \frac{0.346 b}{K_o(\epsilon + \Pi_o)} X Va
\]

The formula on the right applies to a long narrow cylinder, such as the Nitella cell, for which \( V/A = b/2 \). The cell radius \( (b) \) is given (10) as 0.0205 cm; taking 6.5 seconds as a mean value for \( t_{\text{osm}}, K_o = 2.8 \times 10^{-8} \) cm sec\(^{-1}\) atm\(^{-1}\), and thus \( K_o/K_d = 4.4 \times 10^{-2} \) atm\(^{-1}\).

D. Thimann and Samuel (53) followed outward diffusion of tritium-labelled water (THO) from discs of potato tissue, finding half-times of approximately 1.5 minutes for discs 1 mm thick. Virgin (59) followed the progress of osmotic equilibration of strips of potato tissue 1 \( \times \) 1 mm in cross section, by an ingenious resonance method, and found half-times of about three minutes. Direct comparison requires that the difference in tissue geometry be taken into account. The figures given by Philip (43) suggest that \( t_{\text{half}} / t_{\text{osm}} \) should be divided by about three to bring the two into comparison. The value of \( (\epsilon + \Pi_o) \) for potato tissue can be estimated as 35 atm from data of Falk, Hertz, and Virgin (17). Hence, \( K_o/K_d = 5 \times 10^{-4} \) atm\(^{-1}\). The ratio should actually be somewhat greater, since the diffusion experiments

---

6 The equation for osmotic water exchange upon which formula XV is based was derived (41) only for water absorption by a cell, initially without turgor, when placed in pure water. It is readily verified, however, that under the assumptions made in deriving it, the half-time should be the same for osmotic exchange between any initial and final water deficits of the cell not greater than \( \Pi_o \).
(59) experiments (59) were conducted at 30° C while the osmotic experiments (59) were at room temperature.

E. Ordin and Kramer (37) found half-times of about 0.6 minutes for diffusion of DHO out of root segments of *Vicia faba*. To compare this with available data on osmotic permeability, it is necessary to compute an apparent diffusion coefficient *k*.

Information given by Philip (43) indicates that for a cylindrical piece of tissue of radius *b*, *k* = 0.062 mm$^2$/min. Since Ordin and Kramer give the diameter of the root sections as 0.5 mm, *k* = 6.5 × 10$^{-6}$ cm$^2$ min$^{-1}$.

Brewig (3) and Brouwer (6) measured steady osmotic water movement into *Vicia faba* root segments, in a method by which water deficit (S) difference could be determined. Their lowest values are about 0.5 mm$^3$ atm$^{-1}$ hr$^{-1}$ per cm of root length. If we assume, as was done in computing *k* above, that resistance to water flow is evenly distributed through the tissue, then the rate of water movement (v) is in through each cylindrical shell of tissue, at radius *b*, will be

$$ v = -2\pi b k_0 \frac{dS}{db} \quad \text{XVI} $$

where *l* is the length of the root segment. Since the same volume of water per minute moves in through each successive cylindrical shell until the vascular tissues are reached, *v* can be regarded as a constant and the equation integrated between the external surface of radius *b*$_0$ and the outer boundary of the stele, of radius *b*$_1$. This gives the formula

$$ k_0 = \frac{v}{2\pi l (S_1 - S_0)} - \ln \frac{b_0}{b_1} \quad \text{XVII} $$

The fraction *v/S*$_1 - S_0$ is the osmotic permeability, given above. From figures given by Brewig (3) the ratio of external to stele radii *b*$_0$/*b*$_1$ averages 3.6. From these figures we find *k*$_0$ = 1.7 × 10$^{-6}$ cm$^2$ atm$^{-1}$ min$^{-1}$, and the ratio *k*$_0$/*k*$_d$ = 2.6 × 10$^{-2}$ atm$^{-1}$.

The computed values of *K*$_0$/*K*$_d$ fall in the range 4 to 44 × 10$^{-2}$ atm$^{-1}$, as compared with 7.5 × 10$^{-4}$ expected on the basis of the diffusion hypothesis. Although in all cases but the first one, osmotic and diffusion permeabilities were not measured at the same time with the same object; and while in every case there are uncertainties about some of the values used, the comparisons are nevertheless in agreement in indicating that *K*$_0$/*K*$_d$ is several times larger than anticipated.

Among the possible reasons for this is the extent to which the actual situation deviates from one in which the approximations used in deriving equations XIV and XV hold good. The most serious deviation is likely to be from the assumption, made in deriving equation XV, that change in cell volume is exactly proportional to change in turgor pressure (41), since this can be far from correct (52). However, by averaging half-times for osmotic water loss and water gain this error should cancel out; this was done where possible.

It may be questioned whether permeability of membranes to DHO or THO is not less than to H$_2$O, which would make the measured *K*$_d$ too small. The diffusion coefficients of DHO and THO are not more than 14 percent less than that of H$_2$O$^{-1}$, which is believed to be approximately the same as H$_2$O$^{-1}$ (60). Collander (10) proved that Nitella cells are less permeable to DHO than to H$_2$O, because they exhibit a transient osmotic shrinkage when placed in strong DHO solutions. However, if one plots his data on osmotic transients caused by different compounds (10) against permeabilities for the same compounds, which he measured directly (11), it appears that the diffusion permeability of these cells to H$_2$O cannot be more than a few percent greater than to DHO. This objection has also been set aside in work with animal membranes to be discussed below.

It does not seem possible to explain with experimental errors the differences between expected and observed *K*$_0$/*K*$_d$; it seems significant that in studies on animal cells and tissues, discrepancies in *K*$_0$/*K*$_d$ of similar magnitude have been found (44). Such results were reported as early as 1935 by Hevesy, Hofer, and Krogh (22). They mean that osmosis takes place too rapidly to be explained by diffusion across the membrane. Ussing (28, 56) and Pappenheimer (40) have accounted for this by concluding that osmosis is not a diffusion process, as so often assumed in plant physiology, but takes place instead by bulk flow of water through pores in the membrane. It is assumed that if the membrane has pores through which water flow can be caused by a hydrostatic pressure difference across the membrane, then under a difference of osmotic potential the membrane will behave as if an equivalent pressure difference existed across it. With artificial membranes it has been proved conclusively that osmotic water movement does occur much more rapidly than by diffusion, and as rapidly as under an equivalent hydrostatic pressure difference (31, 32).

By assuming, as has been done for many years in treating flow through artificial membranes, that the pores are cylindrical and that water flow through them can be described by Poiseuille's law, average pore radii have been calculated, from *K*$_0$ and *K*$_d$ values, for several animal membranes, in careful work by Solomon and collaborators (16, 38, 49, 58). It is interesting to note that as long ago as 1930 Huber and Höfler (25), who considered osmotic water movement through plant membranes as a flow rather than a diffusion, attempted to calculate radii for pores in the Salvinia cell membrane by using a formula which had been worked out for artificial membranes.

**CAUSE OF FLOW THROUGH MEMBRANES.** It is not obvious that a concentration difference across a membrane should have the same effect as a pressure difference, and thus lead to flow rather than diffusion of water through pores in it. Chinard (7, 8) has objected to the concept of water flow, pointing out...
that in the presence of a concentration difference alone, no hydrostatic pressure difference capable of causing a flow exists across the membrane. Dick (14) and Harris (21) also reject the idea of bulk flow through cell membranes, stating that Poiseuille's law should not hold in channels of molecular dimensions. No physical explanation of why water flow should occur under a concentration difference seems to have become widely accepted. This section presents a proposal about the mechanism of osmotic water movement from which, it is felt, the occurrence of water flow through membranes having pores can be seen to be natural and inevitable.

We shall consider, as shown in figure 3a, a membrane of thickness \( l \), containing pores of radius \( b \), which allow the entry of water but not of osmotically active solutes present in the adjacent solutions. If, first, pure water is present on both sides of the membrane, and isotopically labelled water is introduced on one side, it will diffuse through the membrane along a concentration gradient \( (c_1 - c_2)/l \). If, however, an osmotic solution is placed on one side \( c_2 \) and pure water at the same pressure on the other side \( c_1 \), it is seen that the concentration gradient is, effectively, restricted to the aperture of the pore opening into \( c_2 \), since only water, not solute, can pass into the pore. The distance over which the concentration changes from \( c_2 \) to pure water will be about the same as the pore radius \( b \), since solute molecules which are, for example, larger than the pore aperture will not be able to penetrate any farther into the pore. Thus, for a given difference in water concentration induced osmotically, the concentration gradient will be steeper, and diffusion will tend to be more rapid, than for labelled water in proportion as \( l \) is larger than \( b \). If the pore presented little resistance to water flow, water would flow into and through the pore from \( c_1 \) as fast as it diffuses out along the concentration gradient into \( c_2 \) at the pore aperture, so causing osmotic water movement to take place by bulk flow and to be more rapid than can be accounted for by measuring diffusion of water across the membrane.

However, with thick artificial membranes, and probably with natural membranes as well, the relation between \( b \) and \( l \) is such that considerable viscous resistance to water flow is offered by the pore. Rather than preventing water flow, this proves to be the feature by which pressure effects and osmotic effects become closely comparable, as we shall now see. Diffusion of water from within the pore aperture into \( c_2 \), if not compensated for by flow from \( c_1 \), will result in a decrease in the volume of water within the part of the pore adjacent to the aperture, and hence a decrease in pressure there. Thus there arises a pressure gradient within the pore, between solution \( c_1 \) and the aperture of the pore next to solution \( c_2 \), along which water must flow (and diffuse) from \( c_1 \) to \( c_2 \). This situation is illustrated in figure 3b.

Diffusion out of the pore aperture into \( c_2 \) can be described by equation XI or, more simply, with its approximate form, equation XIV. If we call \( \Delta P \) the pressure drop within the pore aperture and remember that there is only water within the pore, then the rate of diffusion of water through the aperture will be

\[
v = \frac{Ak'_w \bar{V}}{RTb} (\Pi_2 - \Delta P)
\]

where \( A \) represents the cross-sectional area of the pore, and \( k'_w \) the diffusion coefficient of water in the pore. Considering now water movement within the pore as the sum of diffusion and bulk flow under the pressure gradient \( \Delta P/l \), then if flow is described by Poiseuille's law

\[
v = \frac{Ak'_w \bar{V} \cdot \Delta P}{RTl} + \frac{\Delta b^2 \cdot \Delta P}{8\eta l}
\]

During steady osmosis, \( \Delta P \) must attain such a value that the rate of water movement through the pore is equal to the rate of movement out of the pore aperture.
into $c_2$. Hence we may set equations XIX and XIX equal to one another and solve for $\Delta P$.

$$\Delta P = \frac{\Pi_2}{b \frac{RT \delta^2}{1 + \frac{\delta^2}{l} \frac{8\eta k'_w V}} \text{XX}}$$

This indicates that the pressure drop within the pore will approach the numerical value of the osmotic potential difference between the external solution and that inside the pore, provided $l$ is sufficiently larger than $b$. This is equivalent to saying that under these conditions, diffusion equilibrium will practically prevail between the water in solution $c_2$ and the contents of the pore just inside the aperture, and that osmotic water movement is controlled by the rate of water flow within the pore. The range of pore dimensions within which this will be the case can be seen by computing the value of the denominator in equation XX for arbitrary values of $b$ and $l$, which has been done in table I. Whenever this value is not significantly greater than one, the pressure drop within the pore will approach the osmotic potential of the external solution $c_2$.

If diffusion equilibrium practically prevails at the pore aperture next to $c_2$, it should do so also at the aperture next to $c_1$, so if $c_1$ is now an osmotic solution, the pressure drop induced within the length of the pore should be equal to the difference in pressure drops $\Delta P$ which arise at its two apertures, or equal to $\Pi_2 - \Pi_1$. It thus becomes apparent why an osmotic potential difference should cause the membrane to behave as if a comparable hydrostatic pressure difference existed across it. The rate of water movement through the pore will be equal to the water flow and diffusion induced along its length by the total pressure difference between its ends, this being the pressure difference induced osmotically plus any hydrostatic pressure difference between the two solutions, so from equation XIX,

$$\nu_{12} = \frac{A}{l} \left[ \frac{k'_w V}{RT} + \frac{b^2}{8\eta} \right] \left[ (\Pi_2 - \Pi_1) - (P_2 - P_1) \right] \text{XXI}$$

This has the same form as equation XIV, but a larger value because of the appearance of the bulk flow term $b^2/8\eta$. As shown by Pappenheimer (40), this term becomes less and less important as the pore radius is reduced, until at very small radii osmotic water movement would have the appearance of pure diffusion; it is to be noted, however, that within the membrane this diffusion is considered to be occurring along a pressure gradient rather than a concentration gradient. On the other hand, at radii where the bulk flow term is large compared with the diffusion term, flow is the principal mechanism of osmotic water movement, and osmosis occurs more rapidly than diffusion of water across the membrane, as in the examples examined in the preceding section.

For membranes in which the pressure drop $\Delta P$ induced osmotically is less than the osmotic potential difference $\Pi_2 - \Pi_1$ (the denominator in equation XX being greater than one), it appears that the rate of osmotic water movement must be less than the water flow under a numerically equal hydrostatic pressure difference, so that equation V would not hold true. The limiting case, where $\Delta P$ approaches zero, was the case discussed initially in this section. Actually, the pore dimensions in which this situation could arise (table I) are mostly such as to make the membrane rather or very permeable to dissolved substances, a situation which would also decrease osmotic flow in comparison with pressure flow, as will now be discussed.

**Diffusible Solute.** The restricted diffusion permeability of a porous membrane to a solute is, compared to water, may be considered as the result of two effects:

I. Within the pores of the membrane, the diffusion coefficient of the solute ($k'_w$) is restricted, due to frictional hindrance to molecular movement, to a greater extent than is that of water ($k'_w$).

II. At the pore aperture entry of solute molecules is restricted, by comparison with water molecules, because molecules which impinge upon the pore aperture can enter the pore only if they are not deflected by striking its edge: for the larger solute molecules, a smaller fraction of the total pore area can be hit without involving collision with an edge, than for water molecules. This geometrical effect is discussed by Pappenheimer (40). That fraction of the pore area available to water, which is not available to solute in consequence of this effect, will be called the reflection factor $\phi$ for the solute. Its maximum value is one, in the case of a membrane completely impermeable to the solute, as in the preceding section.

Diffusional entry of molecules into the pore will be in proportion to the number of collisions with the.

---

*The solutes referred to are, throughout, lipid-insoluble ones incapable of penetrating the membrane at an appreciable rate by solution in a lipid phase.*

**Table I**

<table>
<thead>
<tr>
<th>Pore Radius, Å</th>
<th>Pore Length, Å</th>
<th>10</th>
<th>100</th>
<th>1,000</th>
<th>10,000</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>1.5</td>
<td>1.05</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>10</td>
<td>9.2</td>
<td>1.8</td>
<td>1.08</td>
<td>1.01</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>199</td>
<td>21</td>
<td>3.0</td>
<td></td>
<td>1.2</td>
</tr>
<tr>
<td>100</td>
<td>7,200</td>
<td>721</td>
<td>73</td>
<td>8.2</td>
<td></td>
</tr>
</tbody>
</table>

*Calculated from equation XX using the viscosity and diffusion coefficient (60) of water at 25°C.*
pore aperture which do not result in reflection at the edges. Effective collisions of solute and of water molecules will be in proportion to their mole fractions $X_s$ and $X'_w$, and to the relative pore areas available to them ($[1 - \phi]$ to one). Hence during steady diffusion of solute from a solution to pure water across the membrane, the mole fractions of solute and water just inside the pore aperture ($X'_s$, $X'_w$) will be related to those outside by the expression

$$\frac{X'_s}{X'_w} = (1 - \phi) \frac{X_s}{X_w} \quad \text{XXII}$$

$$\nu_{s-w} = \frac{A}{l} \left\{ \phi \left( \frac{b^2}{8\eta} + \frac{k'w\overline{V}}{RT} \right) + (1 - \phi) \frac{(k'_w - k'_s)\overline{V}}{RT} \right\} \Pi_2 - \left\{ \frac{b^2}{8\eta} + \frac{k'w\overline{V}}{RT} \right\} (P_2 - P_1) \quad \text{XXIV}$$

The resulting solute mole fraction profile is diagrammed in figure 3c.

For ordinary solutions we may, as before, with sufficient accuracy take $X_w$ and $X'_w$ equal to one. Thus the difference in solute mole fraction outside and inside the aperture ($X_s - X'_s$) will be $\phi X_s$. Water will diffuse towards solution $c_2$ along the resulting concentration gradient at the pore aperture, and, for the reasons given in the previous section, if the pore presents sufficient resistance to flow of solution, the pressure inside the aperture will fall until it differs from the pressure at $c_2$ by the difference in osmotic potential; this difference is seen to be $\phi \Pi_2$. Figure 3c shows the resultant pressure profile within the pore. Along the pressure gradient inside the pore a bulk flow of solution towards $c_2$ will take place. As before, we shall assume this flow to be described by Poiseuille's law.

The net volume movement from solution $c_1$ (pure water) to solution $c_2$ will be the sum of the forward flow of solution along the pressure gradient within the pore and the diffusion of water along the gradient of pressure and concentration within the pore, less the back diffusion of solute along its concentration gradient inside the pore:

$$\nu_{s-w} = \frac{A}{l} \left\{ \phi \left( \frac{b^2}{8\eta} + \frac{k'w\overline{V}}{RT} \right) + (1 - \phi) \frac{(k'_w - k'_s)\overline{V}}{RT} \right\} \Pi_2 - \left\{ \frac{b^2}{8\eta} + \frac{k'w\overline{V}}{RT} \right\} (P_2 - P_1) \quad \text{XXV}$$

$$\nu_{s-w} = \frac{A}{l} \left\{ \phi \left( \frac{b^2}{8\eta} + \frac{k'w\overline{V}}{RT} \right) \right\} \left( \frac{\chi \Pi_2 - [P_2 - P_1]}{\nu_{s-w}} \right) \quad \text{XXVI}$$

To obtain volume equilibrium between solutions 2 and 1 it would be necessary to impose such a pressure difference ($P_2 - P_1$) that $\nu = 0$. This required pressure is called the "effective osmotic pressure" of solution $c_2$, and from equation XXIV it is seen to be as independent of flow of solution. This approximation is satisfactory as long as the solute concentration difference is sufficiently small in relation to the hydraulic conductivity of the membrane, as can be seen from the equations given by Jacobs (27). It appears that this condition holds sufficiently well for biological situations and membranes with small pores, such as cell membranes, which are of interest here. Otherwise, the relationship between osmotic flow and solute concentration becomes more complex. The value of $\eta$ to be used in equation XXIII and those following, is that for the average composition of the solution flowing within the pore.

Substitution, for $\Delta P$ and $X'_s$, of the values given above, leads to

$$(P_2-P_1) = \left[ \phi + (1 - \phi) \frac{(k'_w-k'_s)\overline{V}/RT}{b^2/k'_w\overline{V}} \right] \Pi_2 - \left[ \frac{b^2}{8\eta} + \frac{k'w\overline{V}}{RT} \right] (P_2 - P_1) \quad \text{XXV}$$

$$(P_2-P_1) = \left[ \phi + (1 - \phi) \frac{(k'_w-k'_s)\overline{V}/RT}{b^2/k'_w\overline{V}} \right] \Pi_2 - \left[ \frac{b^2}{8\eta} + \frac{k'w\overline{V}}{RT} \right] (P_2 - P_1) \quad \text{XXV}$$

The coefficient $\chi$ will be called the "osmotic effectiveness" of the solute being considered. It varies from zero, for a solute lacking any osmotic effect, to one, for a solute to which the membrane is completely impermeable. Substitution into equation XXIV gives

$$(P_2-P_1) = \left[ \phi + (1 - \phi) \frac{(k'_w-k'_s)\overline{V}/RT}{b^2/k'_w\overline{V}} \right] \Pi_2 - \left[ \frac{b^2}{8\eta} + \frac{k'w\overline{V}}{RT} \right] (P_2 - P_1) \quad \text{XXVI}$$

It can be seen that the osmotic flow induced by a diffusible solute should be governed by the effective osmotic pressure of the solution $\chi \Pi_2$ rather than by its osmotic potential $\Pi_2$. This fact was deduced on thermodynamic grounds by Staverman (50, 51). Meschia and Setnikar (32) recently showed that osmosis across a collodion membrane, with a series of solutes to which the membrane differed in permeability, obeys an equation of this type. The general expression for osmotic movement, developed as above
but considering the effect of different solutes, and of solutes on both sides of the membrane, is

\[ n_{w-s} = \frac{A}{l} \left[ \frac{b^2}{8\eta} + \frac{k_s V}{RT} \right] \left[ \sum \chi_i (\Pi_{w-s} - \Pi_{w-r}) - (P_w - P_s) \right] \] XXVII

It is clear that in the presence of solutes to which the membrane is permeable, osmosis should not follow equation V. This has important consequences. It is not correct to treat osmotic flow induced by diffusible solutes as proportional to water deficit difference, as has been done [e.g., (41)]; the osmotic effectiveness \( \chi \) of the solutes must be included. Moreover, equation V fails in that most important aspect of water movement in plants, transport through the xylem, for the cell walls of xylem elements are considerably permeable to solutes. Evidence showing that equation V cannot be applied to the xylem was obtained, for example, by Jaccard and Frey (26), who measured osmotic permeability (with sucrose) and hydraulic conductivity of several wood membranes. Their data show that the latter conductivity exceeded the former by a large factor in all cases; this was associated with substantial permeability to sucrose. Therefore, it is feasible to include water movement in the xylem in equation VI only if differences in solute concentration within it are quite small.

According to the present considerations, the relationship between \( \chi \) and the diffusion permeability of the membrane to water and solute will not in general be a simple one. Since diffusion permeabilities to water (\( K_w \)) and solute (\( K_s \)) are proportional to \( k_w \) and \( k_s'(1-\phi) \), respectively, it can be shown from equation XXV that for a diffusion membrane (bulk flow term small in comparison with diffusion term), \( \chi \) reduces to \( 1 - K_s/K_w \). For a membrane through which movement by bulk flow predominates under a pressure difference (bulk flow term large compared with diffusion term), \( \chi \) is essentially equal to \( \phi \) except at small values of \( \phi \), or to \( 1 - K_w k_w'/K_s k_s' \), so that osmotic effectiveness should be less than \( 1 - K_s/K_w \).

According to the theory of Renkin (46), with small or moderate restriction of permeability, the contributions of restriction at the pore aperture and to diffusion within the pore should be of comparable magnitude. From equation XXV this would lead to the relationship

\[ \chi = 1 - \left( \frac{K_w k_w'}{K_s k_s'} \right)^{\frac{1}{6}} \left( 1 + \frac{V(K_w - K_s)}{RTH} \right) \] XXVIII

where \( k_s \) is the free diffusion coefficient of the solute, and \( H \) is the hydraulic conductivity of the membrane. At moderately restricted permeability to solute, the second term in brackets may be neglected for flow membranes. If restriction to diffusion of water within the pores is only slight, the first term in brackets could be evaluated using measured permeabilities and known free diffusion coefficients of water and solute. At very slight restrictions to diffusion of solute, this term becomes practically equal to one; then the principal contribution to \( \chi \) is made by the last term of equation XXVIII, or the \((1-\phi)\) term of equation XXV, which specifies the pressure required to cause a bulk flow just sufficient to offset the difference in diffusion rates of water and solute through the membrane. This represents the situation in which virtually no bulk flow is caused by the solute concentration difference, and a weak, purely diffusional osmotic movement can occur. This seems to have been the case in experiments with diffusible solutes by Meschia and Setnikar (32), for \( K_w k_w'/K_s k_s' \) was very nearly equal to one with glucose, sucrose, and raffinose [cf. diffusion coefficients given in (46)], and the observed \( \chi \) can be calculated fairly closely using the last term in equation XXVIII. These authors (32) employed the hydraulic conductivity of the membrane to calculate \( \chi \) from rate of osmotic movement observed under a diffusible solute concentration difference, which gave an appearance of occurrence of bulk flow which we suggest was a purely formal one, and in reality pertained to the bulk flow which occurred when a pressure difference was imposed to maintain volume equilibrium. In any event, the experiments show clearly that \( \chi \) was much smaller than \( 1 - K_s/K_w \), which is predicted for flow membranes by the present hypothesis of the mechanism of osmosis, but might not have been expected intuitively [cf. (40)].

Meschia and Setnikar’s (32) permeability data are given on the conventional concentration basis, rather than on the mole-fraction basis adopted here to simplify the treatment of pressure effects. Osmotic movement can be derived, using diffusion coefficients on a concentration basis, in a fashion similar to that employed above, yielding an expression for \( \chi \) slightly more complex than equation XXV. It seems likely that the real relationship should lie somewhere in between mole-fraction and concentration basis. In evaluating Meschia and Setnikar’s data the concentration basis was adhered to.

The above interpretation of osmotic water movement is not basically dependent upon any of the simplifying assumptions made about the shape or path of the pores, or the applicability of particular diffusion coefficients or of Poiseuille’s law to movement within pores. As has frequently been remarked, it is unlikely that Poiseuille’s law in unmodified form can accurately describe bulk flow through channels of molecular dimensions; which is not to say that bulk flow cannot occur, as has sometimes been implied, but that the term \( b^2/8\eta \) in the equations should be replaced by some other term dependent on \( b \) and \( \eta \). Such departures from the simple assumptions used here are equivalent to having channels in the membrane related to \( b \) and \( l \) in the equations and in table I by some numerical factor. Furthermore, consider-
ing the nature of processes at molecular dimensions, the pressure and concentration gradients expected within the pores should constitute a time- or number-
average of the situation, rather than the invariable
state of every pore. Finally, the basic osmotic equa-
tion XXVII cannot be expected to hold except for
dilute solutions and low pressures, as it contains the
approximations which are the basis for equation XIV,
and depends additionally upon pore geometry.

One point which has been omitted entirely is the
possibility of a backflow from solution $c_2$ into the pore
aperture along the pressure gradient expected to de-
velop in the aperture of the pore. A flow from solu-
tion into pore aperture would be an ultrafiltration
rather than a simple flow, since for a membrane not
permeable to solute, only water would pass. Such a
flow would involve viscous resistance between solute
molecules and water as well as between water and
the pore, and hence must be slow by comparison with
water flow within the pore. In any case, the supposed
flow would not be possible thermodynamically unless
the pressure drop in the pore aperture exceeded the
expected $\Delta P$ (18).

Regardless of these questions, the important point
appears to be that osmotic flow of water through
membranes can be viewed as the consequence of
pressure gradients set up within the pores by rapid
diffusion at the pore apertures, across the sharp con-
centration gradients prevailing there. Even the idea
of discrete pores, useful in quantitative treatment, is
not essential to the occurrence of osmotic flow, the
only requirements being that water permeate the
membrane as a continuous phase while entry of solutes
be restricted at the membrane surfaces. An intuitive
treatment of osmotic water movement based on this
picture of membrane structure was presented long
ago as 1935 by Jacobs (27). The writer’s attention
has lately been called to the discussion of osmosis given
by Ussing and Andersen (57), who depict a porous
membrane as similar to figure 3a, and regard the
cause of bulk flow to be lack of penetration of solute
into the pore, as was arrived at independently in the
present study.

**Summary**

The mechanism of osmotic water movement and
the factors which determine its rate are reexamined
from a quantitative point of view. Diffusion pressure
and diffusion pressure deficit are held to be self-
contradictory concepts, and hence not tenable. Suc-
tion force, which is an acceptable concept relating to
states of osmotic equilibrium, is renamed “water defi-
cit” to avoid undesirable implications of the former
term which have previously been criticized. Rate of
water movement cannot be proportional to differences
in water deficit as a general law, contrary to the usual
assumption. The idea that transpiration rate is pro-
ditional to the suction force of atmospheric water
vapor is completely erroneous. However, on the as-
sumption that osmosis is due to diffusion across mem-
bres, proportionality between its rate and differ-
ences in water deficit is an approximation good for
low pressures and dilute solutions. The osmotic
permeability of a membrane is then expected to be
related to the diffusion permeability to water, as meas-
ured with labelled water, by the factor $V/RT$. Available
measurements on plant cells and tissues indicate
that osmotic permeability exceeds that expected on
the basis of diffusion by a factor of at least several
fold, which cannot be explained by experimental
errors. It thus appears, as previously observed with
animal membranes, that osmosis is not strictly a dif-
fusion process. The idea is examined that osmosis
occurs by bulk flow of water through pores in the
membrane. Occurrence of flow through pores ap-
pears to be an inevitable result of pressure gradients
induced within the pores by diffusion at pore aper-
tures. This explains why an osmotic potential differ-
ce across a membrane causes as fast a water flow
as a numerically equal hydrostatic pressure differ-
ence. The hypothesis can also be applied to osmosis
induced by diffusible solutes, which is not proportional
to differences in water deficit.

**Acknowledgments**

I wish to thank Dr. Karl F. Guthe and Dr. Kenneth
V. Thimann for valuable discussion and criticism.

**List of Symbols**

- $A$ Area (cm²) of membrane, or of pore cross
  section
- $b$ Radius (cm)
- $c$ Concentration (moles liter⁻¹)
- $d_1$ Rate of outward diffusional movement of water
  molecules, from solution 1, through a membrane (cm³
  sec⁻¹)
- $H$ Hydraulic conductivity of membrane (cm
  sec⁻¹ atm⁻²)
- $K_d$ Diffusion permeability of membrane to water,
  equal to $k_d/l$ (cm sec⁻¹)
- $K_o$ Osmotic permeability of membrane, equal to
  $k_o/l$ (cm sec⁻¹ atm⁻¹)
- $K_s$ Permeability of membrane to a solute (cm
  sec⁻¹)
- $k_d$ Diffusion coefficient of water across mem-
  brane, mole fraction basis (cm² sec⁻¹)
- $k_o$ Osmotic permeability coefficient (cm² sec⁻¹
  atm⁻¹)
- $k_s$ Restricted diffusion coefficient of solute with-
  in pore (mole fraction basis, cm² sec⁻¹) ($k_s$ is the
  free diffusion coefficient)
- $k_w$ Restricted diffusion coefficient of water with-
  in pore (mole fraction basis, cm² sec⁻¹) ($k_w$ is the
  free diffusion coefficient)
- $l$ Membrane thickness (cm); length (cm) in
equations XVI and XVII
- $P$ Hydrostatic pressure, in atm greater (+) or
  less than (−) atmospheric.
- $\Delta P$ Pressure difference between external solution
  and contents of pore just inside aperture (atm)
- $p$ Partial vapor pressure of water (atm)
R Gas constant (82.0 cm³ atm deg⁻¹ mole⁻¹)
\( r_{21} \) Resistance to flow between points 1 and 2 (atm sec cm⁻³)
S Water deficit (suction force), defined by equation I (atm)
\( S' \) Suction force of atmospheric water vapor (atm), defined in the section on transpiration.
T Absolute temperature (deg K)
\( t_{50} \) Time for process to proceed halfway from initial state toward completion. Subscripts 0 and d refer to half-times for osmotic equilibration and diffusion exchange of labelled water (external concentration constant), respectively.
V Partial molal volume of water (cm³ mole⁻¹)
V₀ Cell volume (cm³)
\( \nu_{1-2} \) Rate of volume movement from unit 1 to unit 2 (cm³ sec⁻¹)
X Mole fraction of water in a solution, in osmolar units.
Xₛ Mole fraction of solute, in osmolar units.
Xᵢ Mole fraction of solute inside pore aperture.
\( \epsilon \) Elastic modulus of the cell wall (atm), defined as in (41)
\( \eta \) Viscosity (atm sec). The usual unit of viscosity is the poise (dyne cm⁻² sec), with which pressure must be expressed in dynes cm⁻². Since it is customary and convenient in plant physiology to express pressure in atmospheres, viscosity as used here is in atm sec, which is equal to viscosity in poises multiplied by 9.87 \times 10⁻⁶.
\( \Pi \) Osmotic potential (atm)
\( \Pi_0 \) Osmotic potential at zero turgor (atm)
\( \Pi_{s1} \) Contribution of a particular solute to the osmotic potential of solution 1 (subscript s, 1 is the same for solution 2) (atm)
\( \phi \) Reflection factor for a solute, defined in the section on diffusible solutes.
\( \chi \) Osmotic effectiveness of a solute, defined so that \( \chi \Pi \) is the pressure required to effect volume equilibrium between the solution and water through a particular membrane.

**Literature Cited**

30. Martin, E. 1943. Studies of evaporation and tran-
spiriation under controlled conditions. Carnegie
31. MAURO, A. 1957. Nature of solvent transfer in
32. MESCHIA, G., and I. SETNIKAR. 1958. Experimental
study of osmosis through a colloidion mem-
33. MEYER, B. S. 1938. The water relations of plant
34. MEYER, B. S. 1945. A critical evaluation of the
terminology of diffusion phenomena. Plant Phys-
iol. 20: 142–164.
Auxin-induced water uptake by Avena coleoptile
36. ORDIN, L., and J. BONNER. 1956. Permeability of
Avena coleoptile sections to water measured by
31: 53–57.
37. ORDIN, L., and P. J. KRAMER. 1956. Permeability of
*Vicia faba* root segments to water as measured by
38. PAGANELLI, C. V., and A. K. SOLOMON. 1957. The
rate of exchange of tritiated water across the human
277.
39. PALVA, P. 1939. Die Wasserpermeabilität der
Zellen von *Tolypellopsis stelligera*. Protoplasma
40. PAPPENHEIMER, J. R. 1953. Passage of molecules
through capillary walls. Physiol. Revs. 33: 387–
423.
41. PHILIP, J. R. 1958. The osmotic cell, solute dif-
fusibility, and the plant water economy. Plant
Physiol. 33: 264–271.
42. PHILIP, J. R. 1958. Propagation of turgor and
other properties through cell aggregations. Plant
Physiol. 33: 271–274.
43. PHILIP, J. R. 1958. Osmosis and diffusion in tis-
ue: half-times and internal gradients. Plant
Physiol. 33: 275–278.
44. PRESCOTT, D. M., and E. ZEUTHEN. 1953. Com-
parison of water diffusion and water filtration across
45. PRESTON, R. D. 1954. The transpiration of plants.
46. RENKIN, E. M. 1954. Filtration, diffusion, and
molecular sieving through porous cellulose mem-
47. RENNER, O. 1929. Versuche zur Bestimmung des
Filtrationswiderstandes der Wurzeln. Jahrb. wiss.
Botan. 70: 805–838.
48. SEYBOLD, A. 1933. Zur Klärung des Begriffes
49. SIDEL, V. W., and A. K. SOLOMON. 1957. Entrance
of water into human red cells under an osmotic
257.
50. STAEYERMAN, A. J. 1951. The theory of measure-
ment of osmotic pressure. Rec. trav. chim. 70:
344–352.
51. STAEYERMAN, A. J. 1952. Apparent osmotic pressure
52. TAMARA, H. 1938. Zur Theorie der Turgordeh-
nung und über den funktionellen Zusammenhang
zwischen den einzelnen osmotischen Zustandsgrö-
53. THIMANN, K. V., and E. W. SAMUEL. 1955. The
permeability of potato tissue to water. Proc. Nat.
der Saugkraftmessung. Ber. deut. botan. Ges. 34:
525–539.
der Saugkraft. V. Ber. deut. botan. Ges. 39:
139–148.
56. USSLING, H. H. 1952. Some aspects of the applica-
tion of tracers in permeability studies. Advances
57. USSLING, H. H., and B. ANDERSEN. 1956. The
relation between solvent drag and active transport
58. VILLEGAS, R., T. C. BARTON, and A. K. SOLOMON.
1958. The entrance of water into beef and dog
59. VIRGIN, H. I. 1955. A new method for the deter-
mination of the turgor of plant tissues. Physiol.
Plantarum 8: 954–962.
60. WANG, J. H., C. V. ROBINSON, and I. S. EDELMAN.
Ill. Measurement of the self-diffusion of liquid
water with *H*2, *H*3, and *O*18 as tracers. Jour.
Amer. Chem. Soc. 75: 466–470.
61. WARTIOVAARA, V. 1944. The permeability of Tolyp-
ellopsis cells for heavy water and methyl alcohol.