

THE OSMOTIC CELL, SOLUTE DIFFUSIBILITY, AND THE PLANT WATER ECONOMY ¹

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The question which prompts the present work is: "How can the concept of the plant cell as an osmometer with semi-permeable walls be justified, when solutes may enter the plant cell vacuole?" Textbooks of plant physiology and physical chemistry treat osmosis in detail only for equilibrium conditions and non-diffusible solutes. To extend the quantitative treatment to the case of a diffusible solute we must abandon the equilibrium approach and study the problem dynamically. We introduce the dynamic approach by applying it to the classical cell osmometer; then we proceed to the case of a diffusible solute.

DYNAMICS OF THE CLASSICAL CELL OSMOMETER: We use the following symbols:

V , cell volume (cm^3). V_0 , cell volume at zero turgor pressure.

$v = V/V_0 - 1$, relative departure of cell volume from V_0 .

A , external surface area of cell (cm^2). A_0 , value of A at zero turgor pressure.

P , osmotic pressure of cell contents (in the sense of Meyer (14), i.e., as a concentration-dependent property of the solution, independent of the hydrostatic system) (atm).

T , turgor pressure (atm). [Broyer and others (4, 21, 22, 27) have shown the general equivalence of T and "wall pressure," and that it is a mistaken over-emphasis of an infinitesimal second-order effect to dwell on the distinction between them (6)].

K_w , permeability of cell wall to water ($\text{cm sec}^{-1} \text{atm}^{-1}$). t , time (sec).

We suppose that, initially, $T = 0$, and $P = P_0$, and that the solutes in the system are non-diffusible. If the cell is now placed in free water, water will enter the cell until the (increasing) turgor pressure becomes equal to the (decreasing) osmotic pressure. The dynamics of this process is described exactly by the equation.

$$dV/dt = K_w A [P - T] \quad (1)$$

subject to the initial condition

$$t = 0, V = V_0 \quad (2)$$

Quite generally, K_w , A , P and T are functions of V . If these functions are known, equation 1 may be integrated. If experimental values of these functions are used, numerical integration will generally be necessary.

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This presents no great difficulty, but it is simpler to use certain approximations which enable the problem to be solved analytically.

A increases with V (in fact $A \approx A_0(1 + 2v/3)$ for isotropic swelling and shrinking) and K_w may vary with V (e.g., (2)). This is unlikely to change the order of magnitude of $K_w A$, which affects the time scale of osmometer dynamics, though not its general character. We therefore simplify the analysis by taking $K_w A$ as constant and equal to $K_w A_0$.

If we take P proportional to solute concentration (as it is to a first approximation)

$$P = P_0 V_0 / V = P_0 / (1 + v) \quad (3)$$

If we assume that change of cell volume is proportional to change in turgor pressure, we have for the $T(V)$ function

$$T = (V/V_0 - 1) \cdot \text{i.e. } T = \epsilon v \quad (4)$$

The elastic modulus, ϵ , corresponds to the "coefficient of enlargement" of Broyer (5). As Broyer states, ϵ is not strictly constant for perfectly elastic cell walls, except for infinitesimal volume changes. Since the assumption that the wall obeys Hooke's law is, in any case, an approximation (9), it seems permissible to adopt ϵ as constant in the present analysis.

We recognize that, in real plants, marked deviations from the linear $T(v)$ relation to be used here may occur. In this sense the present work may be considered a first approximation. Essentially similar results would follow from a more precise, though more elaborate analysis along the same lines in which non-linearity in $T(v)$ was taken into account.

The existence of a unique $T(v)$ function implies, however, that the cell volume changes are elastic. Obviously, the plastic, irreversible, deformations associated with cell elongation are beyond the scope of the present treatment, though it may prove possible to include these in a similar, but more complicated, analysis. Insofar as our special concern here will be with cells at low levels of turgor, this is not a serious limitation.

Using equations 3 and 4 in equation 1 then gives

$$\frac{dv}{dt} = \frac{K_w A_0}{V_0} \left[\frac{P_0}{(1 + v)} - \epsilon v \right] \quad (5)$$

This is integrable, but the further developments will be simplified if we use the fact that v is generally rather smaller than unity and introduce the approximation

$$P_0 / (1 + v) = P_0 (1 - v) \quad (6)$$

Equation 5 may then be rewritten

$$\frac{dv}{dt} = \frac{K_w A_o}{V_o} [P_o - (\epsilon + P_o)v] \quad (7)$$

The particular integral of equation 7 which vanishes for $t = 0$ (in accord with equation 2) is

$$v = \frac{P_o}{(\epsilon + P_o)} \left[1 - \exp \left(- \frac{(\epsilon + P_o)K_w A_o}{V_o} t \right) \right] \quad (8)$$

Figure 1 shows the approach of the ideal osmometer to the new equilibrium, $v = P_o/(\epsilon + P_o)$, according to equation 8. The predicted behavior is quite similar to the observed behavior of plant tissues (e.g., (7, 16, 23)), though certain inherent differences are to be expected between the behavior of an individual cell and of a tissue which is an aggregation of cells.

The half-time of the approach to the new equilibrium is $\frac{0.693V_o}{A_o K_w (\epsilon + P_o)}$. That is, for a given cell

dimensions and permeability, the speed of adjustment is directly proportional to $(\epsilon + P_o)$. Thus both the elastic properties of the cell wall and the quantity of solute in the cell exert important influences on cell dynamics.

It will be noted that the relationships used here fail for the plasmolyzed cell, and that the analysis is restricted to cells in the normal unplasmolyzed condition.

The preceding treatment may be applied to more general problems in the dynamics of the classical cell osmometer. No new principles are involved in such generalizations.

“OSMOSIS” IN THE PRESENCE OF A DIFFUSIBLE SOLUTE: The propriety of the term “osmosis” is open to question if the solute is diffusible. Strictly, the process is one of dialysis. Just as in the ideal osmometer, a diffusion pressure (14, 1) difference is set up across the membrane. In the ideal case, net movement of solvent across the membrane may be prevented by applying a constant hydrostatic pressure difference. In the present case, however, “osmotic” equilibrium would require that the applied pressure difference vary in accord with changes in concentration produced by diffusion of the solute.

The question arises as to whether the “osmotic pressure” depends only on the concentrations of solute or whether it is influenced by the permeability of the membrane to the solute. An argument similar to that given by Ostwald (quoted in (10)) to demonstrate the equality of the osmotic pressures developed by all ideal membranes shows that the transient osmotic pressures we examine here also depend only on the solute concentrations. The viewpoint of Hildebrand (12) that osmosis “is primarily a consequence of the tendency of two different liquid species, under the impulse of thermal agitation, to achieve a state of maximum disorder by any available path, and that the route via osmosis is no more significant theoretically

than one via the vapor state” leads to the same conclusion.

CELL DYNAMICS IN THE PRESENCE OF A DIFFUSIBLE SOLUTE: After the cell we have considered above attains its final equilibrium, let it be removed and immersed in a large body of a solution of diffusible solute. In considering subsequent cell behavior, we use the following additional symbols:

P_n , osmotic pressure of the cell contents due to non-diffusible solutes (atm).

P_d , osmotic pressure of the cell contents due to diffusible solute (atm).

P_1 , osmotic pressure of the external solution (of diffusible solute) (atm).

K_s , apparent permeability of cell wall to diffusible solute, essentially defined by equation 10 (cm sec⁻¹).

c_1 , concentration of diffusible solute in the external solution (g cm⁻³).

c , concentration of diffusible solute in the cell contents (g cm⁻³).

q , quantity of diffusible solute in the cell (= cV) (g).

Our model of solute movement consists of purely passive diffusion. It is for this reason that we call K_s apparent permeability. The simple proportionality between rate of solute movement and concentration difference implicit in the model is certainly not always realized in plant cells. Nevertheless the model enables some exploration of the effects of solute diffusibility on osmotic behavior of the cell.

The system of equations describing the movement of water and diffusible solute is then

$$dV/dt = K_w A (P_n + P_d - P_1 - T) \quad (9)$$

$$dq/dt = K_s A (c_1 - c) \quad (10)$$

Equations 4 and 6 enable us to rewrite equation 9 as

$$\frac{dv}{dt} = \frac{K_w A_o}{V_o} [P_o + P_d - P_1 - (\epsilon + P_o)v] \quad (11)$$

We must establish P_d as a function of time before we can integrate equation 11. All volume changes are relatively small, so we may introduce the approximation that, even though K_s , A and V all vary, the quantity $K_s A/V$ is constant and equal to $K_s A_o/V_o$. This enables equation 10 to be reduced to

$$\frac{dc}{dt} = \frac{K_s A_o}{V_o} (c_1 - c) \quad (12)$$

Then, for P_1 , P_d proportional to c_1 , c (as they will be to a first approximation) equation 12 becomes

$$\frac{dP_d}{dt} = \frac{K_s A_o}{V_o} (P_1 - P_d) \quad (13)$$

Now $P_d = 0$ at $t = 0$, so P_d is given by the particular integral of equation 13,

$$P_d = P_1 \left[1 - \exp \left(- \frac{K_s A_o}{V_o} t \right) \right] \quad (14)$$

Using equation 14 in equation 11, we obtain

$$\frac{dv}{dt} = \frac{K_w A}{V_o} \left[P_o - P_1 \exp\left(-\frac{K_s A_o}{V_o} t\right) - (\epsilon + P_o)v \right], \quad (15)$$

which is subject to the initial condition

$$t = 0, v = P_o/(\epsilon + P_o) \quad (16)$$

Numerical solutions of equation 15 subject to condition 16 are shown in figure 2. The most important quantity governing the time-dependence of the cell-behavior is $K_s A_o/V_o$. For this reason the curves are plotted against the dimensionless quantity $K_s A_o t/V_o$. The other significant parameter of the system, $(\epsilon + P_o)K_w/K_s$, influences the relative rate of approach to the initial quasi-equilibrium.

An idea of orders of magnitude can be gained by inserting numerical values. $A_o/V_o = 10^3$ for a spherical cell of radius 3×10^{-3} cm. K_s is difficult to evaluate, but may be about 5×10^{-8} for plant cell membranes and the salts of interest here (19, 8). The experimental data on K_w indicates 5×10^{-7} as typical for plant cells (11). Broyer (3) has deduced $\epsilon \approx 60$ for potato tuber tissue while Ordin and Bonner's data for *Avena coleoptiles* (16) yield $(\epsilon + P_o) \approx 100$. We may therefore take $(\epsilon + P_o)$ of order of magnitude 50 to 100. On the basis of these values, the unit of dimensionless time scale of figure 2 would be about 6 hours, while $(\epsilon + P_o) K_w/K_s$ would be of order 500 to 1000. The curves of figure 2 cover the range 50 to 5000.

It is seen that the behavior of the cell on immersion in a solution of diffusible solute has three phases: (i) a very rapid adjustment to V and T values little different from those which would be developed by the ideal osmometer; (ii) a period of quasi-equilibrium, during which the classical equilibrium values of V and T continue to be approximately realized; (iii) a slow drift back to the initial condition of cell volume and turgor.

It must not be supposed, however, that the cell has returned to its initial state. Whereas the osmotic pressure of the cell contents was initially $P_o \epsilon/(\epsilon + P_o)$, it has now increased to $P_o \epsilon/(\epsilon + P_o) + P_1$.

Accordingly, if the cell is now removed from the solution of diffusible solute and replaced in free water, it will increase in volume rapidly until v approaches the value $P_o/(\epsilon + P_o) + P_1/\epsilon$ (i.e., T approaches the value $P_o \epsilon/(\epsilon + P_o) + P_1$). This will be followed by a gradual (nearly exponential) return to a state in which $v = P_o/(\epsilon + P_o)$. If, after this state is attained, the cell is removed from the free water and placed in a solution of non-diffusible solute of osmotic pressure P_o , the volume decreases rapidly to V_o , the turgor pressure to zero and the osmotic pressure of the cell contents to P_o . The cell has now returned to the state in which it was originally introduced. Figure 3 presents schematically the cycle of operations to which we have subjected it. The osmotic pressure history of

both external solution and cell contents, and the volume (or turgor) changes which the cell undergoes, are shown.

CELL DYNAMICS WITH CHANGING EXTERNAL CONCENTRATION OF DIFFUSIBLE SOLUTE: It will be clear from the preceding section that deviations from classical osmotic behavior induced by the presence of diffusible solutes become apparent only some time after external conditions change. We now consider cell behavior when the external concentration of diffusible solute changes gradually but continuously, as one might expect in nature.

Let us interrupt the previous cycle of operations on the cell at the point where it has reached equilibrium with free water (C of fig 3). We now suppose that a diffusible solute is introduced continuously into the water, so that, at any time, t , the osmotic pressure of the external solution is αt .

The equation governing the increase of osmotic pressure of the cell contents due to the entry of diffusible solute is again equation 13. P_1 is not constant here, but is equal to αt , so that we have

$$\frac{dP_d}{dt} = \frac{K_s A_o}{V_o} (\alpha t - P_d) \quad (17)$$

The particular integral of equation 17 which vanishes for $t = 0$ is:

$$P_d = \alpha t - \frac{\alpha V_o}{K_s A_o} \left[1 - \exp\left(-\frac{K_s A_o}{V_o} t\right) \right] \quad (18)$$

Equation 11, describing the volume change of the cell, holds here also. However, $(P_d - P_1)$ is now

$$-\frac{\alpha V_o}{K_s A_o} \left[1 - \exp\left(-\frac{K_s A_o}{V_o} t\right) \right],$$

so that the equation becomes

$$\frac{dv}{dt} = \frac{K_w A_o}{V_o} \left[P_o - \frac{\alpha V_o}{K_s A_o} \left[1 - \exp\left(-\frac{K_s A_o}{V_o} t\right) \right] - (\epsilon + P_o)v \right] \quad (19)$$

subject to the condition

$$t = 0, v = P_o/(\epsilon + P_o) \quad (20)$$

Provided $(\epsilon + P_o) K_w/K_s$ is much greater than unity (we have estimated the probable range of values at 50 to 5,000), the solution of equation 19 subject to 20 is, to a high degree of accuracy

$$v = \frac{P_o}{\epsilon + P_o} - \frac{\alpha V_o}{(\epsilon + P_o) K_s A_o} \left[1 - \exp\left(-\frac{K_s A_o}{V_o} t\right) \right] \quad (21)$$

This result is shown graphically in figure 4. It will be seen that, no matter how high the external concentration of diffusible solute becomes, the consequent change in v cannot exceed $\alpha V_o/(\epsilon + P_o) K_s A_o$. Thus,

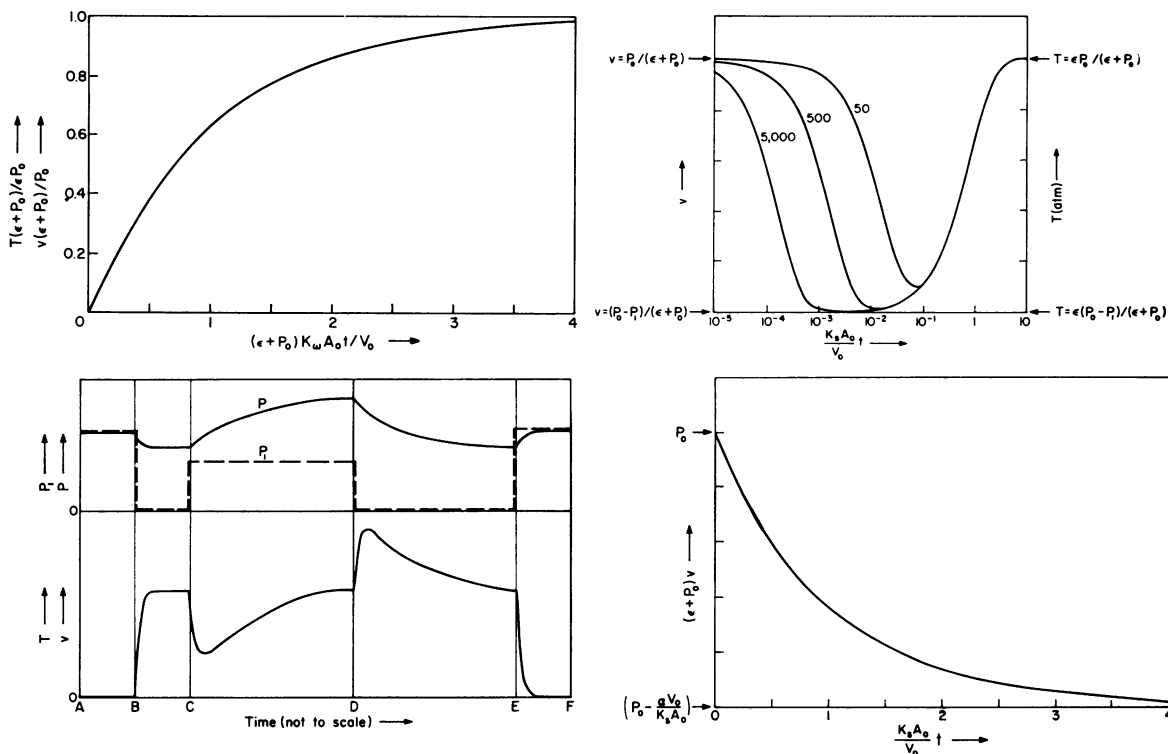


FIG. 1 (top left). The dynamics of the classical osmometer. Transition from zero to full turgor on immersion in free water.

FIG. 2 (top right). Cell behavior on immersion in solution of diffusible solute. The numbers on the curves denote values of $(\epsilon + P_0)K_w/K_s$.

FIG. 3 (bottom left). Schematic diagram of cycle of operations to which cell is subjected. Upper full curve represents osmotic pressure of the cell contents, P . Broken curve represents osmotic pressure of the external solution, P_1 . Points in the time sequence:

- A. Cell at zero turgor in equilibrium with non-diffusible external solution of osmotic pressure P_0 .
- B. Cell placed in free water.
- C. Cell removed and immersed in solution of diffusible solute.
- D. Cell returned to free water.
- E. Cell returned to original non-diffusible solution.
- F. Cell at zero turgor in equilibrium with original non-diffusible solution.

FIG. 4 (bottom right). Cell behavior with changing external concentration of diffusible solute.

if we assume a change in external osmotic pressure (due to diffusible solute) of 1 atm per day ($\alpha = 1.16 \times 10^{-5}$) and takes $K_s A_0 / V_0 = 5 \times 10^{-5}$, $(\epsilon + P_0) = 75$, the maximum change in v is 0.0032. That is, the maximum change in cell volume is less than 1 in 300.

The behavior of cell volume, and the osmotic pressure of external solution and cell sap, is shown in figure 5 for this numerical example ($P_0 = 15$). The external osmotic pressure is allowed to increase 1 atm per day for 20 days, after which it remains constant. Note that the slight loss of turgor is quickly regained once the external concentration ceases to increase.

CELL DYNAMICS AND DONNAN PHENOMENA: To this point we have referred to "diffusible" and "non-diffusible" solutes without specifying whether the dissolved material is ionic or molecular. Only where the Donnan phenomenon operates need this be done.

Table I summarizes various combinations of constitution of cell contents and external solution, and indicates the presence or absence of the Donnan phenomenon in each case.

Case 1 occurs, for example, during plasmolytic determination of osmotic pressure. Case 2 arises when the degree of ionization of the cell contents is negligible, and is perhaps improbable. Case 3, the most general one, is relevant, for example, to the interaction of a plant with the soluble salts of the soil.

The effect of the Donnan phenomenon, where it operates, on the previous analysis may be gauged by considering the problem treated under "Cell Dynamics in the Presence of a Diffusible Solute." Let us suppose that certain diffusible ions, originally in the cell, remain bound there, due to the presence of non-diffusible ions of opposite charge, so long as there are

TABLE I

CASE	CELL CONTENTS	EXTERNAL SOLUTION	DOES DONNAN PHENOMENON OPERATE?
1	Diffusible electrolyte or non-electrolyte, plus (possibly) non-diffusible components	Non-diffusible electrolyte or non-electrolyte	No
2	Non-diffusible electrolyte or non-electrolyte, plus (possibly) diffusible non-electrolytes	Diffusible electrolyte or non-electrolyte, plus (possibly) non-diffusible components	No
3	Electrolyte with at least one diffusible ion, plus (possibly) non-diffusible components	Diffusible electrolyte, plus (possibly) non-diffusible components	Yes

no diffusible ions in the external solution. Let these "bound" ions contribute (at zero turgor pressure) a partial osmotic pressure P_1 .

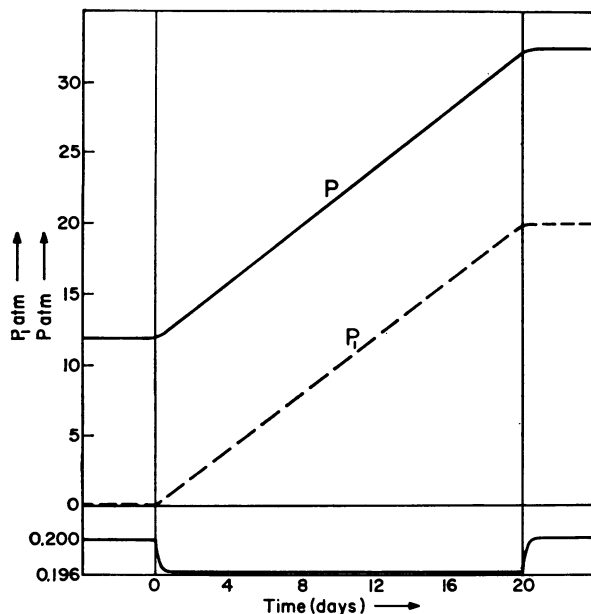


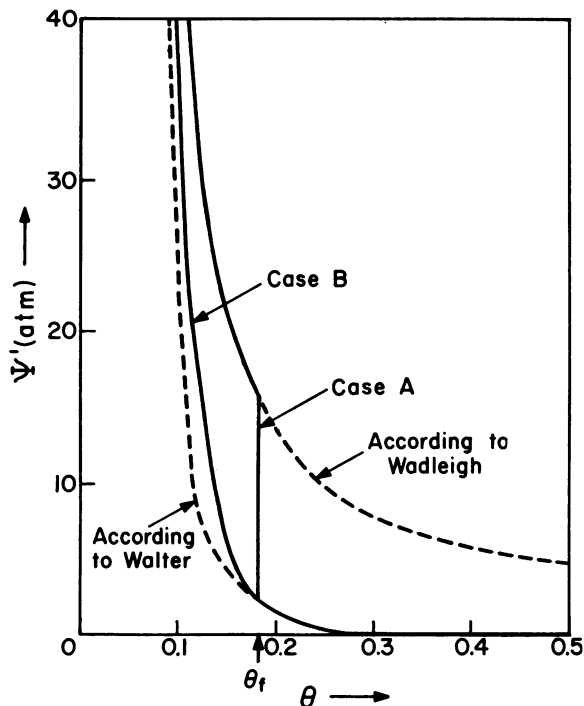
FIG. 5 (left). Cell behavior with changing external concentration of diffusible solute. Upper full curve represents osmotic pressure of the cell contents, P . Broken curve represents osmotic pressure of the external solution, P_1 . Lower full curve shows relative cell volume, v .

FIG. 6 (right). Variation of "effective soil moisture stress," Ψ' , with volumetric moisture content, θ , as implied by various theories. Upper broken curve—according to Wadleigh (25, 24). Lower broken curve—according to Walter (26). Solid curves—behavior indicated by present theory for cases A and B. θ_f denotes value of θ at failure of liquid continuity between soil water and root cell.

It is found that, if these ions are treated as non-diffusible while they remain bound, but as diffusible once the cell is placed in the large body of electrolyte solution, the analysis developed above predicts the final equilibrium osmotic pressure of the cell contents with a fractional error of about $P_1^2/8 P_1(P_0 + P_1)$. This is clearly small if P_1 is rather less than P_0 and P_0 . Thus, for $P_0 = 15$, $P_1 = 5$, $P_1 = 2$, the error is $1/200$. The Donnan phenomenon produces a much greater effect on the concentrations of the individual ionic species than on the total concentration, which is the significant quantity influencing osmotic pressure.

The question of how the Donnan phenomenon affects the dynamics of approach to equilibrium is somewhat obscure. Diffusion rates of electrolytes (or their ions) through membranes may well be of the same order of magnitude whether Donnan effects are present or not. If so, the overall dynamic picture presented above remains relevant in the presence of the Donnan phenomenon.

OSMOMETER ANATOMY AND REAL PLANT CELLS: In this study the model we have used is the classical cell-osmometer, with the complication added that certain solutes are free to diffuse through the cell wall. The classical cell-osmometer wall is envisaged as providing: (i) the geometrical limits of the cell; (ii) the



mechanical strength and elasticity supporting the turgor pressure; (iii) the semi-permeable membrane.

In the mature vacuolated plant cell, there are, as well as the wall and the vacuole, the plasmalemma, the cytoplasm and the tonoplast. Either of the membranes may operate as the effective resistance to the passage of water or of a particular solute; the cytoplasm itself may provide a significant resistance, or may have osmotic properties distinct from those of the vacuole.

A model sufficiently complex to include all these effects could be developed. However, the number of parameters in the system would be large, and the analysis cumbersome, even though the general results would not differ greatly from those we have obtained here for a simpler model. Nevertheless, there are points where some ambiguity arises when we apply the classical model to real plant cells.

Thus we have, throughout, referred to cell volume and cell contents, though we recognize that, where the effective barrier is the tonoplast, it would be more appropriate to work with vacuolar volume and vacuolar contents. The question of how cell volume varies with vacuolar volume raises such matters as change in cytoplasm volume, and the means of transmission of turgor from the cell wall across the cytoplasm to the vacuole. Further, we have referred all permeabilities to cell surface area, though, where the barrier between the external solution and the vacuole resides away from the cell wall, a smaller area (nevertheless, of the same order of magnitude) should, strictly, be used.

SOLUTE DIFFUSIBILITY AND PLANT WATER ECONOMY: In the real plant, both concentration gradients and effective diffusion cross-section per cell may be less than for the single cell, so that one can expect the effects of solute diffusibility to be somewhat retarded. However, with this qualification, the present analysis appears to be pertinent, and we conclude that solute diffusibility exerts a real influence on the water balance of whole plants.

Maximov (13) quotes work by a number of investigators which supports our analysis and this conclusion. Thus Renner added 1% KNO₃ to water cultures of beans, and found that absorption of water was immediately reduced, but that subsequently absorption became more rapid, the plant apparently adapting itself to the change in solution. Monfort observed that a sudden increase in concentration of the external solution caused a temporary cessation of guttation; guttation was subsequently renewed, finally increasing above the original level. Ursprung and Blum found that immersion in concentrated solutions increased the suction pressure of the cells in the absorbing zone of the root. All these experiments follow the course predicted in figure 2, though it is possible that some other effect, such as increase in membrane permeability, operates where the final uptake rate is in excess of the initial one.

Also significant are the experiments of Rybin. After immersion of plant roots in salt solution had reduced water uptake to about half its normal value, the

solution was suddenly replaced by pure water. There was an immediate increase in absorption to about 1.5 times the normal rate. On continued immersion in the water, the absorption rate approached its initial value. Sabinin observed similar phenomena. These experiments follow the course predicted in phases CDE of figure 3, if we regard the observed absorption rate as proportional to the difference in diffusion pressure deficit between the root cells and the solution.

The concept of "physiological dryness" (20) in saline soils has had a long currency in the literature of plant ecology. This viewpoint presupposes that the plant behaves as an ideal osmometer. The osmotic pressure of the soil water due to the soluble salts of the soil (which are diffusible through the plant membranes) is envisaged as opposing the entry of water into the plant via the root system. Wadleigh (25, 24) has used the "total soil moisture stress," defined as the sum of the tension and the osmotic pressure of the soil water, as a measure of the diffusion pressure deficit which must be exceeded in the epidermal cells of plant roots before water may be absorbed by them. Expressed thus, the concept is unexceptionable. However, the concept would seem to be of use only if the external electrolyte fails to diffuse into the cells of the root.

The analysis of solute diffusibility presented here indicates that the concept of salt-induced "physiological dryness" may not always be soundly based. Since, in nature, the osmotic pressure of the soil water is unlikely to change at rates much in excess of the 1 atm per day assumed in the numerical example above, it appears that the direct osmotic effect on plant water uptake is unlikely to be large, provided that liquid phase continuity between the soil water and the root surfaces is maintained. (We discuss this proviso below.) The basis of the deleterious effect of soil salinity in fairly moist soils may need to be sought elsewhere. It is possible that in such cases symptoms which have been interpreted as due to "physiological drought" have in reality been caused by the entry of diffusible solutes in toxic quantities.

Study of the movement of soil water to the absorbing root system (18) indicates that, during transpiration, large moisture gradients may develop near the root surfaces. As a result, even at fairly high mean soil moisture contents, the soil immediately adjoining the absorbing surface may become so dry that the final transfer of water to the root must take place in the vapor phase (17). The failure of continuity may be aggravated by the shrinkage of the root cells as they lose turgor in a drying soil. The vapor gap produced operates as an ideal semi-permeable membrane. Thus, a moderately dry soil, combined with meteorological conditions which impose a high transpiration rate upon the plant, may produce a situation in which the concept of "physiological drought" becomes relevant.

Walter (26) states, "Formerly it was assumed that salty soils, through the osmotic effects of the salts, are physiologically dry for plants. But this osmotic effect

is balanced by the intake of salts." Walter gives no qualification or further explanation of this statement. This total rejection of the physiological drought concept, like its total acceptance, appears to be incorrect. His statement might, however, be accepted by persons working with water cultures. In these no continuity problem arises, and experiment tends to confirm the analysis developed here (13).

The possibility of solute diffusibility makes the term "effective soil moisture stress" useful. We define it here as the minimum value of $(P_n - T)$ in the root cells necessary to produce movement from the soil into the plant. It will be recalled that P_n is the osmotic pressure of the cell contents due to non-diffusible solutes. Now, since diffusible solutes may be present in the root cells as well as in the soil water, we may write, quite generally,

$$\Psi' = \Psi + P_1 - P_d \quad (22)$$

where Ψ' is the effective soil moisture stress (atm), and Ψ is the soil moisture tension (atm). P_1 , P_d now represent the osmotic pressure of the soil solution and the partial osmotic pressure of the cell contents due to diffusible solute, respectively. Let θ be the volumetric moisture content of the soil (cm^3 liquid water/ cm^3 soil) and θ_f the value of θ at which liquid continuity fails. Then

$$\text{for } \theta > \theta_f, P_1 \approx P_d, \text{ so that } \Psi' \approx \Psi \quad (23)$$

When $\theta \leq \theta_f$ matters are more complicated, as the quantity of diffusible material in the plant may depend on the salinity history of the root zone before failure of continuity. When, for example, all the salt accumulates in the soil after the continuity failure (we shall call this the limiting case A),

$$P_1 = P_s \theta_s / \theta, P_d = 0 \quad (24)$$

where P_s denotes the osmotic pressure (atm) of the soil solution, if the soil were at the saturation moisture content θ_s and contained the same amount of salt per unit soil volume. Equation 24 assumes proportionality between osmotic pressure and solute concentration. This gives the result

$$\text{Case A for } \theta \leq \theta_f, \Psi' = \Psi + P_s \theta_s / \theta \quad (25)$$

In this case Ψ' would agree with Wadleigh's "total soil moisture stress" in the range $\theta \leq \theta_f$.

If, on the other hand, we consider the contrasting case B, where the salt in the soil is present in constant (volumetric) concentration before, as well as after the failure of continuity, equation 24 must be replaced by

$$P_1 = P_s \theta_s / \theta, P_d = P_s \theta_s / \theta_f \quad (26)$$

(The expression for P_d neglects the effect of turgor changes in the root and may therefore be somewhat too small.) Equations 22 and 26 then yield

Case B for $\theta \leq \theta_f$,

$$\Psi' = \Psi + P_s \theta_s \left(\frac{1}{\theta} - \frac{1}{\theta_f} \right) \quad (27)$$

This case gives a Ψ' which gradually deviates from Walter's concept of $\Psi' = \Psi$ as θ decreases below θ_f , but which everywhere remains somewhat less than Wadleigh's "total soil moisture stress."

In general terms we may state that, according to the present ideas, $\Psi' = \Psi$ so long as $\theta > \theta_f$. For $\theta \leq \theta_f$ the exact behavior of Ψ' depends on the salinity history of the root zone, but, in general, Ψ' can be expected to assume a value intermediate between that implied either by total acceptance or total rejection of the physiological drought concept.

Figure 6 illustrates the $\Psi'(\theta)$ relationships implicit in the physiological drought theory and in the opposing view of Walter, as well as the relationships for Cases A and B according to the present considerations. The $\Psi(\theta)$ function was based on data of Moore (15) for a soil of moderate clay content, and the value $P_s = 5$ was used.

SUMMARY

The dynamic theory of the classical osmotic plant cell is developed in quantitative form and extended to the case where a diffusible solute is present. It is shown that solute diffusibility may result in marked deviations from classical behavior. Where Donnan membrane phenomena are operative, the analysis needs modification, but the gross character of the dynamic behavior remains similar. The "physiological drought" theory of the influence of soluble salts in the soil on the water economy of plants depends on their non-diffusibility. On the other hand, Walter (26) states, "the osmotic effect is balanced by the intake of salts." Neither view seems wholly correct, since both solute diffusibility and liquid phase continuity may be important factors.

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PROPAGATION OF TURGOR AND OTHER PROPERTIES THROUGH CELL AGGREGATIONS¹

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Inferences are often drawn about the osmotic behavior of pieces of tissue composed of an aggregation of cells, or even of whole plants, by reference to the classical single cell osmometer. Treating the aggregate as an individual introduces no error when the system is in internal equilibrium. However, in the dynamic problems of interest to the physiologist, this is not the case.

We consider first the behavior of a linear aggregation of cells, as shown in figure 1. The cells are identical in the sense that, at zero turgor, their dimensions, and the osmotic pressure of their contents, are equal, and that the elastic and permeability properties of their walls and membranes are equal. A is the effective area of wall available for the passage of water between adjoining cells (cm²), K is the permeability of the surface of an individual cell to water (cm sec⁻¹ atm⁻¹), θ is the diffusion pressure deficit (atm), T is the cell turgor pressure (atm), P is the osmotic pressure of the cell contents (atm), V is the cell volume

(cm³), t is the time (sec), and numerical suffixes denote values obtaining in the appropriately numbered cell. Then, for any sequence of cells, 1, 2, 3,

$$\left. \begin{aligned} \text{Rate of flow of water from 1 to 2} &= \frac{AK}{2} (\theta_2 - \theta_1) \\ \text{Rate of flow of water from 2 to 3} &= \frac{AK}{2} (\theta_3 - \theta_2) \end{aligned} \right\} \quad (1)$$

In attributing definite values $\theta_1, \theta_2, \theta_3$ to the diffusion pressure deficits of cells 1, 2, 3, we imply that osmotic pressure differences within each cell are negligible. Commonly the cell dimensions, and the rates of water transfer, will be so small that this is the case.

It follows that

$$\text{Rate of volume increase of cell 2} = \frac{AK}{2} [(\theta_2 - \theta_1) - (\theta_3 - \theta_2)] \quad (2)$$

By introducing a relationship between V and θ , we could now write down a differential equation express-

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