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PROPAGATION OF TURGOR AND OTHER PROPERTIES THROUGH CELL AGGREGATIONS [1]

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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,

$$\text{Rate of flow of water from 1 to 2} = \frac{AK}{2}(\theta_2 - \theta_1)$$

$$\text{Rate of flow of water from 2 to 3} = \frac{AK}{2}(\theta_3 - \theta_2) \qquad (1)$$

In attributing definite values θ_1, θ_2, θ_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

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

By introducing a relationship between V and θ, we could now write down a differential equation express-
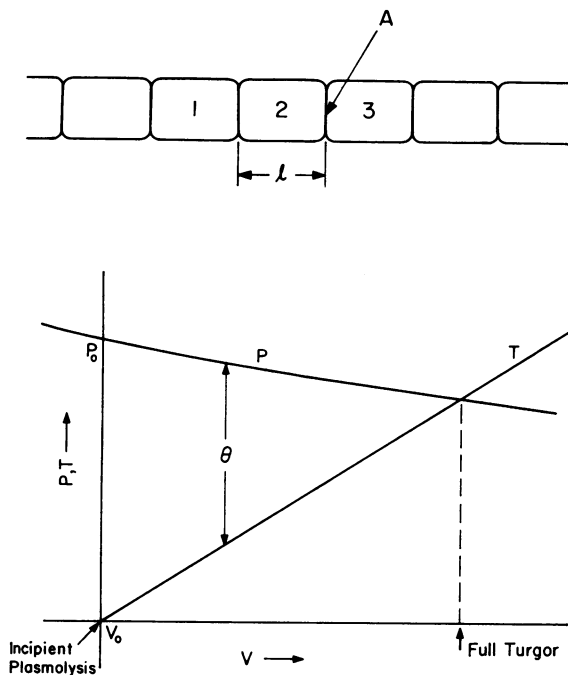
FIG. 1 (*top*). Linear aggregation of osmotic cells.

FIG. 2 (*bottom*). Simplified Höfler diagram. Cell osmotic relations connecting osmotic pressure, P, turgor pressure, T, diffusion pressure deficit, θ, and cell volume, V.

ing $d\theta_2/dt$ in terms of θ_1, θ_2, and θ_3. We could do similarly for each cell of the aggregation. However, since we should then have 1,000 simultaneous differential equations for an aggregation of 1,000 cells, and 1,000,000 equations for 1,000,000 cells, it is simpler and more elegant to use the fact that individual cells are much smaller than the aggregation, and to treat θ as varying continuously along a distance ordinate x directed lengthwise along the aggregation. Then if l is the length of each cell (cm), measured in the x-direction, $[(\theta_2 - \theta_1) - (\theta_3 - \theta_2)]/l^2$ represents in finite difference form (e.g., (3)) the quantity $-\partial^2\theta/\partial x^2$. Thus eq. (2) reduces to

$$\frac{\partial V}{\partial t} = -\frac{AKl^2}{2}\frac{\partial^2\theta}{\partial x^2} \qquad (3)$$

Figure 2 shows in simplified form the well-known relationships between V, P, T and θ. When V is nearly a linear function of θ, it is readily shown (7) by using the fact that cell volume changes are relatively small, that, to a good approximation,

$$\theta = (\epsilon + 2P_o) - \frac{V}{V_o}(\epsilon + P_o) \qquad (4)$$

where V_o, P_o are the values of V, P for T = 0 (incipient plasmolysis) and ϵ is the elastic molulus defined by the equation

$$T = \epsilon(V/V_o - 1) \qquad (5)$$

Note that equation 4 implies that the cell volume at full turgor ($\theta = 0$) is .

$$V_o\left[1 + \frac{P_o}{\epsilon + P_o}\right]$$

As we state in (7), the assumption of linear relations between T and V, and θ and V, is a first approximation. We show later that a more sophisticated analysis permitting any arbitrary form of T(V) and θ(V) functions may be readily developed. It will also be clear from (7) that the present study deals only with elastic changes of cell volume, and does not treat the plastic, irreversible deformations associated with growth.

Combining equations 3 and 4,

$$\frac{\partial V}{\partial t} = \frac{AKl^2(\epsilon + P_o)}{2V_o}\frac{\partial^2 V}{\partial x^2} \qquad (6)$$

The equation is clearly of the diffusion form

$$\frac{\partial V}{\partial t} = D\frac{\partial^2 V}{\partial x^2} \qquad (7)$$

The diffusivity D is a function of K, $(\epsilon + P_o)$ and the cell dimensions. Since Al/V_o is a function of cell shape, and is independent of cell size, it may be replaced by a shape factor a. It follows that

$$D = \frac{\alpha Kl(\epsilon + P_o)}{2} \qquad (8)$$

For plant cells $(\epsilon + P_o)$ is typically of order of magnitude 100 atm (7). a is about 1; it is somewhat less if (gas-filled) free spaces exist between the cells.

Since V, T, θ and P are all assumed to be connected linearly, equation 7 can be recast as a diffusion equation in the other quantities. We may therefore write also

$$\frac{\partial T}{\partial t} = D\frac{\partial^2 T}{\partial x^2}; \frac{\partial \theta}{\partial t} = D\frac{\partial^2 \theta}{\partial x^2}; \frac{\partial P}{\partial t} = D\frac{\partial^2 P}{\partial x^2} \qquad (9)$$

and D is equally the coefficient of diffusion of turgor, diffusion pressure deficit, or osmotic pressure, as well as being the coefficient of diffusion of cell volume (θ(t) will often be fixed at the boundaries, so that the θ-form of the equation will probably be the most serviceable.)

The analysis is simply generalized to three-dimensional aggregations by applying the same considerations in two further directions at right angles to the x-direction and to each other. Where the tissue is isotropic (i.e., a and l are independent of direction in the tissue) the diffusion equations assume the general form

$$\frac{\partial V}{\partial t} = D\nabla^2 V, \text{ etc.} \qquad (10)$$

Where the cells are of different dimensions in the mutually perpendicular principal directions x, y, z, the equations are of the form

$$\frac{\partial V}{\partial t} = D_x \frac{\partial^2 V}{\partial x^2} + D_y \frac{\partial^2 V}{\partial x^2} + D_z \frac{\partial^2 V}{\partial z^2}, \text{ etc.} \quad (11)$$

Here D_x, D_y and D_z are not necessarily equal, each being specified by an equation similar to 8, but with values of α and l appropriate to the particular principal direction in the tissue. (In this more general case the diffusivity becomes a second-order tensor of a form common in the mathematical physics of anisotropic media.)

When the arrangement of cells is other than rectangular, these three-dimensional results do not follow directly from the one-dimensional results. However, provided the tissue is homogeneous (i.e., the individual cells are similar and their spacing is uniform) results of the same nature can be anticipated, though the relationship between the D's and the cell dimensions may now become more complicated.

SOME LIMITATIONS AND POSSIBLE EXTENSIONS: It remains to mention some further aspects of the present approach, mainly dealing with its limitations and its possible extensions.

1. Our analysis deals solely with water exchange between adjoining cells. It must be recognized that, at least in the three-dimensional case of greatest practical interest, there exists the possibility of passage of water between non-adjoining cells through water-occupied intercellular spaces. Fortunately for the present approach, intercellular spaces in plants are normally gas-filled, so that this difficulty will not usually arise.

2. We have not attempted a detailed analysis of the stress-distribution in the framework of cell-walls within the tissue. Obviously the exact stress picture in the structure wall—middle lamella—wall between two cells of differing turgor pressure will depend on the elastic properties of the various components in a manner which may be far from simple. Two extreme working hypotheses are (a) that the middle lamella does not support stress, in which case the cells are elastically independent, and (b) that the two walls plus the middle lamella possess a common tension which depends on the mean of the turgor pressure in the two cells. The present treatment agrees exactly with hypothesis (a) and also, to a first order of small quantities, with hypothesis (b). To this degree elastic interactions between the cells are taken into account. Obviously this aspect needs further study.

3. Here we examine further the approximation that D is constant in a particular tissue. This result depends on (a) neglect of the small changes in l which occur with changes in turgor, and (b) the assumption of a linear relationship between V and the quantity regarded as diffusing (i.e., θ, T or P).

(b) is the more drastic assumption, since it is well known that the Höfler diagram may reveal quite appreciable deviations from linearity. We show here, however, that a more exact expression for D can be found simply in terms of any given Höfler diagram.

In the more precise analysis equation 3 is replaced by

$$\frac{\partial V}{\partial t} = -\frac{\partial}{\partial x}\left(\frac{AKl^2}{2} \frac{\partial \theta}{\partial x}\right) \quad (12)$$

and, instead of using equation 4, we introduce the quantity $d\theta/dV$. Previously with V and θ assumed connected linearly, this quantity was equal to $-(\epsilon + P_o)/V_o$. When the Höfler diagram is non-linear, $d\theta/dV$ is a function of V. Now equation 12 may be rewritten

$$\frac{\partial V}{\partial t} = \frac{\partial}{\partial x}\left(-\frac{AKl^2}{2} \frac{d\theta}{dV} \cdot \frac{\partial V}{\partial x}\right) \quad (13)$$

i.e.,

$$\frac{\partial V}{\partial t} = \frac{\partial}{\partial x}\left(D \frac{\partial V}{\partial x}\right) \quad (14)$$

where

$$D = -\frac{AKl^2}{2} \frac{d\theta}{dV} \quad (15)$$

Equations 13, 14 and 15 correspond to equations 6, 7 and 8 of the linear analysis. As before, we may develop the extensions to three dimensions for both isotropic and anisotropic tissue. It is no longer possible, however, to express the phenomenon as diffusion of θ, T and P, as well as of V. The relevant equations assume the slightly more complicated "heat conduction" form. D is now, evidently, a function of V, and if the manner in which Al^2 depends on V is known, there is no formal difficulty in avoiding approximation (a) as well as approximation (b).

It will be noted that equations 14 and 15 define a diffusion phenomenon with the diffusivity concentration-dependent. The mathematics of this form of diffusion has been considerably advanced in recent years (cf. 2, 6), one of the practical applications being to the problem of water movement in unsaturated soils.

However, it is our view that the linear theory is sufficiently refined for most plant physiological purposes, at least until uncertainties such as those mentioned in 1 and 2 above are resolved. For example very large deviations from linearity in the Höfler diagram would be needed before D would be found to vary in a range of V from, say, 50 to 200 % of some mean value. Yet, even in this extreme case, errors due to using D constant would probably be less than other uncertainties in the problem. Contrast the case of water movement in soils, where D may vary by 1 to 1000, or more, and it becomes much more necessary to take into account the variation of D with concentration.

4. The deformation of the tissue, produced by any given osmotic treatment, can be inferred, once the problem is solved for V, provided always that the relationship between V and the geometry of the individual cell is known. (If the cell deforms isotropically, its external dimensions will vary as $V^{1/3}$.)

5. The analysis, in its present form, does not apply to the case where diffusible salts are present in the

tissue, since P_o is then constant, neither in time nor space.

6. Further, it is valid only for turgid cells, since most of the relations between V, T, θ and P, which we use, hold only for the normal unplasmolyzed cell.

OSMOTIC DIFFUSION AND SELF-DIFFUSION: Molecular and ionic diffusion in tissue is usually complicated by osmotic effects. However, these are apparently absent where the diffusing substance is isotopically labelled water (1, 4, 5). In such cases we may use the methods of the above analysis to arrive at a value for the apparent diffusivity of the labelled water (and, presumably, the apparent coefficient of self-diffusion of H_2O) through the tissue, $D_s(cm^2 sec^{-1})$, namely

$$D_s = \frac{\alpha K_s l}{2}, \qquad (16)$$

where K_s is the permeability of the surface of an individual cell (cm sec^{-1}) to diffusion of the labelled water.

I am indebted to Dr. James Bonner for raising the question of the relationship, if any, between the apparent coefficients of osmotic diffusion, D, and of self-diffusion, D_s. The experiments of Ordin and Bonner (5) suggests $D/D_s \approx 1$, while the somewhat less precise (5) work of Buffel (1) gives $D/D_s \approx 0.1$.

According to the present analysis (equations 8 and 16):

$$\frac{D}{D_s} = \frac{K(\epsilon + P_o)}{K_s} \qquad (17)$$

D involves $(\epsilon + P_o)$, i.e., a quantity depending on both the amount of osmotically active material in the cell and the elastic properties of the cell, while D_s does not. (The argument is, of course, the same when we use equation 15 for D; in qualitative form, the argument is simply that D depends on the Höfler diagram, while D_s does not.) It would seem to be purely coincidence that the two diffusivities are of about the same order of magnitude.

No simple quantitative relationships connecting either D and D_s, or K and K_s, seem possible. Studies of diffusion of labelled water have an interest in their own right, but cannot be regarded as a substitute for osmotic studies. Permeability to water in the osmotic sense, and in the self-diffusion sense, should not be confounded.

SUMMARY

The problem of the propagation of osmotic disturbances through tissue consisting of an aggregation of osmotic cells is analyzed. It is shown that such disturbances can be described mathematically as diffusion phenomena, the diffusivity being a function of the dimensions, permeability, and elastic properties of the individual cell, together with the quantity of osmotically active material in it. The problem of diffusion of isotopically labelled water through such tissue may be treated similarly. The diffusion coefficients of the two phenomena depend on different properties of the system. The experimental result that they are of about the same order of magnitude is, apparently, merely a coincidence, and does not substantiate the idea that diffusion studies of labelled water can give information directly connected with cell water relations.

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