

Osmotically-Induced Mass Transfer in Plant Storage Tissues: A Mathematical Model. Part I*

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ABSTRACT

A mathematical model incorporating cell membrane characteristics for the simulation of water and solute fluxes in complex cellular structures is developed. The overall transport of material in the supporting matrix is considered using relationships associated with an extended form of the second-degree Fickian equation. The interaction of the cells with their immediate environment is described by transport relationships based on irreversible thermodynamics. Because of the complexity of biological tissue structures, a simplified geometrical analogue of the actual cellular matrix is used. This analogue represents the main features of the actual tissue, i.e. apoplastic and symplastic transport, cell volume changes, tissue shrinkage and internal volumetric rearrangements. The mathematical model has been used to simulate movement of water and diffusible permeating and non-permeating solutes in discs of beet roots and potato tubers. The influence of various cellular and tissue properties on the dynamics of mass transport phenomena occurring in the cellular structures was studied. These simulations will be presented in Part II of this study.

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NOTATION

The number in the parenthesis after the description refers to the equation in which the symbol is first used or defined.

<i>a</i>	Thermodynamic activity (dimensionless; eqn (13))
<i>A</i>	Surface area (m^2 ; eqn (6))
<i>C</i>	Effective molar concentration (kg mol m^{-3} ; eqn (14))
<i>C̄</i>	Arithmetic average concentration (kg mol m^{-3} ; eqn (15))
<i>d</i>	Diameter (m ; eqn (5))
<i>D</i>	Binary diffusivity in solution ($\text{m}^2 \text{s}^{-1}$; eqn (26))
<i>D̄</i>	Pseudo-binary corrected diffusivity ($\text{m}^2 \text{s}^{-1}$; eqn (24))
<i>J</i>	Molar flux ($\text{kg mol m}^{-2} \text{s}^{-1}$; eqn (11))
<i>k</i>	Compliance factor (dimensionless; eqn (32))
<i>K</i>	Pseudo-binary mass transfer coefficient (m s^{-1} ; eqn (39))
<i>l</i>	Length of the ECUC (m ; eqn (5))
<i>L</i>	Macroscopic phenomenological coefficient ($\text{kg mol}^2 \text{J}^{-1} \text{m}^{-2} \text{s}^{-1}$; eqn (11))
<i>N</i>	Molar flux with respect to a fixed frame of reference ($\text{kg mol m}^{-2} \text{s}^{-1}$; eqn (25))
<i>p</i>	Macroscopic permeability coefficient ($\text{kg mol N}^{-1} \text{s}^{-1}$; eqn (22))
<i>P</i>	Hydrostatic pressure (N m^{-2} ; eqn (13))
<i>R</i>	Universal gas constant ($\text{J}(\text{kg mol})^{-1} \text{K}^{-1}$; eqn (13))
<i>R</i>	Radius of a given cylinder of the ECUC (m ; eqn (7))
<i>T</i>	Absolute temperature (K ; eqn (13))
<i>T̄</i>	Reference thickness (m ; eqn (37))
<i>v*</i>	Volume average velocity (m s^{-1} ; eqn (24))
<i>v̄</i>	Partial molar volume ($\text{m}^3 (\text{kg mol})^{-1}$; eqn (13))
<i>V</i>	Volume (m^3 ; eqn (1))
<i>z</i>	Macroscopic direction of transfer (m ; eqn (24))
α_p	Fraction of total cell membrane area occupied by plasmodesmata (dimensionless; eqn (6))
β_1	Variation of the cell wall elastic modulus with respect to the intracellular hydrostatic pressure (dimensionless; eqn (17))
β_2	Value of the cell wall elastic modulus at incipient plasmolysis (N m^{-2} ; eqn (17))
ϵ	Void fraction (dimensionless; eqn (1))
θ	Time (s ; eqn (24))
μ	Chemical potential ($\text{J}(\text{kg mol})^{-1}$; eqn (11))
ξ	Cell wall elastic modulus (N m^{-2} ; eqn (16))
τ	Tortuosity (dimensionless; eqn (5))

ϕ	Volume fraction (dimensionless; eqn (1))
Ψ	Effective diffusibility (dimensionless; eqn (26))
$\#_c$	Number of ECUCs in thickness in a representative column (eqn (37))
$\#_c^t$	Number of constituent average unit cells in tissue analogue (eqn (4))
$\#_{\text{col}}^t$	Total number of representative columns in tissue analogue (eqn (38))

Subscripts

a	Osmotically active (in text)
b	Buffer (eqn (9))
c	Cellular (eqn (3))
d	Non-osmotically active (eqn (30))
i, k	Related to species i, k (eqn (11))
I	Interstitium (eqn (1))
m	Plasmalemma (eqn (6))
p	Plasmodesmata (eqn (6))
s	Intercellular free space (eqn (1))
w	Cell wall (eqn (1))
0	Reference state (eqn (3))

Superscripts

1	Related to the average unit cell (eqn (3))
j	Related to the j th cell (eqn (34))
t	Related to the actual tissue (eqn (1))
$+, -$	Related to the $(j, j + 1)$ th and $(j, j - 1)$ th cell interface (eqn (30))
in	Intracellular quantity (eqn (14))
ex	Extracellular quantity (eqn (14))

MASS TRANSFER PROCESSES IN PLANT STORAGE TISSUES

The purpose of this study was to obtain a better understanding of mass transfer phenomena induced by osmotic imbalances when discs of storage tissues of higher plants, such as carrot and beet roots or potato tubers, are immersed in solutions containing diffusible permeating and/or non-permeating solutes (in the present context, the terms 'permeating' and 'non-permeating' solutes refer to the potential of the species to move across the cell membranes, whereas the terms 'diffusible' and 'non-diffusible' refer to their capacity to penetrate the tissue). A mathematical model representing the different aspects of the biological systems under consideration was developed then solved for certain conditions to provide a comprehensive analysis of the system behaviour.

Physiology of plant storage tissues

Although the water relationships in a single plant cell are well understood, the relationships become more complex when osmosis is applied to whole plant tissue structures.

As illustrated diagrammatically in Fig. 1, there are two accepted pathways which water and solutes can follow while traversing plant storage tissues (Moorby, 1981; Nobel, 1983): the apoplast, which is external to the cell membrane (plasmalemma), and the symplast, which is internal to the plasmalemma of neighbouring cells. Apoplastic transport is defined as movement of material into the cell wall and the intercellular free space. Symplastic transport involves transport of material from one cell directly into another by means of small channels (plasmodesmata). Both routes are believed to be significant, their respective contributions to the overall transport processes being related to the nature of the tissue.

Most authors consider a third type of transfer, transmembrane transport, defined as exchanges between the cell interior (cytoplasm and vacuole) and the cell exterior (cell wall and intercellular space) across the cell membrane. However, as discussed by Molz (1976), transport across the plasmalemma cannot be entirely dissociated from transport in the extracellular environment, as all material crossing the cell membrane comes from or goes into the extracellular volume. Transmembrane transport may therefore be regarded as an intrinsic component of the overall apoplastic transport and will hereafter be considered as such.

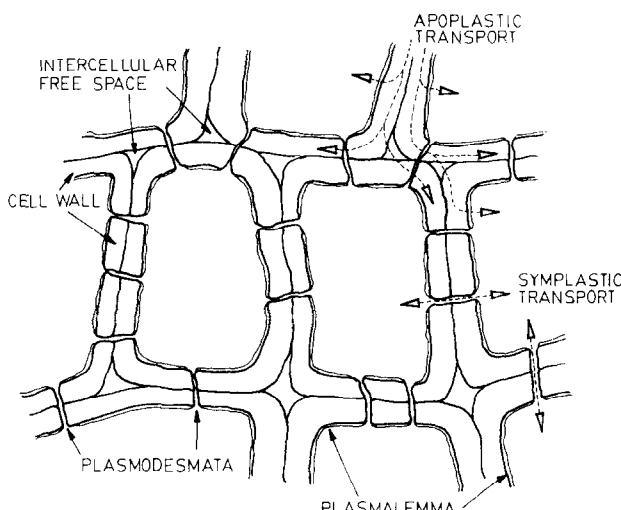


Fig. 1. Mass transport pathways in actual plant storage tissues.

Movement through the cell wall is determined by the width of the interfibrillar and the intermicellar spaces and by the kind and concentration of charged ions fixed there (Lütte & Higinbotham, 1979). Transmembrane transport is controlled by the permeability of the plasmalemma to the solutes and the nature of the mechanisms responsible for the transfer (Briggs, 1957; Cram, 1968; Hall & Baker, 1980).

A modern description of symplastic transport based on irreversible thermodynamics was proposed by Tyree (1970). He used the theory to derive phenomenological equations describing the transport of substances through the plasmodesmata based on macroscopic permeability coefficients (characterizing the overall resistances encountered when molecules negotiate this pathway). This approach is analogous to considering the plasmodesmata as resembling an equivalent membrane which has the permeability characteristics of the channel. Tyree quantified, at least to an order of magnitude, the values of these permeability coefficients, based on properties representing the plasmalemma permeability. He showed that the plasmodesmata was far more permeable than the plasmalemma, with the result that the symplast appears to provide a particularly effective pathway between interconnected cells for water and small solutes.

Review of existing models

Relatively little work has been done on the fundamentals of osmotic dehydration of plant storage tissues. Existing models are mostly based on the assumption that the observed macroscopic mass transfer can be described by the simplified unsteady-state Fickian diffusion model (Loncin, 1980). They are therefore of a correlative nature and, as such, are limited to the studies of interest as they are based on effective diffusion coefficients which are found by regression to satisfy the observed transport phenomena (Hawkers & Flink, 1978; Conway *et al.*, 1983).

The inclusion of a formal description of the tissue structure as part of the diffusion model was examined by Soddu and Gioia (1979) in their study on leaching of sugar from sugar beets immersed in water. Rotstein and Cornish (1978a,b), and more recently, Crapiste *et al.* (1984), introduced similar descriptions in their studies on air dehydration of cellular foodstuffs.

The first major effort to develop a quantitative description of osmotic mass transport in plant tissues based on cellular properties is attributable to Philip (1958a-c). His analysis was restricted, however, to describing movement of water in a linear aggregation of cells in contact with an osmoticum containing a non-diffusible non-permeating solute. He

pointed out that the assumption that the diffusion and osmotic phenomena in whole pieces of tissue were analogous to those in a single cell is not justified. Molz and Hornberger (1973) extended Philip's model to include the effects on a similar structure of a diffusible permeating solute. Nevertheless, both models were relatively limited, as they considered the mass fluxes as having to traverse the cells in series, from surface to interior (and vice versa), and made no attempt to identify a preferential pathway. The above authors used the practical equations for mass transport across biological membranes developed by Kedem and Katchalsky (1958) from irreversible thermodynamics and elaborated for plant cells by Dainty (1963) to describe the solute mass transfer in the structure considered.

In a subsequent paper, Molz and Ikenberry (1974) improved the description by developing a model which allowed for mass fluxes in the cell wall and extracellular space without necessarily traversing the cell membranes. Molz (1976) completed the model by accounting formally for symplastic and apoplastic transport.

In all the aforementioned works it was assumed, to simplify the mathematical treatment of the models, that as the individual cells could be considered much smaller than the aggregation, the anatomy of the tissue could be regarded as a homogeneous continuum, allowing the local continuity equations to be integrated across the whole structure.

Molz *et al.* (1979), employing an electrical circuit analogue to characterize the resistances in the symplast and the apoplast, proposed a model which was used to study the water relations between intra- and extracellular volumes of a matrix composed of a linear arrangement of several plant cells. It is interesting to note that, unlike the previous works, the model devised by these authors included explicitly some of the discrete cellular geometry and anatomy of the actual tissue being modelled. The behaviour of each individual cell could accordingly be simulated.

More recently, McCoy and Boersma (1984) applied continuum mechanics to formulate mathematical expressions for the transport of water and a solute along the direction of deformation in plant tissue. The use of continuum mechanics had, nevertheless, the drawback that it led to a macroscopic description of the tissue with no possibility of simulating the behaviour of its cellular components.

Summary

From the above review it appears that any attempt to study the fundamentals of mass transport in plant storage tissues must involve the

microscopic description of the structures considered (the approach adopted in the present study is thus more in line with the model proposed by Molz *et al.* (1979)). As pointed out by Philip (1958c), the transfer phenomena occurring during osmotic dehydration of plant tissues seem strongly influenced by the nature and interrelation of the transport pathways present in the system and not only by the behaviour of the constituent cells. Osmotically induced mass transport in cellular structures such as plant storage tissues may thus be seen as a transfer of water and solutes from/to the osmotic bath into the apoplast (with possible trans-membrane exchange) and into the symplast.

IDEALIZED REPRESENTATION OF A TYPICAL STORAGE TISSUE

The average unit cell

We now consider the simplified structure of a typical plant storage tissue shown in Fig. 2(a). The total volume of the simplified matrix consists of two main components. The first part is the interstitium, V_l^t , which comprises the total cell wall volume, V_w^t , and the total intercellular free space volume, V_s^t . The intercellular free space is all the space created by gaps

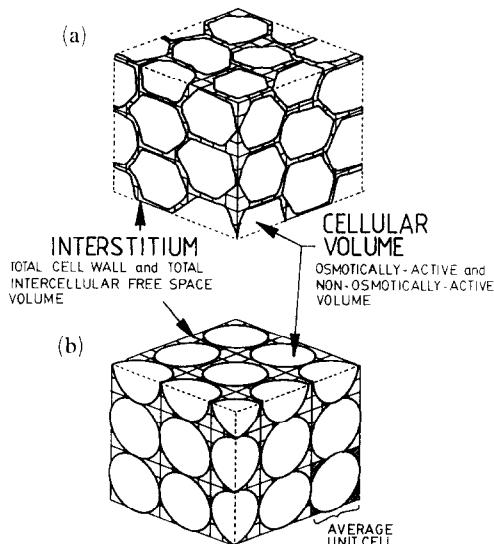


Fig. 2. Simplified structure of a typical plant storage tissue (a) and corresponding analogue (b).

between adjoining cell walls (see Fig. 1). This volume is filled with either air or solution. The second part is the total cellular volume, V_c^t , which is composed of an osmotically active volume, V_a^t , and a non-osmotically active volume, V_d^t . This tissue picture (Fig. 2(a)) considers the constituent plant cells as simple osmotic systems, i.e. the cytoplasm, the tonoplast and the vacuole of any cell are considered to form a single unit (single compartment system), whereas the plasmalemma acts as the sole (semi)permeable barrier. The total cellular volume is therefore all the tissue volume internal to the plasmalemma of the individual cells. The permeability properties of the plasmalemma surrounding a cell are assumed to represent the combined resistances to transfer of the plasmalemma itself and the intracellular structure.

The actual tissue can be regarded as an aggregation of cells possessing a void fraction, ε^t , defined as the fraction of the total tissue volume, V^t , which is interstitial volume, i.e.

$$\varepsilon^t = V_i^t/V^t = \phi_s^t + \phi_w^t \quad (1)$$

where ϕ_s^t and ϕ_w^t are, respectively, the volume fractions of the total tissue intercellular free space and cell wall volume, given by

$$\phi_s^t = V_s^t/V^t \text{ and } \phi_w^t = V_w^t/V^t \quad (2)$$

To make the mathematical treatment feasible, an 'idealized' representation of the parenchymatous structure of plant storage tissues, as shown in Fig. 2(b) (Nilsson *et al.*, 1958) is considered.

The actual tissue may be represented approximately by a homogeneous and isotropic cubic arrangement of representative spherical cells, so that each cell is in contact with six neighbours except at the surface. This process is possible because of the homogeneity and similarity of the structural elements of these plant tissues (Esau, 1940; Poole, 1976).

The diameter of the average cell composing the actual tissue can be measured by microscopic means and the size of this representative cell used to define an average unit cell. This unit cell is composed of a unit cellular volume, $V_{c_0}^1$, represented by a sphere of the average diameter determined above, and its associated unit interstitial volume, V_i^1 , calculated by using the tissue void fraction, ε^t , i.e.

$$V_{i_0}^1 = (\varepsilon_0^t V_{c_0}^1) / (1 - \varepsilon_0^t) \quad (3)$$

where the subscript 0 refers to a reference state of the tissue (usually full turgor).

The number of constituent units in the tissue analogue, $\#_c^t$, is determined by dividing the actual total tissue volume, V_0^t , by the total volume of the average unit cell, V_{u}^t , at the reference state, i.e.

$$\#_c^t = V_0^t / V_{\text{u}}^t = V_0^t / (V_{c_0}^1 + V_{l_0}^1) \quad (4)$$

The equivalent cylindrical unit cell

The prediction of the transport processes within the idealized aggregate of spherical parenchymatous cells requires further analysis to lead to a usable predictive model. More precisely, due to the mathematical complexity of describing diffusive flows within the proposed idealized structure, it appears necessary to introduce an even simpler representation of the system. This further simplification comes also from the necessity to describe the behaviour of a parenchymatous cell undergoing osmotic changes.

The problem at this level is to conceive a realistic model of a cell and its environment. The model not only must provide a means to permit concentration gradients to exist in the interstitium, but also must allow material to cross the plasmalemma over the entirety of its surface of exchange in response to differences in chemical potentials across that membrane.

The equivalent cylindrical unit cell has been conceived to respond to these constraints. The main advantage of this design is that it simulates the continuity of the interstitium and the discontinuity created by the spatial arrangement of the cells in the tissue matrix.

We consider a representative portion of the tissue analogue (Fig. 2(b)), that is, a characteristic portion of the structure which will be assumed to behave exactly as the whole. The selection of this representative subsystem and consequently the usefulness of the proposed approach depend obviously on the type of mass transport phenomenon to be described by the model. Thus, if the analysis is restricted to the description of unidirectional bulk diffusion in plant storage tissue, the most logical choice is to select as a representative section the chain formed by any linear arrangement of adjoining average unit cells in the macroscopic direction of transfer. The length of this chain would then be determined by the geometry of the tissue under study, which in this case will be restricted to systems approximating to an infinite slab of known thickness. The whole structure is therefore represented by a bundle of cellular 'strings', the behaviour of which is assumed to be identical. This approach is identical to using the Krogh capillary concept to represent the beha-

viour of animal tissues which show structural homogeneity (Krogh, 1930; Reneau *et al.*, 1969; Grabowski, 1974).

Although the description of unidirectional mass transport in storage tissue is greatly simplified by dealing thus with one cellular string to represent the tissue behaviour, the transfer within that 'column' remains, at the cellular level, multidimensional, as the migrating molecules have to travel through a linear arrangement of spheres. The phenomenon is also complicated by the interactive role played by the cells in controlling transmembrane transport. The complexity of the problem can, however, be substantially reduced if the system is linearized by geometrically transposing each constituent average unit cell to its cylindrical equivalent (which will be referred to as 'equivalent cylindrical unit cell', abbreviated to ECUC hereafter). The process consists of generating coaxial cylinders which represent each part of the average units. To illustrate the above process, Fig. 3 shows one of the average unit cells composing the selected representative cellular string. The first dimension to be established is the length of the coaxial cylinders which comprise the ECUC, namely, the cellular cylinder representing the cellular volume, the interstitium cylinder representing the interstitial volume and the buffer cylinder which will be introduced below.

To simulate possible shrinkage of the structure and in accord with the decision to restrict the present study to the analysis of mass transport in an infinite slab, the length of the ECUC will be related to the total volume of the average unit cell, such that changes at that level for any

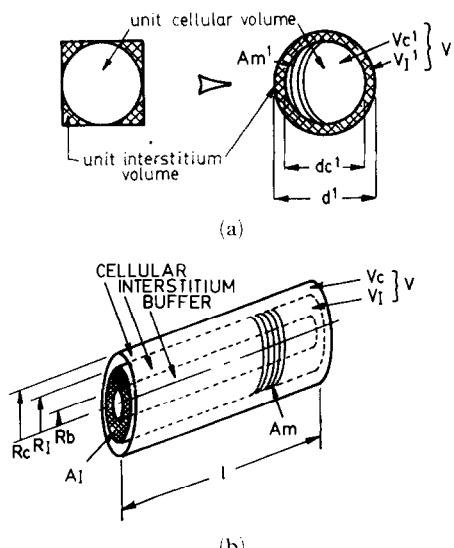


Fig. 3. The average unit cell (a) and the equivalent cylindrical unit cell (b).

unit comprising the column will be represented by an equivalent decrease (increase) in the length of its corresponding cylindrical cell.

Let l , the length of the ECUC, be defined as the diameter, d^1 , of a sphere representing the total volume of the average unit cell, that is, the cellular plus the interstitium volume, times the square root of the interstitium geometrical tortuosity, τ_i , defined as the ratio of the actual distance that a migrating molecule has to travel on average in the interstitium, as part of a macroscopic unidirectional flow, compared with the distance covered normal to the surface, i.e.

$$l = d^1 / \tau_i \quad (5)$$

It should be noted that τ_i does not reflect the microstructural properties of the interstitium complex. It is only an approximation to the length of the path to be negotiated by a molecule diffusing in an empty space around a typical cell, i.e. from one side to the other in a global unidirectional flow, which, for the cubic arrangement introduced previously, leads to a ratio of $\pi/2$ (τ_i is obviously dependent on the arrangement selected to describe the cellular structure). It is also noteworthy that the square root of the tortuosity is a necessary outcome of the requirements of the geometrical similarity in dimensional analysis (Loncin & Merson, 1979).

The radii of the coaxial cylinders representing the components of the average unit cell are calculated in accordance with the following specifications:

(1) Radius of the interstitium cylinder. As the average unit cell is spherical, the surface of exchange between interstitium and cellular volume, that is, the area of the plasmalemma, A_m^1 (excluding the proportion of total cell membrane occupied by plasmodesmata, α_p) is given by

$$A_m^1 = (1 - \alpha_p) \pi (d_c^1)^2 \quad (6)$$

where d_c^1 is the diameter of the sphere representing the unit cellular volume. As, at any time, all the ECUC dimensions are dependent on geometrical properties which change as osmosis progresses, the radius of the interstitium cylinder, R_i , must be found from

$$A_m^1 \equiv A_m = 2\pi R_i l \quad (7)$$

i.e. R_i is calculated to make the area of the interface cellular-interstitium cylinders, A_m , identical to the area of the plasmalemma (see Fig. 3). For convenience, the notation introduced to characterize the properties of the average unit cell will be adopted to describe identical properties of the ECUC. The superscript '1' will, however, be dropped.

(2) Radius of the cellular cylinder. As the cellular cylinder represents the cellular volume of the average unit cell, V_c^l , its radius, R_c , must be such that, at any time,

$$V_c^l \equiv V_c = \pi l(R_c^2 - R_b^2) \quad (8)$$

(3) Radius of the buffer cylinder. The buffer cylinder is introduced as a geometrical artifice to ensure that, as l , R_b and R_c are now fixed, the volume of the interstitium cylinder, V_l , is identical to its average unit cell equivalent, V_l^l , that is

$$V_l^l \equiv V_l = \pi l(R_l^2 - R_b^2) \quad (9)$$

As can be seen, the above design not only transposes the spherical average unit cell into another geometry but it also inverts the whole system. This arrangement and cell shape has the main advantage of linearizing the interstitial diffusion path at the level of each cell. It is therefore possible to simulate the establishment of concentration gradients 'around' any given cell as apoplastic transport processes are now described by transfer in the linearized environment of the interstitium cylinder, with one end representing the 'front' of the average unit cell and the other the diametrically opposite side.

The transposition also satisfies the constraint of constant plasmalemma surface area for a cell undergoing volume changes. As can be seen in Fig. 3, the coaxial arrangement of the ECUC, with the cellular volume being represented by the outer cylinder and the buffer cylinder by the inner one, allows complete freedom in modifying the cellular and/or interstitium volume without altering R_l , as these changes can be implemented by varying the radius of the cellular cylinder, R_c , and/or the radius of the buffer cylinder, R_b (see eqns (8) and (9)).

Another interesting feature of the proposed ECUC is that the ratio of the interstitium cross-sectional area, A_l , to the total cross-sectional area of the ECUC, A , is equal to the void fraction of the average unit cell, ε^l , that is

$$\varepsilon^l = \pi(R_l^2 - R_b^2)/\pi(R_c^2 - R_b^2) = A_l/A \quad (10)$$

which in turn can be shown to be related to the average fractional free cross-section of the tissue (Sherwood *et al.*, 1975).

Equation (10) is particularly important for the derivation of the continuity equations depicting the mass transport in the proposed system (see below). It shows that the dimension of the interstitium cylinder accounts formally for the fraction of the total tissue surface available for apoplastic transport.

The hypothetical parenchymatous tissue

From the redefined cellular unit, a hypothetical equivalent parenchymatous tissue can be generated by replacing each average unit cell by a cylindrical equivalent. The original real structure is now represented by a fascicular arrangement of equivalent cylindrical unit cells.

This design appears particularly appropriate for modelling unidirectional mass transfer in storage tissue because, as can be seen in Fig. 4, the interconnected cylindrical cells provide an extracellular continuum representing the apoplast of the actual tissue, but still allow the cells to remain independent units which are interconnected by plasmodesmata.

MATHEMATICAL ANALYSIS OF MASS TRANSFER PHENOMENA IN THE MODEL TISSUE

Two basic processes will be described: the cell interactions, represented by relationships derived from irreversible thermodynamics, and bulk unidirectional mass transport, represented by relationships associated with the extended form of the second-order Fick equation. The deviation will be covered briefly here, (a detailed treatment was given by Toupin (1986)). For this purpose the j th member of the column of ECUCs selected as a representative portion of the hypothetical parenchymatous tissue will be considered (see Fig. 4).

Exchanges across membranes

The description of mass transfer across the plasmalemma (transmembrane transport) and across the plasmodesmata (symplastic transport) will be considered using irreversible thermodynamics by which phenomenological equations can be used to describe such processes (Toupin, 1986); namely, for transport across the plasmalemma of species i ,

$$J_{i_m} = - \sum_k L_{k i_m} \Delta \mu_{k_m}; \quad i, k = 1, \dots, m \quad (11)$$

and, for symplastic transport,

$$J_{i_p} = - \sum_k L_{k i_p} \Delta \mu_{k_p}; \quad i, k = 1, \dots, m \quad (12)$$

where J_{i_m} and J_{i_p} are, respectively, transmembrane and symplastic molar fluxes (relative to the cell interior) of species i , $L_{k i_m}$ and $L_{k i_p}$ are macroscopic phenomenological coefficients describing the permeability

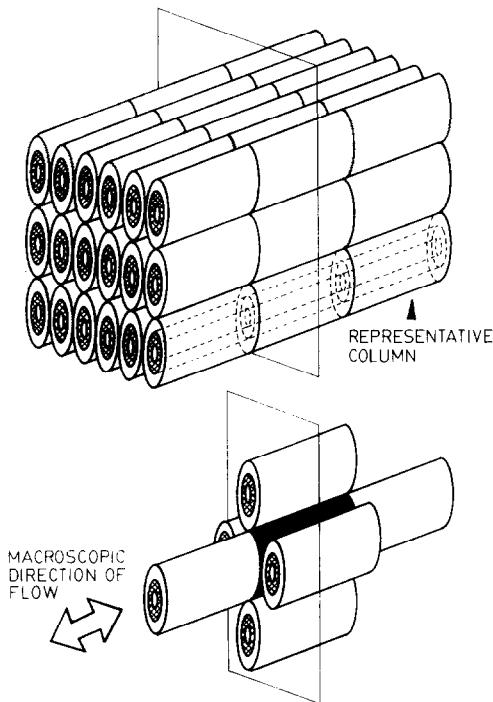


Fig. 4. The hypothetical equivalent parenchymatous tissue.

characteristics of the membranes considered and $\Delta\mu_{k_m}$ and $\Delta\mu_{k_p}$ are differences in chemical potential of species k across those membranes. The symbol Δ indicates a difference between an intracellular quantity and an extracellular quantity, i.e. $\Delta = x^{\text{in}} - x^{\text{ex}}$. The term extracellular in this context encompasses not only the interstitium environment but also the cellular volume of a neighbouring cell. The summations are performed for m diffusible species (permeating and non-permeating) present in the system once the tissue is immersed in the osmotic bath.

The thermodynamic forces are given, by definition, for a plant cell environment (restricting the analysis to the transport of nonelectrolytes) by (Nobel, 1983)

$$\Delta\mu_i = RT\Delta \ln a_i + \tilde{v}_i \Delta P \quad (13)$$

where R is the universal gas constant, T is the absolute temperature of the system, a_i is the activity of species i , \tilde{v}_i is its partial molar volume and P is the hydrostatic pressure (in excess of atmospheric pressure) in the phase considered.

Because of the difficulty of determining the value of a_i in complex multicomponent systems, the first term of eqn (13) will be represented as

follows (Toupin, 1986). For the solvent water ($i = 1$):

$$RT\Delta \ln a_1 \approx -RT\tilde{v}_1 \Sigma_i (C_i^{\text{in}} - C_i^{\text{ex}}); \quad i = 2, \dots, m \quad (14)$$

and for all other species ($i = 2, \dots, m$),

$$RT\Delta \ln a_i \approx RT(C_i^{\text{in}} - C_i^{\text{ex}})/\bar{C}_i \quad (15)$$

where C_i is the effective molar concentration of species i in the phase considered and \bar{C}_i is the arithmetic average concentration of species i across the membranes for which a difference in chemical potential is computed.

The difference in hydrostatic pressure (the second term of eqn (13)) is evaluated in relation to the change of cellular volume, through a measure of the reversible elastic properties of the cell walls in the form of an empirical modulus, ξ , that is (Dainty, 1976; Nobel, 1983)

$$dP_c = \xi dV_c / V_c \quad (16)$$

where P_c is the hydrostatic pressure in the cellular volume above atmospheric pressure.

As discussed by Dainty (1976), the empirical modulus, ξ , is in general strongly affected by the internal pressure. Hence, assuming a relationship of the form (Nilsson *et al.*, 1958),

$$\xi = \beta_1 P_c + \beta_2 \quad (17)$$

where β_1 is defined as the variation of ξ with respect to P_c , that is, $d\xi/dP_c$ and β_2 is the value of the modulus at incipient plasmolysis (i.e. when P_c reaches 0); and integrating eqn (16) with respect to the conditions at the reference state (full turgor), P_c becomes the following function of the cellular volume

$$P_c = [P_{c_0} + (\beta_2/\beta_1)](V_c/V_{c_0})^{\beta_1} - (\beta_2/\beta_1) \quad (18)$$

If, on the other hand, it is assumed that ξ is not a function of P_c , integration of eqn (16) yields

$$P_c = \xi \ln(V_c/V_{c_0}) + P_{c_0} \quad (19)$$

where P_{c_0} is given by (Levin *et al.*, 1979)

$$P_{c_0} = RT\Sigma_k (C_{k_0}^{\text{in}} - C_{k_0}^{\text{ex}}) \quad (20)$$

where the summation is performed for all the non-permeating solutes present in the intracellular and interstitial solutions at full turgor.

The difference in hydrostatic pressure, ΔP , is therefore given by

$$\Delta P = P_c - P^{\text{ex}} \quad (21)$$

where P^{ex} can represent the hydrostatic pressure (in excess of the atmospheric pressure) in the interstitium or in the cellular volume of a neighbouring cell.

Finally, the macroscopic phenomenological coefficients, L_{ik_m} and L_{ik_p} , are assumed to vary with concentration (Toupin, 1986) as

$$L_{ii_*} = p_{ii_*} \bar{C}_{i_*}; \quad i = k \quad (22)$$

and

$$L_{ik_*} = p_{ik_*} / (\bar{C}_{i_*} \bar{C}_{k_*}); \quad i \neq k \quad (23)$$

where the subscript “*” indicates that the above relationships apply for describing plasmalemma ($* = m$) as well as plasmodesmata ($* = p$) permeabilities. $\bar{C}_{i(k)_*}$ is, as before, the average concentration of species $i(k)$ across the membrane considered and p_{ii_*} and p_{ik_*} are macroscopic permeability coefficients, assumed to be concentration independent.

Interstitium equations of continuity

In developing the equations describing the conditions associated with bulk unidirectional mass transport in the interstitium of the j th ECUC of the representative column, the following assumptions will be used:

(1) Only axial diffusion occurs in the interstitium cylinder. Radial diffusion is considered negligible.

(2) The interstitial volume is allowed to vary as well as the cross-sectional area for transfer. However, as the cells are treated as whole entities in their response to volume changes (see below), any transfer of cellular volume to interstitial volume is assumed to be spread equally over the latter volume, which therefore compels recalculation of dimensions to be made over the entire cell. This means that the radii of the cylinders composing the ECUC, its length and its other geometrical characteristics will be functions of time and distance in the column, but on a cell-to-cell basis.

(3) The macroscopic permeability coefficients (p_{ii_m} and p_{ik_m}) describing the properties of the plasmalemma are constant in time and position along the interstitium and are assumed identical for all the cells.

(4) The description is restricted to non-electrolyte transport. There are therefore no Donnan exchange or other form of ionic interactions present in the system.

(5) The extracellular solution is, at all times, sufficiently dilute so that the partial molar volumes of the diffusing species remain constant.

With the above assumptions, considering an element of cross-sectional area A_1 and thickness δl (see Fig. 3), the convective diffusion equations in the interstitium become (for the diffusing species i):

$$\frac{\partial C_i}{\partial \theta} = \frac{\partial}{\partial z} \left[D_i \frac{\partial C_i}{\partial z} \right] - \left[v^* \frac{\partial C_i}{\partial z} + C_i \frac{\partial v^*}{\partial z} \right] - \left[\frac{C_{i_l}}{V_1} \frac{\partial V_1}{\partial \theta} \right] - \left[\frac{A_m}{V_1} J_{i_m} \right] \quad (24)$$

where C_{i_l} is the local concentration of species i in the interstitium, θ is the time variable and z the macroscopic direction of transfer. v^* is the local value of the volume average velocity, defined as (Bird *et al.*, 1960)

$$v^* = \sum_i \tilde{v}_i N_{i_l}; \quad i = 1, \dots, m \quad (25)$$

where N_{i_l} is the molar flux of species i with respect to a fixed frame of reference chosen as the centre of the infinite slab. D_i is the pseudo-binary diffusivity of species i (Bird *et al.*, 1960) corrected to take into account the hindrance effect of the interstitium microstructure, that is,

$$D_i = \Psi_1 D_{i_l}; \quad 0 \leq \Psi_1 \leq 1 \quad (26)$$

where D_{i_l} is assumed identical to the binary diffusivity of species i in water and Ψ_1 is called the effective interstitium diffusibility, and is assumed to be the following function of the interstitium characteristics:

$$\Psi_1 = [(\phi_s \Psi_s) + (\phi_w \Psi_w)]/\epsilon \quad (27)$$

where ϕ_s and ϕ_w are, respectively, the intercellular free space and cell wall volume fractions of the ECUC and ϵ is the ECUC void fraction. Ψ_w is the effective diffusibility of the cell wall microstructure and Ψ_s is that of the intercellular free space volume, which, for structural considerations, will take the value of 1, i.e. its resistance to transfer is negligible.

As can be seen, Ψ_1 is a function not only of the intrinsic diffusibility of each part of the interstitium but also of the fraction occupied by each component. It is therefore possible to simulate the changes in resistance to diffusion which are likely to occur in the different stages of osmotic dehydration (discussed below) where, for example, there might be an increase in intercellular free space volume due to the retraction of the plasmalemma from the cell wall. It should be noted that it is assumed that the cell wall structure is sufficiently rigid to ensure that its total volume remains constant, even though the whole tissue might shrink. This assumption is therefore equivalent to supposing that any volume gain or loss of the whole structure is attributable to changes in the intercellular free space and cellular volume.

From eqn (24), it can be seen that the variation with time of the concentration of species i in the interstitium is explicitly a function of four processes: transport by diffusional forces (first term, obtained after introducing Fick's law in the derivation), transport by convective forces (second term), 'concentration' or 'dilution' due to interstitial volume changes (third term), and production or depletion due to exchanges across the plasmalemma (transmembrane transport, last term).

The equation relating the fluxes of all the components present in the system is developed by considering the volume of the interstitium cylinder. In accordance with the assumption that the partial molar volumes of the diffusing species are constant (assumption (5)),

$$\frac{\partial v^*}{\partial z} = - \left[\frac{A_m}{V_l} \sum_i \tilde{v}_i J_{i_m} + \frac{1}{V_l} \frac{\partial V_l}{\partial \theta} \right] \quad (28)$$

$$i = 1, \dots, m$$

Equations (24) and (28) are, by virtue of the governing assumptions and the nature of the interstitial volume, point functions in time and distance along the interstitium. However, as the geometrical properties of the ECUCs composing the column vary from cell to cell in response to the volumetric rearrangements, these equations are specific to the interstitium of the cell under consideration. Proper boundary conditions are therefore required to link the individual descriptions of interstitial mass transfer, to lead to an overall picture of the transport in the entire apoplastic continuum.

Intracellular equations of change

In the derivation of the equations describing the volume and concentration changes in the intracellular volume, the following assumptions will be considered:

- (1) Perfect mixing of the intracellular phase.
- (2) The plasmalemma surface area, A_m , is allowed to vary, as is the total symplastic area of transfer, A_p , as both are linked by definition (see eqn (6)) through the factor α_p , leading to

$$A_p = [\alpha_p / (1 - \alpha_p)] A_m \quad (29)$$

- (3) The macroscopic permeability coefficients (p_{ii_p} and p_{ik_p}) describing the properties of the plasmodesmata are constant in time and are assumed constant for all the cells.

Hence, referring to Fig. 3, for the j th cellular volume considered as a whole, the following is the variation with time of the intracellular concen-

tration C_{i_c} of species i :

$$\frac{dC_{i_c}}{d\theta} = \left[\frac{2\pi R_I}{(V_c - V_d)} \int J_{i_m} dz \right] - \left[\frac{C_{i_c}}{(V_c - V_d)} \frac{dV_c}{d\theta} \right] + \left[\frac{A_p^-}{(V_c - V_d)} J_{i_p}^- \right] + \left[\frac{A_p^+}{(V_c - V_d)} J_{i_p}^+ \right] \quad (30)$$

The first term describes the contribution of the transmembrane flux (where the integral is carried out over the entire length of the cell), the second term describes the effect of the cellular volume change on the concentration. The last two terms are introduced to take into account the contribution of symplastic transport from/to the neighbouring cells, which by virtue of the design of the hypothetical tissue are restricted to the ends of the 'downstream' and 'upstream' cells, i.e. the $(j-1)$ th cell (superscript $-$) and $(j+1)$ th cell (superscript $+$) of the representative column. Referring to Fig. 4, it can be seen that all the cellular units in any plane normal to the axis of each column are identical, which precludes symplastic transport in that plane.

V_d is a correction factor, usually referred to as apparent cellular non-osmotically active volume, which is introduced to account for the intrinsic non-ideality and non-diluteness of the intracellular solution (Toupin, 1986). This factor is assumed to be constant with time and to occupy the same proportion of total cellular volume for all the cells. A_p^- and A_p^+ are fractions of total symplastic surface area pertaining to the $(j, j-1)$ th and $(j, j+1)$ th cell interface respectively.

By a treatment similar to that leading to eqn (30), the total volume change of the cellular compartment is derived and (assuming the partial molar volumes to be constant) is given by

$$\frac{dV_c}{d\theta} = \left[2\pi R_I \int \sum_i \tilde{\nu}_i J_{i_m} dz \right] + \left[A_p^- \sum_i \tilde{\nu}_i J_{i_p}^- \right] + \left[A_p^+ \sum_i \tilde{\nu}_i J_{i_p}^+ \right] \quad i = 1, \dots, m \quad (31)$$

where again the contributions of the transmembrane (first term) and symplastic fluxes (second and third terms) to the total volume change are included.

Supplementary equations of change

Geometrical relationships

In the development of the model, geometrical relationships were used to evaluate the equivalent cylindrical unit cell dimensions. The description

of the evolution of these geometrical properties as time passes becomes crucial as variables are intrinsically part of the continuity equations presented previously. These dimensions, by virtue of their nature and of the assumptions adopted here, represent the geometrical characteristics of entire cellular units. They are therefore independent of position within a given ECUC (as in eqns (30) and (31)). The geometrical equations of change then become time derivatives which, for the j th unit cell, are obtained readily by differentiating eqns (5), (7)–(9) and (27) with respect to time.

Structural reorganization during dehydration

Referring to Fig. 5, the following model will be adopted to describe the deformation of a cellular unit during osmotic dehydration. All the rearrangements which the cell experiences during dehydration are assumed to be reversible, i.e. the cell is capable of returning to its initial state if the conditions are reversed. Any unit cell will be allowed to reach three stages of dehydration which are functions of the extent of cellular volume losses,

$$\frac{dV_1}{d\theta} = k \frac{dV_c}{d\theta} \quad (32)$$

and

$$\frac{dV}{d\theta} = (1 + k) \frac{dV_c}{d\theta} \quad (33)$$

where the compliance factor, k , takes the values of 0, -1 and 0, for stages 1, 2 and 3, respectively. The limits of each stage are defined as follows:

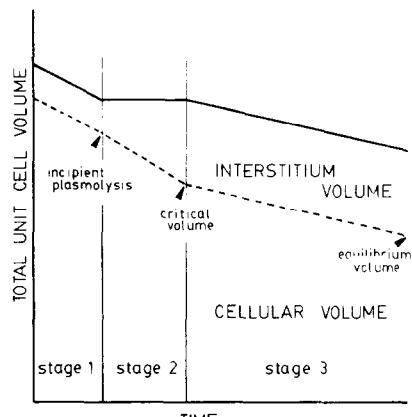


Fig. 5. General behaviour of a typical unit cell undergoing osmotic dehydration. Dehydration stages 1, 2 and 3 are shown.

(1) Stage 1, from full turgor to incipient plasmolysis, i.e. from the maximum volume a typical cell can achieve upon swelling to its volume at which the internal hydrostatic pressure vanishes (which can be determined by solving eqns (18) or (19) for $P_c = 0$). This period describes the loss of turgescence of the tissue.

(2) Stage 2, from incipient plasmolysis to the critical cell volume, i.e. from the point where $P_c = 0$ to the point where the loss of cellular volume is such that the structure starts to collapse. During this stage it is assumed that any loss of cellular volume is directly compensated for by a proportional increase in intercellular free space volume, as the plasmalemma pulls away from its surrounding cell wall (Nobel, 1983).

(3) Stage 3, from the critical cell volume to the equilibrium volume. To account for the shrinkage which is observed in most dehydration processes, the third stage will be considered as a period during which the whole structure collapses due to extreme volume diminution.

The concept of the average unit cell and the ensuing ECUC assumes its importance when the above analysis is extended to the entire tissue. By monitoring the behaviour of each individual cell, it becomes possible to follow the extent of structural reorganization within the tissue, and, therefore, to draw a complete picture of the whole system by 'integrating' the observed individual changes over the total number of constituent units. For example, the change in volume of the tissue will be given by

$$\frac{dV^t}{d\theta} = \sum_j \frac{dV^j}{d\theta}; \quad j = 1, \dots, \#_c^1 \quad (34)$$

where $\#_c^1$ is the total number of ECUCs calculated using eqn (4).

Equations (32) and (33) represent a very simple description of the deformation of the tissue during osmotic dehydration, which can be refined by including mechanical stress analysis and other features relating osmotic changes to momentum transport (McCoy & Boersma, 1984). However, as shown by Suzuki *et al.* (1976) and Lozano *et al.* (1983), the above approximations appear reasonable in the context of osmotic dehydration, in view of the fact that the process stays well within the range of moisture content in which the shrinkage of the tissue can be related directly to the net volume lost by the structure, i.e. the high moisture region (Rotstein & Cornish, 1978c).

The change in area of the plasmalemma and the total symplastic surface are given by

$$\frac{dA_m}{d\theta} = \left(\frac{2A_{m_0}}{3V_{c_0}^{2/3}} \right) V_c^{-1/3} \frac{dV_c}{d\theta} \quad (35)$$

(where a two-thirds power relationship between A_m and V_c (isotropic changes) is assumed) and (see assumption 2)

$$\frac{dA_p}{d\theta} = \frac{\alpha_p}{(1 - \alpha_p)} \frac{dA_m}{d\theta} \quad (36)$$

Equations (35) and (36) will be used only during stage 1. Constancy of these surface areas will be assumed during the two other periods (Morris *et al.*, 1986).

Initial and boundary conditions

Initial conditions

It will be assumed that initially the tissue is at full turgor, that is, it has been equilibrated with pure water. An average unit cell can then be generated from the analysis of the geometrical characteristics of the actual tissue in that state. This presupposes that initially all the constituent cells are identical, that is, on average their dimensions and their contents are equal, as are the elastic and permeability properties of their walls and membranes. Following the approach described earlier, an equivalent cylindrical unit cell is assumed, based on the initial properties of the average unit cell, and the number of ECUCs in the representative column, $\#_c$, is then

$$\#_c = \text{int}[(T_0/d_0^1) + 1] \quad (37)$$

where T_0 is a reference thickness, taken as half the corrected thickness of the tissue (to take into account the percentage of cut cells on the surfaces). It is noted that $\#_c$ is taken as the nearest integer (signified by 'int') greater than or equal to the calculated value, as the model assumes that the cells are physically sound throughout the tissue. The number of columns in the tissue must therefore be such that

$$\#_{\text{col}}^{-1} = \#_c^{-1}/\#_c = (V_0^1/V_0^1)/\#_c \quad (38)$$

Boundary conditions

(1) Conditions at the surface. At any time, the convective mass transfer at the surface (signified by ' $|_{\text{surf}}$ ') of the tissue will be given by (Geankoplis, 1978)

$$N_{i_l}|_{\text{surf}} = K_i(C_{i_l}|_{\text{surf}} - C_{i_l}|_{\text{bath}}) \quad (39)$$

$$i = 2, \dots, m$$

where K_i is the pseudo-binary mass transfer coefficient of the i th solute at the surface and $C_i|_{\text{bath}}$ is the bath concentration of that species (assumed to remain constant).

(2) Conditions at the centre. Because of the requirement of symmetry, the conditions at the centre are

$$\left. \frac{\partial C_i}{\partial z} \right|_{\text{cent}} = 0; \quad i = 2, \dots, m \quad (40)$$

and

$$\left. J_{i_p}^+ \right|_{\text{cent}} = 0; \quad i = 1, \dots, m \quad (41)$$

as well as

$$\left. \frac{\partial v^*}{\partial z} \right|_{\text{cent}} = 0 \text{ and } \left. v^* \right|_{\text{cent}} = 0 \quad (42)$$

(3) Conditions at the interface separating two adjoining cells. As stated previously, the description of the behaviour of the representative column is approached on a cell-to-cell basis. The major consequence of such treatment is that it necessarily creates discontinuities at the interface between two adjoining cells since the two neighbouring units do not behave identically. The interstitium continuity equations (eqns (24) and (28)) are consequently not valid at the interface because of the different cell properties on the two sides.

Thus, assuming that, at any interface, the interstitial concentrations on both sides are the same for all species as well as the density of the interstitial solution, for convective transfer

$$(A_1^j v^{*j})|_{\text{int}} = (A_1^{j+1} v^{*j+1})|_{\text{int}} \quad (43)$$

and for diffusive transfer

$$\left. \left(A_1^j D_1^j \frac{\partial C_1^j}{\partial z} \right) \right|_{\text{int}} = \left. \left(A_1^{j+1} D_1^{j+1} \frac{\partial C_1^{j+1}}{\partial z} \right) \right|_{\text{int}} \\ i = 2, \dots, m \quad (44)$$

where the superscripts j and $j+1$ refer to the j th and $(j+1)$ th cells, respectively.

CONCLUSION

The complexity of modelling mass transfer in plant storage tissues has been considerably reduced by creating a geometrical equivalent of these biological structures. Instead of a complicated tridimensional microscopic process, mass transfer is now conveniently handled unidimensionally. Even so, the model maintains its predictive potential, as it simulates basically all the main phenomena present in the actual system.

The main advantage of the proposed equivalent structure is that it allows each cell to experience the presence of concentration gradients in the interstitial solution all along its surface of exchange. At this level, equations derived from irreversible thermodynamics are used to take into account the selective nature of the plasmalemma with regard to transport of material across it. This approach, which is used also for symplastic transport, results in a more accurate picture of mass transfer in these complex systems as it permits quantification of the resistances of these barriers to permeation.

The second part of this communication will present results of simulations carried out to test the model.

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