Leaf hydraulics I: Scaling transport properties from single cells to tissues

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HIGHLIGHTS
- We describe the transport of water through plant cells as a poroelastic medium.
- We show that an approximate theory with the form of the heat equation has an error less than 12%.
- Local chemical equilibrium between protoplasts, cell walls, and adjacent air spaces is sufficient for modeling as a composite.
- Aquaporin mediated cell-to-cell flow dominates isothermal water transport.
- Importance of internal vapor transport for transpiration depends on the temperature gradient.

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ABSTRACT
In leaf tissues, water may move through the symplast or apoplast as a liquid, or through the airspace as vapor, but the dominant path remains in dispute. This is due, in part, to a lack of models that describe these three pathways in terms of experimental variables. We show that, in plant water relations theory, the use of a hydraulic capacity in a manner analogous to a thermal capacity, though it ignores mechanical interactions between cells, is consistent with a special case of the more general continuum mechanical theory of linear poroelasticity. The resulting heat equation form affords a great deal of analytical simplicity at a minimal cost: we estimate an expected error of less than 12%, compared to the full set of equations governing linear poroelastic behavior. We next consider the case for local equilibrium between protoplasts, their cell walls, and adjacent air spaces during isothermal hydration transients to determine how accurately simple volume averaging of material properties (a 'composite' model) describes the hydraulic properties of leaf tissue. Based on typical hydraulic parameters for individual cells, we find that a composite description for tissues composed of thin walled cells with air spaces of similar size to the cells, as in photosynthetic tissues, is a reasonable preliminary assumption. We also expect isothermal transport in such cells to be dominated by the aquaporin-mediated cell-to-cell path. In the non-isothermal case, information on the magnitude of the thermal gradients is required to assess the dominant phase of water transport, liquid or vapor.

1. Introduction
As stomata open to allow an influx of CO₂, the resulting efflux of water vapor must be balanced by the movement of water molecules through the leaf. As a result, apparent leaf hydraulic efficiency (an observed flux divided by an observed water potential difference, a nominal 'conductance') with which leaves transport water correlates with maximum stomatal conductances over a wide range of plants (Boyce et al., 2009; Brodribb et al., 2007). Nevertheless, we lack a clear understanding of the physical bases for the observed differences between leaves in the hydraulic efficiency with which water is delivered to the stomata. Uncertainties about whether the flow path outside the xylem is predominantly apoplastic or symplastic, as well as the relative importance of liquid versus vapor transport within the leaf interior, continue to cloud the question of what determines the maximum transpiration rate observed for a given leaf.

Each of the three different pathways have been presumed by different authors to dominate water transport in well hydrated leaves: the aquaporin mediated cross-membrane flow path (Cochard et al., 2007; Scoffoni et al., 2008), the apoplastic flow path (Brodribb et al., 2007, 2010), and the diffusive path of vapor through the air space...
The lack of consensus regarding the path of transpiration once outside the xylem derives from the inability of current experimental techniques to resolve the individual transport properties of the cell walls, protoplasts, and air spaces within a leaf, or even to measure the actual water potential gradients driving the flux.

One strategy that addresses the latter limitation is to characterize the hydraulic properties of the tissue under non-transpiring conditions, and then, given the known material properties of air, model the competition between liquid and vapor transport within the leaf in satisfying a known transpirational flux. Isothermal transient hydration experiments, which measure the hydration time required for a leaf to transition between two water contents associated with two equilibrium potential states (Brodribb and Holbrook, 2003; Boyer, 1968), can provide the required estimates of leaf tissue hydraulic properties, albeit averaged over the whole leaf. A model of leaf tissue as a composite of protoplasts, cell walls, and air spaces is then needed to parse the tissue hydraulic properties providing a description of the bulk behavior equal to that obtained by accounting for transport in each domain separately.

2. Plant tissues as poroelastic media

As far as we are aware, Philip (1958b) was the first to analyze flow through a file of plant cells, in a model later extended by Molz and Ikenberry (1974) to make explicit the contribution from flow in the wall space. As these derivations were somewhat ad hoc, the limitations of the theory were not obvious, although Philip did provide some guidance discussed further below. To better understand the limits of this theory, we begin by reconsidering the transport of an incompressible solvent such as water through a porous and elastic medium, such as an aggregate of plant cells, from the perspective of continuum mechanics. Such a theory was derived by Biot (1941), and is well-described in full by Yoon et al. (2010) and Doi (2009); here we recapitulate some steps to illuminate the limits of Philip’s theory in particular, and the physical assumptions latent in the extension of plant cell water relations theory to plant tissues (Table 1).

Given that the physical dimensions of a water absorbing medium change as it swells, as measured in standard laboratory coordinates, it is convenient to adopt a material coordinate system (Gandar, 1983). We label particles $x = (x_1, x_2, x_3)$ according to their position in a reference configuration, and study a material volume phase, we consider the contribution to hydraulic conductivity and capacity of the apoplast (cell wall space) and symplast (protoplast space) separately. We then use a mixture of mathematical analysis and numerical simulation to find the range of component parameters over which the simple idea of volume averaged material properties provides a description of the bulk behavior equal to that obtained by accounting for transport in each domain separately.

Table 1: Symbol definitions.

<table>
<thead>
<tr>
<th>Quantity</th>
<th>Value (25°C)</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area $A$</td>
<td>–</td>
<td>m$^2$</td>
</tr>
<tr>
<td>Volume $V$</td>
<td>–</td>
<td>m$^3$</td>
</tr>
<tr>
<td>Shear modulus $G$</td>
<td>–</td>
<td>Pa</td>
</tr>
<tr>
<td>Volumetric modulus $K$</td>
<td>–</td>
<td>Pa</td>
</tr>
<tr>
<td>Bulk modulus, cell $κ$</td>
<td>–</td>
<td>Pa</td>
</tr>
<tr>
<td>Water content $C$</td>
<td>–</td>
<td>mol m$^{-3}$</td>
</tr>
<tr>
<td>Molecular flux $J$</td>
<td>–</td>
<td>mol m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>Water potential $ψ$</td>
<td>–</td>
<td>Pa</td>
</tr>
<tr>
<td>Chemical potential $μ$</td>
<td>–</td>
<td>J mol$^{-1}$</td>
</tr>
<tr>
<td>Darcy permeability $p$</td>
<td>–</td>
<td>m$^2$</td>
</tr>
<tr>
<td>Porous elasticity $s$</td>
<td>–</td>
<td>m$^2$ s$^{-1}$</td>
</tr>
<tr>
<td>Cell permeability $L_p$</td>
<td>–</td>
<td>m Pa$^{-1}$ s$^{-1}$</td>
</tr>
<tr>
<td>Membrane permeability $P_m$</td>
<td>–</td>
<td>m$^2$ s$^{-1}$ Pa$^{-1}$</td>
</tr>
<tr>
<td>Hydraulic capacity $c$</td>
<td>–</td>
<td>mol m$^{-3}$ Pa$^{-1}$</td>
</tr>
<tr>
<td>Hydraulic conductivity $k$</td>
<td>–</td>
<td>mol m$^{-1}$ Pa$^{-1}$ s$^{-1}$</td>
</tr>
<tr>
<td>Thermal conductivity $k'$</td>
<td>–</td>
<td>J m$^{-1}$ K$^{-1}$ s$^{-1}$</td>
</tr>
<tr>
<td>Kelvin temperature $θ$</td>
<td>–</td>
<td>K</td>
</tr>
<tr>
<td>Density of water $ρ_w$</td>
<td>9.97 $\times$ 10$^3$</td>
<td>kg m$^{-3}$</td>
</tr>
<tr>
<td>Molar volume of water $τ$</td>
<td>1.807 $\times$ 10$^{-5}$</td>
<td>m$^3$ mol$^{-1}$</td>
</tr>
<tr>
<td>Diffusivity, water in air $D_w$</td>
<td>2.5 $\times$ 10$^{-5}$</td>
<td>m$^2$ s$^{-1}$</td>
</tr>
<tr>
<td>Viscosity of water $η$</td>
<td>8.9 $\times$ 10$^{-4}$</td>
<td>kg m$^{-1}$ s$^{-1}$</td>
</tr>
<tr>
<td>Formula weight of water $f_w$</td>
<td>1.8015 $\times$ 10$^{-2}$</td>
<td>kg mol$^{-1}$</td>
</tr>
<tr>
<td>Heat of vaporization $J_w$</td>
<td>44 $\times$ 10$^3$</td>
<td>J mol$^{-1}$</td>
</tr>
<tr>
<td>Gas constant $R$</td>
<td>8.3145</td>
<td>m$^3$ Pa mol$^{-1}$ K$^{-1}$</td>
</tr>
</tbody>
</table>

Dimensionless variables

| Potential $ψ$ | Apoplast | a |
| Time $T$ | Symplast | s |
| Poisson’s ratio $ν$ | Cell | c |
| Transverse strain $ζ$ | Water, liquid | f |
| Area fraction $A$ | Water vapor | $ρ$ |
| Volume fraction $ν$ | Initial state | $o$ |
| Mole fraction $χ$ | Final state | $f$ |
| Tortuosity $ξ$ | Equilibrium | eq |
element \(dV = dx_1 dx_2 dx_3\) that tracks a constant amount of dry matter, even as the volume itself shrinks or swells with changing water content. In this conception, an individual plant cell, taken as approximately cubic, becomes an individual volume element. Conservation of molecules requires that the change in the concentration of water molecules \(C\) in a material volume be equal to the net flux of water into the volume, or

\[
\frac{\partial C(x, t)}{\partial t} = -V \cdot \mathbf{J}(x, t). 
\]  

(1)

The Darcy flux of water molecules in response to a gradient in chemical potential, assuming homogenous and isotropic material properties, is given by,

\[
\mathbf{J} = -\frac{p}{\eta} \nabla \mu(x, t),
\]  

(2)

where \(p\) is the Darcy permeability with units of \(m^2\), and in the context of plant cells, the flux is in relation to the cellular membranes and walls that are themselves stationary in the material coordinate frame. Eqs. (1) and (2) may be combined,

\[
\frac{\partial C(x, t)}{\partial t} = -\frac{p}{\eta V} \nabla \cdot \mathbf{J}(x, t).
\]  

(3)

We can get (3) into a form more familiar to plant physiologists by defining a hydraulic conductivity \(k\), and recalling the definition of water potential \(\psi\), to arrive at,

\[
\frac{\partial C(x, t)}{\partial t} = k \nabla^2 \psi(x, t), \quad k = \frac{p}{\eta V}, \quad \psi = \frac{\mu}{V}
\]  

(4)

The steps to this point have been consistent with theory of poroelasticity, as derived from the perspective of thermodynamics and continuum mechanics (Biot, 1941; Yoon et al., 2010). In addition, for small changes in volume, as typically occur in rehydration experiments in tissues above the turgor loss point, we may neglect the difference between material and laboratory coordinates (Hong et al., 2008a). However, we have not specified the relationship between \(C\) and \(\psi\), and (4) is still a three dimensional equation, relating a volume change to flow over surfaces normal to \(x, y, z\). The next step in deriving the equations is to consider the balance of mechanical forces in the tissue and the deformation of the 'dry' frictional scaffold, which leads to a set of relations between applied forces, water content, the chemical potential of the permeating water, and the field of stress in the tissue (Doi, 2009).

Alternatively, turning to Philip (1958b) for the simpler perspective based on cell water relations, we could find the relation between water potential and water content for a 'big cell' model of a tissue as,

\[
\frac{dC}{d\psi} = \frac{1}{W(e + \pi)} = c,
\]  

(5)

where \(e\) is the bulk or volumetric modulus of a representative cell, and \(\pi\) is the osmotic potential in the reference state. We can assign this expression the symbol \(c\), and give it a name, the hydraulic capacity of the cells. The form then adopted by Philip (1958b) for the propagation of turgor in a file of plant cells, in response to a change in source water potential on the boundary normal to \(x\) is,

\[
\frac{dC(x, t)}{dt} = k \frac{\partial \psi(x, t)}{\partial x}, \quad k = \frac{L_{\psi} l}{2V}
\]  

(6)

Comparison with (3) shows that (6) appears to be a one-dimensional version of the poroelastic equation, with \(k\) now defined in terms of the cell length \(l\), and cell permeability \(L_{\psi}\) for the case of cell-to-cell flow considered by Philip. Here \(k\) arises from 'smearing' the permeability of two membrane and wall sections \((L_{\psi}/2)\) over the length measured from the center of one cell to the next \((l)\) to define a continuum conductivity; dividing by the molar volume simply converts the flux from a volumetric to a molecular basis. The one dimensional form follows from the idea that as long as the principal flux is in \(x\), there is no between-cell flow in \(y, z\), though the cells swell in three dimensions. With these ideas, (6) and (5) can then be combined to find a single equation governing \(\psi\),

\[
\frac{dC}{dt} = \frac{dC}{d\mu} \frac{d\mu}{d\psi} \frac{d\psi}{dt} = k \frac{\partial^2 \psi}{\partial x^2},
\]  

(7)

\[
\frac{d\psi}{dt} = \frac{k}{c} \frac{\partial^2 \psi}{\partial x^2}, \quad k = \frac{K}{c}.
\]  

(8)

This definition of \(c\) has lead us to an equation, (8), which has the form of the heat equation, with the poroelastic diffusivity \(k\) analogous to a thermal diffusivity in that it arises from the ratio of a conductivity to a local storage capacity. To avoid confusion with molecular diffusion, we will refer to the transport of water molecules in a poroelastic body due to potential gradients as permeation (Hong et al., 2008b). The great advantage of the heat equation form is that given appropriate boundary conditions and initial conditions the solutions are well known (Carslaw and Jaeger, 1959).

However, it should be noted that Philip’s definition of \(c\), (5), defines the relationship between potential and water content in terms of equilibrium swelling measurements, and yet we are asking this relationship to hold during transitions between equilibrium states. Philip (1958b) was aware of the problem, noting that his use of an equilibrium relationship between water content and potential neglected mechanical (elastic) interactions between cells during the transient. Indeed, Philip cautioned that rigorous justification of (8) might require that the middle lamella does not support stress, such that each cell wall is mechanically independent of its neighbor. For leaf mesophyll cells bordered by extensive air space, cell-to-cell mechanical coupling may indeed be weak and one might justify (8) simply on those grounds. However, this argument is unlikely to apply in epidermal tissues, or the closely packed cells around the vasculature. In between these two limits of purely elastic mechanical interactions and no mechanical interactions between cells lies the possibility of viscous interactions, such that the stresses imposed on a cell by the swelling of its neighbors may be partly relaxed by slippage or ‘creep’ in their relative positions. Here we focus on the simpler limiting cases of a purely elastic linkage (case 1), versus no mechanical linkage between cells (case 2).

In order to ask what happens if the middle lamella does support elastic stress in a non-trivial way (case 1), we have to return to the more rigorous poroelastic theory of continuum mechanics, from which we departed after equation (4). For the sake of simplicity, we again consider small deformations of a linear elastic material, and therefore neglect the difference between laboratory and material coordinates. Poroelastic theory tells us that because of the mechanical coupling between volume elements (cells), stresses induced by swelling can propagate through a tissue ahead of the swelling front, causing a change in the water potential of the unswollen tissue in advance of any change in water content (Hong et al., 2008a; Doi, 2009). To see this, consider that in poroelastic theory the relationship linking the mean normal stress in a body to the water content (related to the sum of the normal strains) and water potential is given by

\[
dC = \frac{1}{3V K} d\sigma_{ik} + \frac{1}{V K} d\psi.
\]  

(9)

Here \(K\) is the volumetric modulus, \(\sigma_{ik}/3\) is the mean normal stress, the mechanical pressure exerted on a volume element (or by analogy a cell) by its neighbors. For a freely (without external
parameter, that the equilibrium swelling behavior is a function of just one parameter, $K$, which plays the same role for tissues as the quantity $\varepsilon + \pi$ does for cells. However, during the transient the field of stress is generally not zero, and the water potential of the permeating fluid is a function not just of the local water content (i.e., volume), but of the local deformation (i.e., shape) as well, as illustrated in Fig. 1 (adapted from Doi, 2009).

To describe the local deformation, the balance of forces that describes the field of stress in $x, y, z$ must be considered in addition to conservation of mass, and the equation governing the evolution of the water potential field can be shown to take the more complex form (Doi, 2009; Yoon et al., 2010)

$$\frac{\partial \psi}{\partial t} + 4G \frac{\partial \zeta}{\partial t} = \frac{3(1-\nu)\pi K}{1+\nu} A \frac{\partial^2 \psi}{\partial x^2}$$

(10)

The second term on the left hand side describes the stress due to the change in the strain in the $y, z$ directions $\zeta$, that accompanies swelling propagating along the $x$ direction, where $G$ is the shear modulus, such that during the transient the overall shape of the block is conserved; note that this conservation of shape is not imposed, but emerges from a balance of forces in the tissue (Doi, 2009). On the RHS, we see that two parameters are necessary to characterize the swelling behavior, both $K$ and Poisson’s ratio $\nu$, the ratio of transverse ($y, z$) strain that accompanies an imposed axial ($x$) strain. For a linear poroelastic body, $G, K, \nu$ are related by

$$G = \frac{3K(1-2\nu)}{2(1+\nu)}$$

(11)

We can now ask under what conditions do we approach Philip's approximation that mechanical coupling between cells is unimportant ($G=0$). From (11) we see that for $G=0$ requires $\nu=0.5$, meaning that a change in the shape of a volume element or cell leads to no overall volume change, i.e., no fluid migration. Hence, for this special value of $\nu=0.5$ water potential is function only of the water content, and not the shape of the volume element or cell (n.b., in poroelastic theory, $\nu$ is an apparent Poisson’s ratio that results from fluid migration; instantaneously, both the fluid and the dry fraction are considered incompressible. For an illustrative physical example of this idea see Yoon et al., 2010). Inserting $\nu=0.5$ into (10) and (11), we find

$$\frac{\partial \psi}{\partial t} = \nabla k \frac{\partial \psi}{\partial x^2}, \quad \frac{\partial C}{\partial \psi}_{eq} = \frac{1}{\pi K} = c.$$  

(12)

For the special case that the water potential of the ‘cells’ is independent of their shape, one dimensional poroelastic flow (1) does indeed collapse to the heat equation form (8), and the local relationship between water content and potential follows the global equilibrium swelling relationship. Although the cells are mechanically coupled, and shape change propagates ahead of volume change during water uptake, there is no effect on the driving force for flow as the cells have no preferred shape. Note that this way of arriving at the heat equation (8) differs from Philip’s approximation that the middle lamella does not support stress.

However, neither Philip’s justification for the heat equation form (no mechanical linkages between cells), nor the assumption of no shape preference for cells that reduces poroelasticity to the heat equation form, are defensible in the literal sense. First, plant cells adhere to one another to form a macroscopic body capable of withstanding gravity; second, plant cells take on a preferred shape based on the orientation of cellulose microfibrils in their walls (Burgert, 2006). What we have gained by finding the relation between the heat equation form and linear poroelastic theory is an analytical basis for evaluating whether the heat equation form still provides a reasonable approximation to the full poroelastic theory in the case that individual cells have a shape preference ($\nu \neq 0.5$) and the middle lamella supports stress. Based on a mathematical analysis of the structure of the solution to (10) at long times by Doi (2009), it can be shown that the dominance of the dominant term of the solution, the ‘longest relaxation time’, on the value of Poisson’s ratio over the expected range of $\nu = 0.1 \rightarrow 0.5$ that seems appropriate for plant tissues (Niklas, 1992) varies by only 12% (Appendix A).

Such a weak effect of $\nu$ on relaxation times has also been suggested for gels based on numerical implementations of linear poroelasticity (Cai et al., 2010). It appears therefore that the heat equation form (8) that follows from $\nu=0.5$ may provide a good approximation for describing the kinetics of changes in tissue water content and potential in plants. Nevertheless, it is unlikely that plant material is ever an ideal isotropic, homogenous linear poroelastic material. Therefore (8) may be best viewed as a leading order approximation, not necessarily realistic in terms of the details of local deformation. In studies of plant water transport, due to methodological constraints (e.g., the metastability of the water in the xylem) material properties such as hydraulic capacitance as well as water potential and volumetric water content are typically averaged over whole organs, such as leaves (Kramer and Boyer, 1995). As long as the whole organ (e.g., 'leaf level') relationship between water potential and water content remains in a linear range (e.g., much of the range above the leaf turgor loss point, Boyer, 1995), we can apply linear poroelastic theory. According to Doi’s (2009) analysis of longest relaxation times, we should then be able to adopt the approximation $\nu=0.5$ and so find the heat equation form (8) with an expected error of at most 12%. It is on these grounds that we will adopt the heat equation form of Philip (1958b) as the basis for the description of leaf tissue hydraulics below.

![Fig. 1. Free swelling of a plane sheet of tissue, from an initial unswollen (white) state to a final swollen (shaded, or blue (online)) state. During the transition the overall shape of the block is conserved, and the unswollen cells in the center must change shape to accommodate the swelling of the outer tissue. To the extent the cells have a preferred shape, the unswollen cells will experience a change in potential that precedes any volume change.](image-url)
3. Liquid flow in the apoplast versus the symplast

3.1. Thin-walled cells

In deriving a hydraulic conductivity for a population of cells, Philip (1958a) assumed the dominance of cell-to-cell (cross-membrane and plasmodesmatal) flow, neglecting the apoplast. However, we need not assume negligible flow in the wall space to model aggregates of cells as an homogenous material characterized by a single overall conductivity. Previous simulations, employing an electrical circuit analogy, have suggested that as long as a cell is near local water potential equilibrium (LE) with its own wall, simple volume averaging of hydraulic conductivity and capacity to define ‘composite’ (apoplastic and symplastic) material properties agrees well with numerical simulations of transient flow along parallel paths Molz (1976) and Molz et al. (1979). In this case, the poroelastic diffusivity becomes,

\[ k_p = \frac{k_2}{C} = \frac{A_k k_a + A_s k_s}{V_s C_s + V_w C_w} \]  

where \( A \) and \( V \) refer to the area and volume fractions of the two paths, and the subscripts \( l, a, s \) refer to the total cellular liquid phase, apoplast and symplast respectively.

The analyses by Molz, conducted prior to the discovery of aquaporins, assumed that cell-to-cell flow in the symplast occurred primarily through plasmodesmata. Yet the greater limitation of these studies is the lack of a framework for generalizing the analysis of whether local equilibrium could be expected beyond the particular parameter values culled from the literature of the day. Here we account for aquaporin-mediated cross-membrane flow, and investigate the errors associated with the composite description in two stages. First, we undertake a scaling analysis to analyze the structure of the coupled transport problem in thin-walled cells to find three non-dimensional groups of parameters that determine the structure of the solution. Next, we consider four cases based on the relative magnitudes of these groups to identify the conditions favoring close coupling of apoplastic and symplastic potential (LE). Based on one of these parameter groupings, we develop an order-of-magnitude criteria for the assumption of local equilibrium. We then use this criteria to guide a numerical analysis of the parameter values for which the composite description converges with the numerical solution to the coupled set of equations for apoplastic and symplastic flow.

We start by defining thin-walled cells as cells with an individual length \( l_w \) much greater than the thickness of their wall, \( w_o \), and expect this geometrical condition, \( l_w \gg w_o \), to describe most of the parenchyma inside a leaf (Essau, 1960). Transport cell-to-cell and through the wall can be written in the form of two diffusion type equations describing the propagation of a change in potential accompanying flow in the two paths, coupled by an exchange of water in response to the local water potential difference across the plasma membrane. Beginning with the geometry in Fig. 2, and the condition that \( l_w \gg w_o \), the areas and volumes of the two compartments (neglecting terms of size \( w_o^2 \) or smaller) are,

\[ A_l = l_l^2 \approx l_l^2 - 4w_a l_l \]
\[ A_s = l_s^2 \approx l_s^2 - 4w_a l_s \]
\[ V_l = l_l^2 \approx l_l^2 - 2w_a l_l^2 \]
\[ V_s = l_s^2 \approx l_s^2 - 6w_a l_s^2 \]  

The subscripts \( a \) and \( s \) refer to the apoplastic and symplastic paths respectively, \( l_l \) is the length of a cell in the flow direction (middle lamella to middle lamella), \( l_s \) is the length of the protoplast, and \( w_a \) is the thickness of the cell wall, such that \( l_w = l_l - 2w_a \). Conservation of water molecules in the two compartments then can be written as

\[ A_l \Delta x \Delta C_l = -[A_l J_{lx,l} \Delta x - A_s J_{lx,s} \Delta x] \Delta t + 4l_v \Delta x J_{x,s,l} \Delta t \] \hspace{1cm} (15)

and

\[ A_s \Delta x \Delta C_s = -[A_s J_{lx,s} \Delta x - A_l J_{lx,l} \Delta x] \Delta t - 4l_v \Delta x J_{x,l,s} \Delta t \] \hspace{1cm} (16)

The fundamental theorem of calculus then leads directly to,

\[ \frac{dC_l}{dt} = -\frac{\partial J_{x,l,s}}{\partial x} + \frac{4l_v}{l_s} J_{x,s,l} \] \hspace{1cm} (17)

and

\[ \frac{dC_s}{dt} = -\frac{\partial J_{x,l,s}}{\partial x} - \frac{4l_v}{l_s} J_{x,l,s} \] \hspace{1cm} (18)

Note that in writing the exchange terms we have chosen to regard the exchange flux \( J_{x,s,l} \) as positive when net exchange occurs into the symplast. The individual fluxes, with the hydraulic conductivity as the proportionality between the potential gradient and the molar flux, are

\[ J_{x,s,l} = -k_a \frac{\partial \psi_a}{\partial x} \] \hspace{1cm} (19)

where \( k_a \) is the permeability of the membrane system between the vacuole and cell wall. For cell-to-cell flow dominated by aquaporins (rather than plasmodesmata), symplastic conductivity comprises the permeability of two protoplasts in series with two wall sections ‘smeread’ over the cell length,

\[ k_a = \frac{L_p k_a}{2 \bar{V}'} = \left[ \frac{L_m k_a}{2 \bar{V}'} \right]^{-1} + \left[ \frac{k_a L_w}{2 \bar{V}'} \right]^{-1} \] \hspace{1cm} (21)

where \( L_m \) is the permeability of a cell including its wall. This leads to a condition for neglecting the contribution of the wall to cell-to-cell flow.

\[ L_m \approx 1 \] \hspace{1cm} (22)

Assuming the above constraint is satisfied, which is not too onerous for small \( w_o \), then the transfer conductance from apoplast to symplast can be approximated,

\[ l_m \approx k_w \frac{L_m}{L_w} \] \hspace{1cm} (23)

To eliminate \( C_a \) and \( C_s \) from (17) and (18), we need to define the hydraulic capacities that characterize the symplastic and
apoplastic paths. As with $k_c$, above, the capacity of the symplastic path, which we call $c_s$, has a small contribution from the abutting walls that separate two adjacent protoplasts:

$$c_s = \frac{V_s}{V_p} c_t + 2L_w \frac{V_s}{V_p} c_c = \frac{L_c}{c_t} c_t + 2L_w c_c$$  \hfill (24)

However, as plant tissues decline in volume, losses of water from cell walls are thought to be negligible relative to losses in volume from the symplast (Kramer and Boyer, 1995), or $L_c c_t > 6L_w c_c$, and therefore $L_c c_t > 6L_w c_c$. We then neglect the contribution of the wall sections, and take $c_s = c_t$. Substituting $c_t$ and $c_c$ into (17) and (18) brings us to two equations in terms of $\psi$ and $t$,

$$\frac{\partial \psi}{\partial t} = k_s \frac{\partial^2 \psi}{c_s \partial x^2} + \frac{8k_s}{c_s L_c} (\psi_a - \psi_s),$$  \hfill (25)

$$\frac{\partial \psi_a}{\partial t} = k_s \frac{\partial^2 \psi_a}{c_s \partial x^2} - \frac{2k_s}{c_seL_w} (\psi_a - \psi_s).$$  \hfill (26)

In order to study the structure and behavior of these two equations, we take the standard step of re-scaling to dimensionless variables, with the goal of assessing the relative importance of the individual terms (Deen, 1998). To this end, we re-scale potential and the spatial coordinate to new variables that range from zero to one,

$$\psi = \psi_a \frac{x}{L} = X,$$

where $\psi_a$ is the potential of some source at $x=0$, $\psi_s$ is the initial potential of the tissue, $L$ is the length of the cellfile, and $n$ the number of cells, such that $L = n \cdot l$. We next re-scale time by a characteristic time $\tau$, with units of seconds,

$$\frac{\tau}{\tau_0} = T.$$

(28)

This is the step of introducing dimensionless variables. Note that at this point we do not know yet what $\tau$ is; instead we will let the process of making each term dimensionless determine the characteristic time scale. Substituting the new variables into (25) and (26) yields,

$$\frac{\partial \psi_c}{\tau \partial t} = k_s \frac{\partial^2 \psi_c}{c_s \partial X^2} + \frac{8k_s}{c_s L_c} (\psi_a - \psi_s),$$  \hfill (29)

$$\frac{\partial \psi_a}{\tau \partial t} = k_s \frac{\partial^2 \psi_a}{c_s \partial X^2} - \frac{2k_s}{c_seL_w} (\psi_a - \psi_s).$$  \hfill (30)

From (29) and (30) we can identify four candidate time scales that characterize the problem: the characteristic times for changes of potential to propagate along each path independently ($\tau_c, \tau_a$), and the characteristic times for potential changes in each domain due to transfer of water from the other ($\tau_{ca1}, \tau_{ca2}$).

Here we choose $\tau = \tau_c$, which results in three dimensionless groups,

$$\frac{\partial \psi_c}{\partial t_a} = \frac{k_s c_s \frac{\partial^2 \psi_c}{c_s \partial X^2}}{c_{ca2}} (\psi_a - \psi_s),$$  \hfill (31)

$$\frac{\partial \psi_a}{\partial t_a} = \frac{\partial^2 \psi_a}{c_s \partial X^2} + \frac{8k_s}{c_s L_c} (\psi_a - \psi_s).$$  \hfill (32)

Group I represents the efficiency of potential relaxation through the symplast relative to the apoplastic, which is order one, hereafter, $O(1)$, by our construction. Group II represents the relaxation of the symplast by the adjacent apoplast, and III the tensioning of the apoplastic by the adjacent symplast. However, the importance of these transfer processes, relative to transport within a compartment, depends also on the potential difference ($\psi_a - \psi_s$), which may range from zero to one.

Note too that although the spatial derivatives are both $O(1)$, the magnitudes of the time derivatives are not, and are instead set by the need to balance the RHS of each equation. That is, we do not know how many $T$ it takes for $\psi$ to go to $\psi_\infty$ in either the apoplast or symplast; it depends on the magnitudes of the parameter groups I, II, and III and the difference in potential between the two domains. We can now organize the behavior of the coupled equations with regard to whether the apoplast–symplast potential difference tends toward one or zero (i.e., LE) into five cases, based on whether I, II, and III are each much more or much less, or about the same, as one.

Case 0: $\tau_c = 1$. If group I is about one, then potential relaxes at the same rate in both domains, and ($\psi_a - \psi_s$) $\rightarrow$ 0: local equilibrium holds by definition, and we can write a composite transport equation in terms of a single poroelastic diffusion summing area and volume weighted conductivities and capacitances.

For the remainder of the possibilities, we can ask which poroelastic time scale is faster (i.e., how large group I is), and then consider the efficiency of transfer between compartments relative to transport within them (the size of II and III). Note that the groups I and II differ only by a geometrical factor that has to be large, meaning that in the symplast, potential change due to transport out will always be fast relative to potential change due to transport within. The cases we need to consider are thereby reduced to four, based on the behavior of groups I and III:

Case 1: $\tau_c > 1$, $\tau_{ca} > 1$: Propagation of potential changes within the symplast is faster than in the apoplastic, and, within the apoplastic, potential changes due to transfer is more important than diffusion. As a result, apoplastic potential is a slave to symplastic transport—just contributes capacitance to the governing equation, slowing down the kinetics from what would be expected for the symplast alone. LE holds.

Case 2: $\tau_c > 1$, $\tau_{ca} < 1$: Again, propagation of potential changes in the symplast is faster than in the apoplastic, while the effect of transfer on the time for relaxation in the apoplast is weak. Note that this case requires $c_s > c_t = \frac{8L_c^2}{L_w}$ to satisfy both conditions, which seems unlikely as changes in total cell volume for changes in water potential are typically dominated by changes in the volume of the vacuole, included in the symplastic compartment (Kramer and Boyer, 1995). Efficient transfer slows the symplast to the point that it follows the diffusive time scale of the apoplastic LE.

Case 3: $\tau_c = 1$, $\tau_{ca} > 1$: Propagation of potential changes in the apoplastic is faster than in the symplast, but transfer of potential out of the apoplastic is even faster, holding the two domains close together. LE holds.

Case 4: $\tau_c < 1$, $\tau_{ca} > 1$: As in Case 3, propagation of potential changes in the symplast is very slow relative to the apoplastic, however transport within the apoplastic is much more efficient than transfer out. The kinetics of the two compartments therefore ‘uncouple’ in time

$$\frac{\partial \psi_a}{\partial t_a} = \frac{k_s c_s \frac{\partial^2 \psi_a}{c_s \partial X^2}}{k_{ca2}} (\psi_a - \psi_s),$$

and

$$\frac{\partial \psi_a}{\partial t_a} = \frac{\partial^2 \psi_a}{c_s \partial X^2} + \frac{8k_s}{c_s L_c} (\psi_a - \psi_s).$$

The apoplastic goes to source potential before it ever sees demand from the symplast, and, from the symplastic perspective, the
entire apoplast goes instantly from $\Psi_s = 1$, to source potential $\Psi_\infty = 0$. LE fails.

With uncoupling, water permeates into the symplast from the apoplast over all six surfaces of a cubic cell, requiring an update to the geometry for the net radial flux in (15). After returning to dimensional variables, the uncoupled governing become

$$ \frac{\partial \Psi_a}{\partial t} = \frac{k_s}{C_s l_s} \Psi_a - \Psi_s, \tag{35} $$

$$ \frac{\partial \Psi_s}{\partial t} = \frac{k_s}{C_s l_s} \frac{\partial^2 \Psi_s}{\partial x^2}. \tag{36} $$

Recalling the definitions of $k_s$ and $C_s$ in terms of cellular parameters, given by (6) and (5), and that for a cubic cell $6/l_s$ is the ratio of surface area $S_A$ to volume $V$, (35) becomes,

$$ \frac{\partial \Psi_a}{\partial t} = k_s \frac{S_A}{l_s} (\kappa + \pi)(\Psi_a - \Psi_s). \tag{37} $$

The result is that in Case 4, the entire tissue follows the same kinetics as a single cell. As tissues appear to have at least an order of magnitude longer relaxation time than individual cells, tens of seconds versus seconds (Kramer and Boyer, 1995), the complete uncoupling of Case 4 seems outside the realm of realistic solutions for plant tissue. Nevertheless, leaf tissues are often implicitly assumed to follow first order kinetics, following an ohm’s law analogy whereby the tissue is treated as an ideal capacitor (Brodribb and Holbrook, 2003; Scoffoni et al., 2008; Johnson et al., 2009). For the case of hydrating leaves, such a ‘lumped capacity’ model may yet be justified if cavitation results in the xylem becoming the limiting resistance to flow (Rockwell et al., in submission). However, in general tissues should not be expected to follow the first order kinetics of single resistor–capacitor model.

Instead, for tissues the interesting case appears to be Case 3, for which the critical condition for LE is,

$$ k_s \frac{2l^2}{k_c w_c} > 1. \tag{38} $$

The LHS of (38) describes the local leakiness, from apoplast to symplast, relative to permeation through the apoplast; when this leakiness is relatively large the potential of the two compartments converges. In considering the magnitude of this term, it is helpful to note that we can express $L$ as $n - k_c$, where $n$ is the number of cells across which transport occurs. The LHS of (38) can then be estimated as,

$$ k_s \frac{2l^2}{k_c w_c} = \frac{k_s}{k_c} \frac{2n^2}{l_s} \frac{l_c}{l_s} \sim 5000. \tag{39} $$

The ratio of the conductivities comes from potato parenchyma (Michael et al., 1997), for which $k_s = k_c$, 2.8 and $2.7 \times 10^{-12}$ mol m$^{-1}$ Pa$^{-1}$ s$^{-1}$ respectively. While comparable estimates of $k_a$ appear to be scarce, estimates of $k_c$ from other pressure probe experiments appear to be consistent with the potato data, with $k_c$ on the order of 1.6 and 1.5 $\times 10^{-12}$ mol m$^{-1}$ Pa$^{-1}$ s$^{-1}$ for Zea mays and Tradescantia leaf epidermal cells (Kim and Steudle, 2007; Ye et al., 2008). For a cell file five cells long, with $l_c$ 25 $\mu$m and $w_c$ 0.25 $\mu$m, the RHS of (39) evaluates to $\sim 5000$, which is indeed much larger than 1, and LE seems a good assumption. Yet, estimates of $l_c$ from cell pressure probe experiments, and $L_c$, from protoplast swelling assays, can range over orders of magnitude even in a single plant organ (Kramer and Boyer, 1995; Ramahaleo et al., 1999), and so we must regard $k_s/k_c$ $\sim$ 1 as very poorly constrained. We can then ask how small group III can be before LE becomes a bad assumption, such that, more to the point, adopting the composite model leads to large errors. To address this question, we compared the solutions based on the composite description of the poroelastic diffusivity, (13), to numerical solutions of the coupled equations.

3.2. Numerical solutions for thin-walled cells

We solved the coupled equations, non-dimensionalized using the apoplastic poroelastic time scale as in (31), (32), using the partial differential equations solver pdepe in Matlab (Mathworks, Natick, MA, USA). We studied the problem of potential relaxation in a file of cells with an initial uniform potential $\Psi_0$, hydrating at time $t > 0$ from a source of water at constant potential $\Psi_\infty$, located at $x=0$. At $x=L$, an impermeable cuticle provides a ‘no flux’ boundary. The non-dimensionalized boundary and initial conditions for both the apoplastic and symplastic domains become,

$$ \text{source boundary: } \Psi'|_{x=0} = 0, \tag{40} $$

$$ \text{no flux boundary: } \frac{\partial \Psi}{\partial x}|_{x=1} = 0, \tag{41} $$

$$ \text{initial condition: } \Psi'|_{t_\infty} = 1. \tag{42} $$

For the sake of comparison to the numerical results, we then sought the solution to the composite problem in terms of the apoplastic time scale $T_a = t/\tau_a$. Starting with,

$$ \frac{\partial \Psi}{\partial T_a} = k_s \frac{\partial^2 \Psi}{\partial x^2} \tag{43} $$

and multiplying both sides by $\tau_a$ brings us to,

$$ \frac{\partial \Psi}{\partial T_a} = \gamma \frac{\partial^2 \Psi}{\partial x^2}, \quad \gamma = \frac{A_s k_s}{V_s C_s + V_a C_a} \tag{44} $$

subject to the boundary and initial conditions above. As an aside, we note that $\gamma$ shows the mathematical linkage underlying the coincidence of local equilibrium and the composite model. With the geometry considered here, $L > w_c$, the area and volume fractions of the symplast are much greater than those of the apoplast, and taking $A_s \equiv V_s$, we find $\gamma$ is equal to group I in (31). Hence, (44) has the form of the symplast equation (31), excepting the transfer term. This means that if the composite model holds, in the symplast equation the transfer term must be negligible relative to the poroelastic–diffusive term, and since the derivative is $O$ (1) by construction, we find the inequality,

$$ \frac{k_s C_s}{k_c C_c} \frac{2l^2}{k_c w_c} \frac{\Psi_a - \Psi_s}{\Psi_a - \Psi_s} \ll 1. \tag{45} $$

Dividing through by the RHS and using the relation $L = n l_c$ and the thin walled condition $w_c \ll l_c$, leads to,

$$ (8n^2)^{-1} (\Psi_a - \Psi_s) \ll (8n^2)^{-1} (\Psi_a - \Psi_s) \tag{46} $$

which shows the role of cell number in inhibiting potential differences between compartments during transients.

In comparing the composite solution with the numerical results, we need to account for the fact that plant physiologists are currently limited methodologically to equilibrium measurements of plant water potentials. In this context, this means that the only potential that can be measured accurately is the potential of the tissue once all gradients induced by transient flow have collapsed, and the cell file is once again characterized by a single, uniform potential. We therefore integrated the composite solution with respect to $X$ to find the equilibrium potential predicted for the tissue after hydration for $t$ seconds. The solution to (44) is well
known; after integration it becomes,
\[
\Psi_n(T_a) = \frac{8}{\pi^2} \sum_{n=0}^{\infty} \frac{\exp(-\lambda_n^2 T_a)}{(2n+1)^2}, \quad \lambda_n = \left(\frac{2n+1}{2}\right) n.
\]  
\begin{equation}
(47)
\end{equation}

and, for numerical evaluation, it is generally sufficient to retain only the first ten terms of the infinite series, as the individual terms die off with both increasing \( n \) and \( T \) (Crank, 1957). The numerical solutions for the apoplast and symplast domains were also integrated over \( X \) and the equilibrium potential of the cell file, as a function of hydration time, found as the volume fraction \( \nu \) and hydraulic capacity weighted average of the symplastic and apoplastic potentials,
\[
\Psi^*_n(T_a) = \frac{\nu c_s \Psi_s(T_a) + \nu c_a \Psi_a(T_a)}{\nu c_s + \nu c_a},
\]
\begin{equation}
(48)
\end{equation}

Fig. 3 shows the relaxation curves with the ratio of the hydraulic conductivities, \( k_i/k_o \), lowered to 0.01 and 0.001, with group III evaluating to 50 and 5 respectively. For the first case (panel A), the composite and numerical solutions follow similar kinetics, and the apoplastic and symplastic domains remain well coupled (inset).

For the case that group III drops to five \( (k_i/k_o = 0.001 \text{, panel B}) \), the composite solution diverges from the numerical, and the difference in the average potential of the symplast and apoplast becomes large, especially at very early times (inset). The initial rapid decrease in the apoplast occurs as it would if it were an isolated domain, which would approach zero by \( t/\tau_a = 2 \); as the average potential of the apoplast falls while the symplast has yet to change, flow into the apoplast falls even as the amount of transfer-flow to the symplast increases, and the progress of the apoplast toward zero slows.

We can quantify the failure of the composite model, as a function of group III varying from 5 to 50, by comparing the ratio of the half-times \( t_{1/2} \); that is the times at which the composite and numerical solutions predict the cell file will have relaxed to half its initial value. This is an appropriate metric for comparison as rehydration transients in plant tissue are generally fit near the half-time (Brodribb and Holbrook, 2003). The halftime predicted by the composite solution (47) can be found by evaluating the solution for \( \Psi_n = 0.5 \), retaining a finite number of terms in the series (here, 10), with the well known result \( t_{1/2}^n = 0.197 \tau_a/\gamma \) (Crank, 1957). The halftime predicted by the numerical solution is by definition \( t_{1/2}^n = T_{1/2}^n \), where \( T_{1/2}^n \) is the solution time \( T_a \) at which \( \Psi_n = 0.5 \). The test of the competence of the composite model is then,
\[
\frac{t_{1/2}^n}{t_{1/2}^c} = \frac{0.197 \tau_a}{T_{1/2}^n} = 0.197 \frac{\tau_a}{T_{1/2}^n} \approx 1.
\]
\begin{equation}
(49)
\end{equation}

Fig. 4 shows that the composite halftime is still within 10% of the numerical result for the coupled transport model until group III drops below 20, and that agreement drops precipitously once group III falls below 10. We note that this result is broadly consistent with the result of the scaling analysis that group III should be at leaf an order of magnitude greater than 1 to justify an assumption of LE and the composite model. However, the comparison of half-times as function of group III provides more specific criteria for adopting the composite model. For example, for an expected error in hydraulic conductivity estimates of less than 10%, Fig. 4 provides,
\[
\frac{k_i}{k_o} \frac{2L^2}{\nu c_o l_w} \geq 20.
\]
\begin{equation}
(50)
\end{equation}

This result means that, with the typical parenchyma geometry considered for the evaluation of group III in (39), even if the estimate of \( k_i/k_o \) based on the potato parenchyma Michael et al. (1997) is one hundred times higher than the true typical case, the composite model can still be justified. This is so even though, with this conductivity ratio of \( k_i/k_o = 0.01 \), the flux through the apoplast is four times that through the symplast. If, on the other
hand, the material properties $k$, $c$ for the symplast and wall space are indeed of the same order of magnitude, then for thin-walled cells the total poroelastic diffusivity (13) will be well approximated by the symplast properties alone, and the diffusivity is well approximated by the form given by Philip (1958b),

$$k_i \approx L_p (e + \sigma).$$

(51)

The advantage of this equation is that it connects the parameter governing tissue behavior ($k_i$) to cell-level properties.

The above differs slightly from Philip (1958b) in that the latter includes a shape factor, which represents the proportion of cell-to-cell contact area to cell cross-sectional area. This factor may generally be neglected in the case of experimentally derived estimates of $L_p$: if cells adjacent to probed cells serve as the sink for flows induced in pressure probe experiments, as it seems they must given the small volume of the adjacent wall space, then such a correction would be already reflected in the experimentally measured values. Yet this raises an issue with the usual interpretation of pressure probe data typically assumes a sink of constant potential surrounds the cell of interest outside the plasma membrane (Kramer and Boyer, 1995). This assumption, while justified for the algal cells for which the mathematics were originally formulated, likely fails for cells embedded in tissues of thin-walled parenchyma, and we expect that two sets of membranes are crossed in the transient cell-to-cell flow induced by the pressure probe.

3.3. Numerical analysis for thick walled cells

Based on the above arguments, (39) offers strong support for the existence of local equilibrium in aggregates of thin walled cells, such as commonly make up the mesophyll and epidermal tissues of leaves. However, cells packed around major veins may often be thick-walled, and therefore we might question whether the composite model can be expected to adequately describe leaf tissue. To extend our analysis to thick walled cells, we relax the assumption that the radial gradients through the wall are negligible, and model the resulting 3D potential relaxation problem using a finite element analysis software package (Comsol 4.2a, Comsol Inc., Burlington, MA, USA). By symmetry, we study a quarter section of symplastic path and adjacent $L$ shaped wall path for cells with a symplastic length $l_s = 20 \mu m$, wall thickness $w_a = 10 \mu m$, through a thickness of 100 $\mu m$ or five cells; coordinates are then normalized by the longest length for transport, $L$. The non-dimensional variables are taken as,

$$X = \frac{x}{L}, \hspace{1cm} Y = \frac{y}{L}, \hspace{1cm} Z = \frac{z}{L}.$$  

(52)

$$\Psi = \frac{\psi(t) - \psi_\infty}{\psi_0 - \psi_\infty}, \hspace{1cm} T_a = t \cdot \frac{k_a}{c_a L}.$$  

(53)

Substituting (52) into the 3D form of Philip’s poroelastic equation (8) provides the non-dimensional form governing transport along the central symplastic path,

$$\frac{\partial \Psi}{\partial t_a} - \frac{k_c k_o}{c_c c_o} \left[ \frac{\partial \Psi}{\partial X} + \frac{\partial^2 \Psi}{\partial Y^2} + \frac{\partial^2 \Psi}{\partial Z^2} \right],$$

and along the peripheral wall path,

$$\frac{\partial \Psi}{\partial t_a} = \left[ \frac{\partial \Psi}{\partial X} + \frac{\partial^2 \Psi}{\partial Y^2} + \frac{\partial^2 \Psi}{\partial Z^2} \right].$$

(54)

(55)

The boundary and initial conditions are given by,

source boundary $\Psi|_{x=0} = 0,$  

(56)

no flux (epidermis) $\frac{\partial \Psi}{\partial X}|_{x=1} = 0,$  

(57)

no flux (symmetry) $\frac{\partial \Psi}{\partial Y}|_{y=1} = \frac{\partial \Psi}{\partial X}|_{x=1} = 0,$  

(58)

at an interface $\Psi_a = \Psi_s, (u_s - f_s) \cdot \hat{n} = 0$  

(59)

initial condition $\Psi|_{t_a = 0} = 1.$  

(60)

Fig. 5 shows the numerical solutions to the 3D problem for values of $k_c/k_s = 0.1, 0.01, 0.001$ at their halftimes. For the first two values, the halftimes predicted by the composite model (44) and (47) are within 99% and 94% of the halftimes for the respective numerical solutions, while for the third agreement drops to 82%. For $k_c/k_s = 0.001$, the gradients in the symplast are almost entirely lateral, and the dominant flow into the symplast is through the radial walls. Indeed, even for $k_c/k_s = 0.01$ the 94% agreement in halftimes occurs despite that fact that radial flows appear an important path for hydration of the symplast, and LE is not very well supported. As in the thin walled Case 3, the composite model can provide an apt description of the bulk behavior even when the apoplast is the dominant path for flow.

Finally, considering that in Michael et al.’s (1997) data the $Lp$ of cells as measured by the pressure probe as reported is on the order of $10^{-7}$ m s$^{-1}$ MPa$^{-1}$, while the range for plant cells is reported to be $10^{-8}$ to $10^{-5}$ (Boyer, 1995), then apoplastic and symplastic conductivities may in general be within an order of magnitude of each other ($k_c/k_s = 10^{-0.1}$), and the composite model justified for thick walled cells as well. At the very least, the presence of thick-walled cells in a tissue should not constitute grounds for rejecting the composite model.

4. Isothermal water vapor transport in leaves

We next consider how to account for the fact that leaf tissues are not just aggregates of cells, but include significant intercellular air spaces, typically 5–50% by volume (Byott, 1976) (Fig. 6). As in considering the symplast and apoplast fractions of the cells, we are again interested in whether we can represent the air and cell volumes as a homogenous medium, whose material properties are again a volume weighted combination of the properties of the two domains, and to what degree success depends on local equilibrium between the two phases (liquid in the cells, vapor in the air space) along axes perpendicular to the principal flux.

To address this problem, it is convenient to express transport in the two phases as a function of a common driving force. Based on the Clausius–Clapeyron equation, and the relation between saturated vapor pressure and water potential (Nobel, 2005), we can write the molar concentration of water molecules per unit volume of air, $C_v$, in equilibrium with a tissue inhabited by a liquid with water potential $\psi$ at temperature $\theta$ as,

$$C_v(\theta, \psi) = C_{v0} \exp \left[ \frac{\theta - \theta_0}{R} \left( \frac{\psi}{R} \right) \right] + \left( \frac{\psi + p_{atm} - p_v(\theta) \psi}{R} \right),$$

(61)

where the reference concentration and temperatures are taken as $1.28$ mol m$^{-3}$ and $298.15$ K. As Clausius–Clapeyron describes the coexistence of the pure phases, and water potential is defined as zero at atmospheric pressure, the liquid ‘pressure’ dependent term ($\psi + p_{atm} - p_v(\theta) \psi$) is written so that it will be zero (and the effects of liquid pressure on vapor concentration vanish) when the liquid phase has an absolute ‘pressure’ ($\psi + p_{atm}$) equal to the vapor pressure $p_v(\theta)$.  

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mean in the air spaces 260 transport will be minimal where the composite model is only 18%, despite the breakdown in local equilibrium between the symplast and its adjacent wall space. However, we expect that for most leaves conduction in the liquid is more efficient than vapor diffusion, the effective hydraulic conductivity of the air space, and describes the capacity of air to store water molecules as vapor. Here we are neglecting the thermal cooling and heating that must accompany the inter-duction experiments on leaves in thermal equilibrium with their surroundings.

\[ J_v = -D_v \left( \frac{\partial C_v}{\partial \psi} \nabla \psi + \frac{\partial C_v}{\partial \theta} \nabla \theta \right), \]

where \( C_v \) and \( D_v \) are constants found by linearizing the partial derivatives around the temperature and potential that characterize the problem. For the isothermal problem, applicable to rehydration experiments on leaves in thermal equilibrium with their surroundings, \( k_v = D_v C_v \) defines the effective hydraulic conductivity of the air space, and \( D_v \) describes the capacity of air to store water molecules as vapor. Here we are neglecting the thermal gradients within the leaf that would be induced by the evaporative cooling and condensing heating that must accompany the internal redistribution of water molecules through the vapor phase. However, we expect that for most leaves conduction in the liquid phase is efficient enough that such a thermal feedback on vapor transport will be minimal (Appendix C), and in this ‘quasi-isothermal’ limit consider the concentration of water vapor in equilibrium with the adjacent liquid phase to be a function of the liquid phase water potential alone.

We can now write isothermal transport within the leaf in both phases in terms of a common driving force,

\[ \frac{\partial \psi}{\partial t} = k_v C_v \nabla \psi = D_v \nabla \psi, \]

in the cells, \( \frac{\partial \psi}{\partial t} = \frac{k_v}{C_v} \nabla \psi = \kappa_v \nabla \psi, \]

at an interface \( \psi_i = \psi_f, \) \( J_1 = J_v. \)

Comparing the diffusivities for the two phases, \( D_v \) is on the order of \( 10^{-5} \text{ m}^2 \text{s}^{-1}, \) while \( k_v \), taken as \( k_v \) as estimated from pressure probe experiments, ranges in order of magnitude from \( 10^{-12} \) to \( 10^{-9}, \) with a consensus value about \( 10^{-10} \) (Kramer and Boyer, 1995). This does not mean however that transport through the vapor phase outweighs transport through the tissue. The difference in diffusivities is largely due to the vanishingly small quantity of water it takes to change the potential of the air compared to the tissue; that is, \( C_v / C_f \sim 10^{-5}. \) As a result, the expected values of both \( k_v \) and \( k_s, \) the parameters that determine the magnitude of the fluxes, are much closer. For example, at \( 25 \text{ C}, D_v = 2.5 \times 10^{-5} \text{ m}^2 \text{s}^{-1}, \) \( C_v = 9 \times 10^{-9} \text{ mol m}^{-3} \text{ Pa}^{-1}, \) and \( k_v = 2.3 \times 10^{-13} \text{ mol m}^{-1} \text{ Pa}^{-1} \text{ s}^{-1}. \) This is an order of magnitude lower than \( k_l \) values found above. However, data for Arabidopsis protoplasts in Morillon and Chrispeels (2001) provide a mean membrane permeability \( (P_m) \) of 70 \text{ mm} \text{s}^{-1}, for an \( L_p \) of \( 5 \times 10^{-13} \text{ m Pa}^{-1} \text{s}^{-1}, \) and a \( k_s = 4.2 \times 10^{-13} \text{ mol m}^{-1} \text{ Pa}^{-1} \text{s}^{-1} \) (for the relation between \( P_m \) and \( L_p, \) see Appendix B).

Arriving at an expected value for a population of cells is challenging, as the range for individual protoplasts spans an order of magnitude above and below the mean. In addition, in leaves these distributions appear to have a long tail at the high end (Ramahalo et al., 1999; Martre et al., 2002), and the median value, which may be more important for determining tissue behavior, typically lower than the mean. Thus, while the hydraulic capacity of the gas phase is negligible relative to the cells, transport may not be, with the relative area available for vapor diffusion an important factor. To try to clarify the limits of describing a 1D domain composed of both air and cells with a composite model, we again compare the results of the composite description with a numerical solution for the 3D domain (Comsol 4.2a, Comsol Inc., Burlington, MA, USA).
To simplify the analysis, we rescale the spatial coordinates $x, y, z$ by a length that characterizes transport. Choosing that length again as $L$, we adopt the new variables $X = x/L, Y = y/L, Z = z/L$, with the resulting domain of interest as in Fig. 7A. To consider transport in a part of a leaf most favorable to vapor transport, we model our domain on a spongy mesophyll with air filled pore space diameters 2R twice the characteristic size of the cells 2r. The later is generous to vapor movement as in the spongy mesophyll of temperate woody leaves air space diameters appear to be about equal to those of the neighboring cells (Wylie, 1939). Symmetry reduces the representative domain of interest to a quarter air space plus an L-shaped region equal to the half thickness of the adjacent cells, and by definition the boundaries normal to $Y, Z$ then have a no-flux condition. We adopt the non-dimensional variables,

$$X = \frac{x}{L}, \quad Y = \frac{y}{L}, \quad Z = \frac{z}{L}. \quad (68)$$

Substituting (68) and (69) into (65) and (66) provides the non-dimensional forms of the governing equations for transport through the air space,

$$\frac{c_v}{c_l} \frac{\partial \Psi}{\partial \tau} = k_v \left( \frac{\partial^2 \Psi}{\partial X^2} + \frac{\partial^2 \Psi}{\partial Y^2} + \frac{\partial^2 \Psi}{\partial Z^2} \right). \quad (70)$$

and in the cellular space,

$$\frac{\partial \Psi}{\partial \tau} = \left[ \frac{\partial^2 \Psi}{\partial Y^2} + \frac{\partial^2 \Psi}{\partial Z^2} \right]. \quad (71)$$

The boundary and initial conditions are given by,

source boundary $-\Psi|_{X = 0} = 0,$ \quad (72)

no flux (epidermis) $-\frac{\partial \Psi}{\partial x}|_{X = 1} = 0,$ \quad (73)

no flux (symmetry) $-\frac{\partial \Psi}{\partial z}|_{X = 1, 0} = 0,$ \quad (74)

at an interface $-\Psi_v = \Psi_i, \quad (j_1 - j_v) \cdot \vec{n} = 0.$ \quad (75)

For a quantitative measure of the effect of neglecting in plane gradients between cells and adjacent airspace, we can again consider the halftimes for transport predicted by the solution to the composite model expressed in terms of $T^{3D}, \tau^{1D}$, in relation to that observed for the numerical simulation, for which time is denominated in terms of $t^{3D}$. With the above boundary conditions, the halftime predicted by the composite model is $0.197 \tau^{10},$ and the test for the competence of the composite model is just

$$\frac{\tau^{10} T^{3D}_{1/2}}{\tau^{1D} T^{1D}_{1/2}} \approx 1 \rightarrow \frac{\kappa_v}{\kappa_t} 0.197 \rightarrow 1,$$ \quad (78)

where the unknown $T^{3D}_{1/2}$ is found from averaging the potential field in the cellular domain at each time step of the numerical solution (note that the hydraulic capacity of air is negligible relative to that of the cell fraction, and so the potential in the airspace is immaterial in determining the potential attained by the whole domain as it comes to equilibrium after hydration for $t$ seconds). Fig. 7 shows the iso-surfaces of the potential field in the domain in the halftime given by the numerical simulations. Qualitatively, we can see that for vapor conductivity less than or about equal to that of the liquid path, near local equilibrium is observed between air and cell fractions. Even for vapor conductivity 10 times greater than the cell fraction, the phases do not show too much separation in potential. However, for $k_v/k_t = 0.1, 1, 10$, the quantitative test for the composite model based on the ratio of the halftimes, (78), evaluates to 0.999, 0.99,
that calculated according to volume fraction to the effect of a tortuosity (Cussler, 1997), to which we give the symbol \( \xi \). In this view, tortuosity accounts for the fact that in substances with heterogeneous material properties transport may not be strictly one-dimensional, depending on the arrangement of the component materials.

As a ‘tortuous’ bend in a cell file implies a similar bend in the adjacent airspace, it might be assumed that the tortuosity of the two phases must be equal. However, it seems that observed tortuosities can be larger than might be reasonably attributed simply to the increase in path length (Cussler, 1997); that is, the definition of tortuously as the difference between an observation and theoretical expectation makes it a catch-all parameter in which various physical effects may lurk. We thus define separate tortuosities, \( \xi_{\ell} \) and \( \xi_{v} \), for the two phases. With respect to the liquid phase, the parameter defined by experiment is the effective conductivity of the liquid path, \( k_{l}/\xi_{l} \); only in rare situations is it likely to be possible to arrive at separate estimates of \( \xi_{l} \) and \( k_{l} \). In contrast, for the vapor phase, the effective hydraulic conductivity, \( k_{v}/\xi_{v} \), must be built up from the known material properties \( D_{v} \) and \( c_{v}^{\ell} \), and an independent estimate of \( \xi_{v} \). In general, tortuosity may be expected to be about three, with a typical range from two to six (Cussler, 1997); in the context of leaf internal air spaces, a value of 1.5 has been suggested (Pierschka et al., 2005). Accounting for tortuosity, the poroelastic diffusivity of the tissue becomes,

\[
\kappa'_{f} = \frac{k_{l} \cdot \frac{1}{\xi_{l}}}{\frac{1}{c_{l}}},
\]

Eq. (81), together with (13) and (5), completes the description of leaf tissue as a composite media in terms of the constituent material properties of membranes, cell walls, and air.

4.1. Impact of cell size and number on hydration times

We began this analysis by discussing how discrete cellular properties, such as membrane permeabilities and cell size, could be scaled to a continuous property such as hydraulic conductivity. Doing so allowed us to adopt the ideas of continuum mechanics,
and avoid the complexity of a fully discrete description. However, in some cases it may be illuminating to return to the original discrete variables. For example, in the limit that cell-to-cell flow dominates transport, the dependence of the characteristic time $\tau$ on cell permeability can be found simply as,

$$\tau = \frac{c_l n^2}{k_c} = \frac{2}{A_0} \frac{\nu L}{l_c} n^2.$$  \hspace{1cm} (82)

For such tissues, the time for changes in potential or water content to propagate will be linearly related to the characteristic cell size $l_c$, but will grow as the number of cells $n$ squared. Hydraulic limitation may then arise from the number of cell-to-cell transitions, rather than linear distances, and $n \cdot l_c$ may be a more useful variable than $L$ in analyzing internal leaf structure. The steady state conductance $K_n$ for transport over $n$ cells is then,

$$K_n = \frac{A_0 l_c}{2 \nu n}.$$  \hspace{1cm} (83)

Notably, (83) emphasizes that, in the limit that tissue conductivity is dominated by membrane permeability, cell number, and not actual tissue dimensions, may provide the most informative measure of how far a cell can be from the vasculature before transport limitations become too great. For example, the relatively low value of $k_t$ calculated here for Arabidopsis may be explained by its small cell size, $l_c = 30 \mu m$, while its mean $l_p$ falls within the range of the other species discussed ($2 \cdot 7 \cdot 10^{-13} m Pa^{-1} s^{-1}$).

5. Discussion

5.1. Poroelasticity and plant water relations

It will be noted that in considering the permeation of water molecules through plant tissues from the perspective of poroelastic theory, we have nevertheless arrived at the same mathematical form as Philip (1958b), and so might be argued the extra effort was superfluous. However, the exercise did make explicit the approximations and limitations entailed by the use of the heat equation to describe water transport in elastic tissues, and therein lies some of its value. The rest of the value lies in pointing plant physiologists towards a well developed body of theory linking liquid transport within a tissue, all of our estimates of hydraulic conductivity may be expected to be similar. As the thermal conductivity of air is an order of magnitude lower than that of liquid phase, whose thermal conductivity may be expected to be of the same order of magnitude as water (Vogel, 1983), and because the thermal capacity of air is likewise an order of magnitude lower than that of water, the case for a composite model for heat transport would appear to be stronger than for water molecules. The gas phase cannot ‘short circuit’ the liquid phase heat flux, as it might if the thermal conductivity of air were very high; nor will it provide a large lateral impedance, as the combination of high thermal capacity and low conductivity might, which would slow the time for heat transport from what might be expected based on the composite model. The thermal diffusivity of the composite will then just be dominated by that of the liquid fraction, or $\kappa_f = A_k/\nu c_f$, where the superscript $T$ refers to thermal properties.

5.3. Pathway of isothermal water flux in leaf tissue

With regard to the competition between isothermal vapor and liquid transport within a tissue, all of our estimates of $k_l > k_t$, though the low end of the $k_t$ distribution for individual protoplasts is comparable. Experimental estimates of $k_l$ greater than $\sim 2 \cdot 10^{-12} mol m^{-1} Pa^{-1} s^{-1}$ would suggest a dominant role for liquid flow over vapor diffusion. Mott and Peak (2011) proposed that vapor diffusion might be more important than liquid flow for transport through the mesophyll under isothermal (dark) conditions in leaves of Tradescantia, but based on a $k_l > 1.6 \cdot 10^{-12} m mol m^{-1} Pa^{-1} s^{-1}$, estimated earlier from data in Ye et al. (2008), our estimate of $k_l$, and a whole leaf volumetric air fraction of 15% (Byott, 1976), would this appear unlikely.

While the non-isothermal case is beyond the scope of this paper, temperature gradients within the leaf have the potential to
shift more of the flux into the vapor phase than is predicted to occur in the isothermal case developed here. An idea of the expected for leaves (Yianoulis and Tyree, 1984), are as efficient at moving water as liquid phase gradients on the order of 1 MPa. In addition, while to define average tissue hydraulic properties from experiments we needed the volumetric air fraction averaged over the entire leaf, the appropriate air fraction for considering the transpirational flux between the veins and lower epidermis is that of the spongy mesophyll, further contributing to the competitiveness of the vapor phase. These issues will be further explored in a subsequent analysis.

The important point with regard to the experimental determination of material properties is that as long as rehydration experiments are conducted at a temperature close to transpiring ‘leaf temperatures’ (i.e., the temperature measured by a thermocouple at the leaf surface), the isothermal value of \( k \) should still be appropriate for modeling liquid phase transport under non-isothermal conditions. This is because temperature variations in the leaf are expected to be less than \( 1^\circ \mathrm{C} \), while the conductivity of the cell fraction is thought to have a Q10 of about 2 (Matzner and Comstock, 2001), from which it follows we can safely neglect variation in \( k \) due to temperature gradients within a leaf.

With the respect to the question of whether most of the liquid flux in the leaf mesophyll occurs through the walls or symplast, for the thin wall aspect ratio considered here, \( w_s / L = 0.01 \), we found that even for ratios of the symplast to apoplast hydraulic conductivity of \( k_s / k_a > 0.05 \) the steady flux across the symplast will be larger, simply due to the relatively small area available for apoplastic flow. Experimental values of \( k \) on the order of \( 10^{-11} \) mol m\(^{-1}\) Pa\(^{-1}\) s\(^{-1}\) would be higher than could be explained by the symplastic path, based on the estimates of \( k_s \) given here. Such values, if observed, would support the concept of a predominantly apoplastic path in leaf mesophyll tissue, as some work on leaves assumes (Brodribb et al., 2007, 2010). Despite this assumption, the fit to the data in Brodribb et al. (2007, Fig. 1B) implies a universal \( k \) for ferns, gymnosperms, angiosperms, and lycopsids of \( 2 \times 10^{-15} \) mol m\(^{-1}\) Pa\(^{-1}\) s\(^{-1}\), which may readily be accounted for by the estimates of \( k_s \) based on pressure probe estimates of \( L_p \) given here. Thus it seems unnecessary to invoke a large apoplastic flux to account for water transport in leaf tissue.

According to Martre et al. (2002), in *Ambipodos* estimates of \( L_p \) of this magnitude, \( \sim 10^{-13} \) m Pa\(^{-1}\) s\(^{-1}\), correspond to \( P_{w,v} > 10 \) m s\(^{-1}\) that are indicative of active aquaporins. \( L_p \) measurements from pressure probes do not discriminate between cross-membrane and plasmodesmatal mediated fluxes, so it is notable that \( P_{w,v} \) values appear capable of accounting for the magnitude of observed cell-to-cell conductivities. An important role for aquaporins within the symplastic compartment is also consistent with the negative effect of anoxia, known to gate aquaporins (Tournaire-Roux et al., 2003), on the rehydration of *Quercus rubra* leaves (Rockwell et al., 2011).

It is perhaps surprising then that Martre et al. (2002) found no effect of down regulation of aquaporins on leaf hydraulic conductance, defined as the proportionality between transpiration and the difference between covered leaf (presumably in equilibrium with the stem xylem) and transpiring leaf water potentials, while an effect was seen in roots. Martre et al. conclude these results are consistent with a dominantly apoplastic path for transpiration. However, while the potential difference driving flow across the root was well defined in that study, the relationship between whole leaf volume averaged water potential measurements and the potential at the evaporation sites in leaves is not (Sack et al., 2002).

Evaporative methods can also give highly nonlinear potential-flux relations, in which the potential differences between transpiring and non-transpiring leaves appears insensitive to increases in the flux, a problem particularly for measurements of detached leaves of young, growing herbaceous plants (Boyer, 1985). In addition, the potential difference between transpiring and non-transpiring leaves may be well-defined in plants in which xylem resistance is much greater than the post-xylem path through the tissue, such that all the living tissue in the leaf may be approximated as at one potential, but, in the case of angiosperms, tissue resistance is not negligible (Cochard et al., 2004). As a result, the capacitance of tissue not between the minor veins and the stomata (e.g., palisade and upper epidermis in hypostomatus leaves, rib tissues) will reduce the sensitivity of the average potential of the leaf, as measured by the pressure chamber, to changes in vein to stomata gradients. While attractive for characterizing flux-potential relations at phylogenetic scales (e.g., Brodribb et al., 2007), evaporative methods do not appear sufficiently well-defined physically to probe finer scale leaf structure-function relationships.

In the case of Martre et al. (2002), the method may simply have been to crude to detect a change in leaf tissue permeability. In conclusion, our analysis has shown that all of the pathways considered here, apoplastic, symplastic, and through the air spaces as vapor, may be important for water transport within a particular tissue depending on the volume fractions, wall thicknesses, and temperature gradients that characterize the tissue. Modeling the path of transpiration in leaf tissues should therefore take all of these factors into account. Yet while the topology of the walls, protoplasts and air spaces is complex, a simple composite model of leaf tissue as a homogenous isotropic medium characterized by the area and volume averaged material properties of the component sub-domains appears to offer a good working hypothesis or starting point for exploring leaf structure-function relationships related to water transport.

**Appendix A. Sensitivity of poroelastic relaxation times to \( \nu \)**

The solution to diffusion type boundary value problems can be expressed at any particular time as a sum of \( n \) exponential terms, where the contribution to the solution of any particular term decays as both \( n \to \infty \) and \( t \to \infty \) (Crank, 1957). As a result, at ‘long times’, or after about one quarter of the progress of the transient to the final equilibrium state has occurred, the solution maybe well described by a single dominant term. While no closed form solution to the free swelling linear poroelastic problem exists, Doi (2009) sketches the expected form of the longest relaxation time, which will determine the half time of the swelling kinetics.

According to Doi’s (2009) solution, the time constant \( \tau_o \) of the dominant term, or ‘longest relaxation time’, is given by (in our notation, with \( L \equiv h/2 \)),

\[
\tau_o = \frac{L^2}{3k^\lambda}, \quad \kappa = \frac{3K(1-\nu)}{1+\nu} k, \quad (A.1)
\]

where \( \lambda \) is the smallest positive solution to,

\[
\lambda \cot \lambda = \frac{4G}{3K+4G} = \frac{2(1-2\nu)}{1-\nu}. \quad (A.2)
\]

Note that the second equality simply follows from the relationship between \( G \) and \( K \) given by (11). Inspection of (A.1) and (A.2) shows that, for a given hydraulic conductivity \( k \) and volumetric modulus \( K \), the longest relaxation time \( \tau_o \) is just a function of the poroelastic Poisson’s ratio, \( \nu \). For \( \nu = 0.1 \) and \( \nu = 0.5 \), the longest relaxation
Appendix B. Relating osmotic and potential flows

The relationship between $P_{os}$, the permeability defined by protoplast swelling assays, and $L_p$, the hydraulic permeability as measured by the pressure probe, can be found by relating the absolute volume fluxes (Boyer, 1995; Ramahaleo et al., 1999),

$$\frac{\partial \psi}{\partial t} = P_{os} S_0 \cdot \nabla \rho_o \Delta C_{os} = L_p S_0 \cdot \Delta \psi,$$

where $S_0$ is the initial surface area of the protoplasm, and $C_{os}$ is the osmolality, in mol/kg solvent, as reported in Ramahaleo et al. The limit of dilute solutions, $\rho_o C_{os}$ gives the concentration $C$ in mol/m$^3$, and $\nabla \rho_o C_{os}$ the dimensionless mole fraction, that describe the osmotic driving force across the membrane. Using the relation between dilute concentrations and water potential, $\psi_w = -RT C$ (Kramer and Boyer, 1995), and recognizing that the ‘positive’ differences in $C_{os}$ and $\psi$ driving inward flow have opposite signs when written more formally as gradients, leads to,

$$\frac{\Delta C_{os}}{\Delta \psi} = (\rho_o RT)^{-1} \cdot L_p = \frac{P_{os} \psi}{RT}.$$

This is indeed for the above boundary conditions the longtime solution to (12), the heat-equation form we found the equations of poroelasticity reduce to in the special case $\nu = 0.5$, equivalent to Philip’s (1958b) model (8).

Appendix C. Approximately isothermal vapor transport

Here we consider vapor transport within the leaf tissue, in the absence of radiative loading of the leaf. Because of the low capacity of air for water molecules relative to the cells, effectively all of the water entering the leaf in the liquid phase during a hydration experiment ultimately resides in the cells, again in the liquid phase. This means that to the extent water moves through the internal air space as vapor during a change in hydration, energy must flow towards the evaporative surfaces (i.e., the bundle sheath) as well as away from the condensing and absorbing cells in the mesophyll and epidermals. Only if the amount of energy removed by evaporation is small relative to the heat capacity of the tissue, will temperature variations at the evaporating and condensing sites truly be negligible. Yet, if we treat the entire tissue (noting that the heat capacity of the air fraction is negligible compared to that of water) as a reservoir of heat energy, we find that for a typical oak leaf containing 1.2 g of water in a typical hydration experiment that results in the uptake of 0.04 g, or ~3% of the leaf’s water content, the energy required to evaporate the hydration flux relative to the energy required to change temperature of the leaf water 1 °C is,

$$\frac{T}{C_P} = 0.03 \approx 17.5 \, ^\circ C,$$

which tells us that, in the absence of a flow of energy to the evaporation sites, the thermal gradients induced in the tissue by a vapor flux would not be negligible. Of course, in the absence of radiative loading from an external source, energy can flow to the leaf from the surrounding air, but this potential source is separated from the leaf tissue by a conductive boundary layer resistance.

A more important source of energy is likely to be the sites of condensation within the leaf itself. To estimate how important thermal gradients might then be in slowing vapor transport, we can find an approximate thermally ‘corrected’ hydraulic conductivity of the air by imposing the requirement (which would be exact in steady state) that any latent heat transport must be conducted back to the evaporating site a distance $\Delta x$ away. In terms of the latent heat flux that arises due to vapor transport in the air fraction $\Delta \rho$, during rehydration, the conduction of heat through the leaf tissue required to deliver the heat of condensation back to the evaporative surface is given by,

$$\Delta \rho \Delta \tau = k_p A \frac{\Delta \rho}{\Delta x},$$

where $k_p$, the thermal conductivity of the leaf, is given by $A \Delta \rho + A \Delta k$. Solving (C.2) for the temperature gradient (induced by vapor transport and driving heat transport from the site of condensation back to the site of evaporation), and substituting back into (64), we find an expression for the vapor flux in the air space that accounts for the adverse impact of a temperature gradient on vapor transport,

$$J_v = \frac{\Delta \rho \psi}{\Delta \theta} = \frac{A \Delta \rho \Delta \tau}{k_p \Delta \rho},$$

Re-arranging (C.3) defines an effective hydraulic conductivity of the air space, $k_p$, that takes into account thermal effects,

$$J_v = k_p \frac{\Delta \rho \psi}{\Delta \theta} = \frac{A \Delta \rho \Delta \tau}{1 + A \Delta \rho \Delta k}.$$

For an oak leaf with a tissue thermal conductivity about a third that of water, or 0.25 J m$^{-1}$ K$^{-1}$ s$^{-1}$, and a whole leaf air fraction of 12.63% (unpublished data), the correction amounts to only a 4% reduction in the hydraulic conductivity of the vapor path, a result due to the efficiency of conduction in the leaf tissue relative to vapor transport. A full thermal budget would also account for convective heat transport as well as radiative transfer across the air spaces; it can be shown these are negligible effects, but formal development of the arguments will be left to a more complete description of non-isothermal water transport in leaves, in preparation.

References


