Transport in Sieve Tubes and Plasmodesmata

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SUMMARY. Fluid transport in sieve tubes and in plasmodesmata of plants is considered from a theoretical framework. The effects of filaments on reducing the flow rates in sieve tubes are considered while that of variable geometry and a Newtonian and power-law fluid are evaluated in the plasmodesma model. It appears in the case of the sieve tube that the filaments may have a profound effect on reducing flow rates while in the plasmodesma "necking" at the ends has the same effect.

1. INTRODUCTION

In a recent article by Canny (1977), flow and transport phenomena in plants was reviewed from the plant physiologists viewpoint. Many unresolved problems, or ones needing serious fluid mechanical study, were outlined. One of these involves sucrose translocation in the phloem and in particular concerns flow in the sieve tubes and plates. Another one, that was only briefly mentioned, concerns flow in plasmodesmata. In this paper we look at aspects of flow in both sieve tubes and plasmodesmata.

Before we attempt any fluid mechanical analysis it is necessary to describe briefly the physiology and morphology of the seive tube and a (single) plasmodesma. There are two separate transport tissues, one for movement of water, called the xylem, the other, the phloem where sugars are translocated. Sieve tubes are thought to be the main route for transport of sucrose from the leaves where it is formed to other parts of the tree such as the roots, trunk, branches and twigs. The rate of mass transfer is proportional to the gradient of sucrose concentration. The morphology or shape of the sieve tube is illustrated in Figure 1(a). The sieve tube has a length in the range 200-500 μm and a diameter of 10-25 μm. The sieve plates can be quite thick compared to other cells with a pore length of up to 5 μm. The sieve pores which, again, are much larger than the normal connection through cell walls have radii in the range of 0.08-5.0 μm. They can occupy up to 50% of the cross-sectional area. Micro-filaments of P-protein (radius 5·10 nm) pass through the pores. From this description of the morphology it is clear that the flow patterns are much more complicated than Poiseuille flow; which is the model commonly used by plant physiologists.

Plasmodesmata are common in a wide range of plants (see e.g. Tyree 1970, Gunning and Robards 1976). They are narrow strands of cytoplasm that connect neighbouring plant cells through the common cell wall. It is thought that cells and tissues which are remote from sources of nutrient can be nourished by a bulk flow or diffusion through plasmodesmata and that materials can pass through them to and from the long distance transport tissues of the vascular system (Gunning *et al.* 1976). Plasmodesmata occupy a very small percentage (less than 1%) of the mutual cross-sectional area between the two cells. There are two directions of flow across the root endodermis with sugars moving outwards from the phloem and water and ions inwards into the

xylem. However it is not known if they take separate paths, but it is thought that plasmodesmata play an important role in these transport processes.
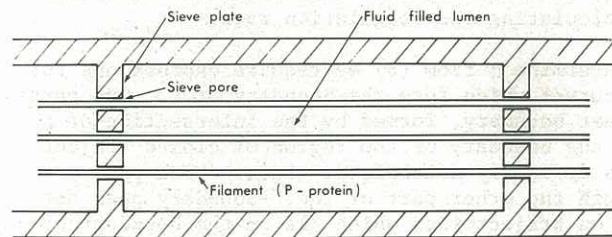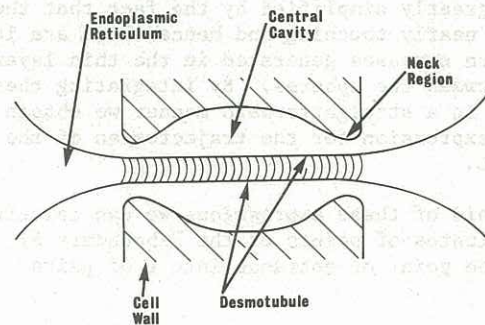
Figure 1 Illustrates the geometry and nomenclature of (a) a sieve tube and (b) a plasmodesma

A schematic diagram of a plasmodesma is shown in Figure 1(b). Nomenclature is taken from Robards (1975). Plasmodesmata are narrow cytoplasmic channels bounded by plasmalemma with an internal diameter of 30-60 nm and a length of 0.5-1.0 μm. It is normally depicted with a hollow axial strand which is called a desmotubule and which is thought to be continuous with the endoplasmic reticulum. The internal and external diameters of the desmotubule are 7-10 nm and 16-20 nm respectively. Thus there are two possible pathways via (a) the desmotubule or (b) the central cavity.

In the succeeding sections we will investigate the effects of fibrils on the flow field in sieve tubes

and then analyse the effects of geometry on the flow rate and pressure change across a plasmodesma for a Newtonian and a power-law fluid. Because of the very small dimensions and flow rates and the possibility of high viscosities, the Reynolds numbers are extremely small, hence we can entirely neglect inertial effects on the flow field. The equations of motion for the incompressible fluid will be those of Stokes flow, or appropriate approximations for the case of these long slender cells and connections. In the final section, the conclusions of this paper will be appraised.

2   MODELLING THE RESISTANCE OF SIEVE PLATES AND PROTEIN FIBRILS

To model the resistance of the sieve plates and P-protein fibrils in complicated on the micro-scale. We may estimate the pressure change ΔP across a sieve tube element by using Poiseuille's law in both the tube and the pore as follows,

$$\Delta P = \frac{8\eta Q}{\pi} \left(\frac{\ell}{a^4} + \frac{L}{NR^4} \right) \tag{1}$$

where Q is the volume flow rate, ℓ the length and a the radius of the sieve tube and L, the length and R, the radius of the sieve-pore respectively while N is the number of pores in the sieve plate. It is often stated (e.g. Canny 1977) that the sieve pores occupy approximately half the area of the sieve plate. Canny (1977) cited examples, based on the above formula, of the pressure gradient along a sieve tube in the absence of a plate and also including it for physiologically relevant data. The overall pressure gradient varies from 0.25 bar m^{-1} in the absence of the sieve plate to 800 bar m^{-1} for the very finest sieve pore (of radius 0.05 μm). Clearly the shape and size of the sieve plate and pores are very important.

To model flow in both the sieve tube and the plasmodesmata in more detail we need to resort to the uni-directional Stokes flow equations in a cylindrical tube,

$$\frac{dp}{dx} = \frac{\eta}{r} \frac{\partial}{\partial r} \left(r \frac{\partial u}{\partial r} \right) \tag{2}$$

where u is the axial velocity and r the radial coordinate. For one protein fibril in the centre of the sieve tube the relation between the pressure drop ΔP across a length ℓ and the volume flow rate Q would be,

$$\Delta P = \frac{8\eta Q \ell}{\pi} \left[a^4 - r_0^4 + (r_0^2 - a^2)^2 / \log(r_0/a) \right]^{-1} \tag{3}$$

where r_0 is the radius of the protein fibril. If the radius of the fibril is only 1/100 that of the sieve tube the pressure change for the same flow rate will be increased by over 25% on that in Poiseuille flow.

However, it is thought that there are a large number of filaments and fibres occupying the sieve tube lumen so a model incorporating this additional resistance is needed. An approximation can be obtained by considering a volume resistance term on the R.H.S. of (2), and since we are concerned with Stokes flow, this term will be proportional to u, the axial velocity, (i.e. we add a term $-\gamma u$ onto the R.H.S. of (2), γ = force/unit volume, see e.g. Brinkman (1949), Saffman (1971), Blake (1975)). It is straightforward to calculate the volume flow rate Q in a cylinder of radius a which includes a volume resistance and compare this with that due to Poiseuille flow (Q_p) in the same tube. The expression is,

$$\frac{Q}{Q_p} = \frac{16}{\alpha^2} \left[\frac{1}{2} - \frac{I_1}{\alpha I_0(\alpha)} \right] \tag{4}$$

where α is the volume resistance parameter ($= (\gamma a^2 / \mu)^{1/2}$) and I_0 and I_1 are modified Bessel functions of the first kind of zeroth and first order respectively. When α tends to zero (i.e. no volume resistance) Q/Q_p obviously tends to 1, while for large α it asymptotes to,

$$\frac{Q}{Q_p} = \frac{8}{\alpha^2} - \frac{16}{\alpha^3} + 0(\alpha^{-4}) \tag{5}$$

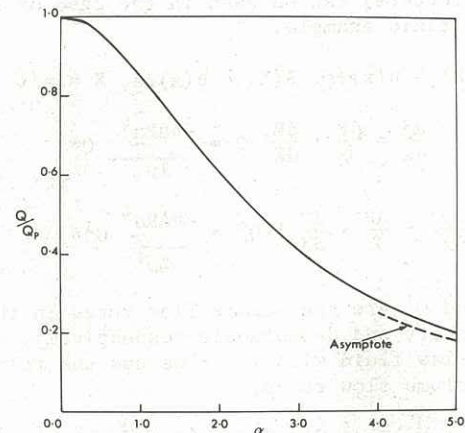from above. A graph of Q/Q_p against α can be seen in Figure 2.

Figure 2   Comparison of the volume flow rates for resistive media with that in Poiseuille flow as a function of the volume resistance parameter α

It is hard to estimate α accurately. However, from Happel and Brenner (1965), we can obtain an approximate value by using their results for an infinite array of cylindrical rods, which gives,

$$\alpha = \left(\frac{2\pi a^2}{(\log(d/r_0) - 1.32)d^2} \right)^{1/2} \tag{6}$$

where d is the spacing of the rods and r_0 their radius (see also Blake 1975). Thus we can assume that $\alpha = 0(a/d)$. Using data based on Canny's review, $d = \sqrt{2\pi} R$ (R = radius of sieve pore) which would give values of α in the range $0(1) - 0(100)$. Thus the hydraulic conductivity for flow in a sieve tube may hardly vary from Poiseuille flow for small values of α but may decrease by up to 3 orders of magnitude for large values of α (see (5), taking $8 = 0(10)$). The pores will increase the resistance further, presumably compressing the fibres closer together and leading to larger values of α there.

3   PLASMODESMATA

The geometry of a plasmodesma is shown in Figure 1(b). We take it to be of length ℓ and the radius of the inner and outer tubes to be $b(x)$ and $h(x)$ respectively, x being the distance along the axis. We will consider two different fluids in the lumen of the plasmodesma (i.e. in the central cavity and desmotubule), a Newtonian fluid in the first example satisfying (2), and a power-law fluid for the second one which satisfies the following equation between the pressure and the viscous stresses,

$$\frac{dp}{dx} = \frac{K}{r} \left(r \left| \frac{\partial u}{\partial r} \right|^\gamma \operatorname{sgn} \left(\frac{\partial u}{\partial r} \right) \right) \tag{7}$$

Here K is a constant analogous to viscosity in a

Newtonian fluid, γ is the index of the power-law fluid and sgn(x) is 1 if $x > 0$ and -1 if $x < 0$. These equations (2) and (7) are valid approximations because the plasmodesma is long and slender. It is straightforward to obtain the linear relationship between the volume flow rate and pressure change across the plasmodesma for the case of a Newtonian fluid and the special case of $\gamma = \frac{1}{2}$ for the power-law fluid. Further details on velocity profiles and additional calculations can be found in Blake (1978).

It is more convenient for computation to use non-dimensional quantities. If we define $\underline{a}$ as the radius of the symmetric desmotubule and the entry and exit point of the flow (i.e. $\underline{a} = b(0) = b(\ell)$), then the following non-dimensional quantities (capital letters) can be used in the case of the Newtonian fluid example,

$$H(X) = h(x)/\underline{a}, \quad B(X) = b(x)/\underline{a}, \quad X = x/\ell$$

$$\frac{dp}{dx} = \frac{\Delta P}{\ell} \cdot \frac{dP}{dX}, \quad Q = \frac{-\pi \Delta P \underline{a}^4}{\ell \mu} Q^* \qquad (8)$$

$$\frac{dp^1}{dx} = \frac{\Delta P}{\ell} \cdot \frac{dP^1}{dX}, \quad Q^1 = \frac{-\pi \Delta P \underline{a}^4}{\ell \mu^1} Q^{1*} $$

where Q and Q^1 are the volume flow rates in the central cavity and desmotubule respectively. For the power-law fluid with $\gamma = \frac{1}{2}$ we use the following for the volume flow rates,

$$Q = -2\pi \left(\frac{\Delta P}{2\ell K}\right)^2 \underline{a}^5 Q^*, \quad Q^1 = -2\pi \left(\frac{\Delta P}{2\ell K^1}\right)^2 \underline{a}^5 Q^{1*} \quad (9)$$

The primes are used to denote quantities in the desmotubule. On dropping the asterisks from the Q's we obtain the following first order differential equations. In the case of the Newtonian fluid we obtain,

$$\frac{dP}{dX} = 8Q[\, H^4 - B^4 + (B^2 - H^2)^2/\log(B/H)]^{-1} \qquad (10)$$

$$\frac{dP^1}{dX} = 8Q^1 B^{-4} \qquad (11)$$

while for the case of the power-law fluid

$$\frac{dP}{dX} = [\, Q/F\,]^{\frac{1}{2}} \qquad (12)$$

$$\frac{dP^1}{dX} = [\, Q^1/F^1\,]^{\frac{1}{2}} \qquad (13)$$

where

$$F = \frac{\delta^6}{2} \left(\frac{1}{B} + \frac{1}{H}\right) - \frac{16}{5}\delta^5 + \frac{3}{2}\delta^4 (B + H)$$

$$- \frac{1}{2}\delta^2 (B^3 + H^3) + \frac{1}{10}(B^5 + H^5)$$

and

$$F^1 = \frac{1}{10} B^5$$

The cylindrical surface in the central cavity where $\partial u/\partial r = 0$ (i.e. shear is zero) is defined by $r = \delta(x)$. It can be obtained by solving a quartic (see Blake 1978).

In the calculations, we have taken,

$$H(x) = \begin{cases} C + (D-C)\sin^2(\pi X/2A) & : \ 0 \leqslant X \leqslant A \\ D & : \ A \leqslant X \leqslant 1-A \quad (14) \\ C + (D-C)\sin^2(\pi(1-X)/2A) & : \ 1-A \leqslant X \leqslant 1 \end{cases}$$

with B(X) being taken as a constant equal to 1 (as $b(x) = \underline{a}$), $A = 0.2$, $D = 3.0$ and C is to be varied $(1.2 \leqslant \tilde{C} \leqslant 3.0)$. This geometry appears to be a reasonable representation of the shape and relative dimensions of an idealised plasmodesma (see Gunning and Robards 1976). With the above geometry it is straightforward to obtain values for Q and Q^1. In the case of Q^1 its value is 0.125 for the Newtonian fluid case and 0.1 for the power-law fluid, but to calculate Q we will need to resort to numerical techniques. It is simplest if we express this gap thickness in terms of a non-dimensional ratio, ε, of the neck gap thickness to maximum thickness of the central cavity. For the geometry represented by (14) we define

$$\varepsilon = \frac{C-B}{D-B} \qquad (15)$$

In Figure 3(a), the ratio Q/Q^1 is plotted as a function of ε on a log/linear plot for both the Newtonian and power-law fluid case. They both show a similar shaped curve with the rapid decrease in
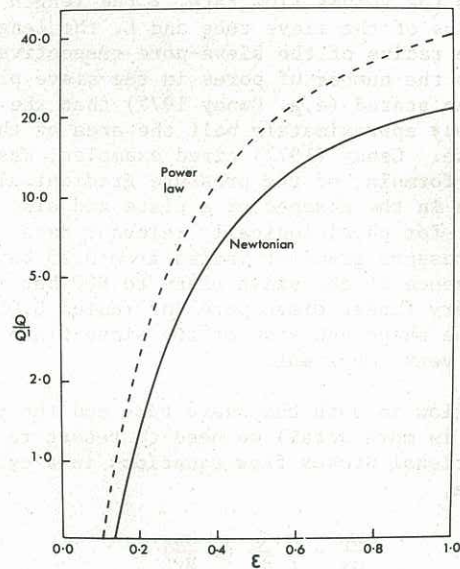
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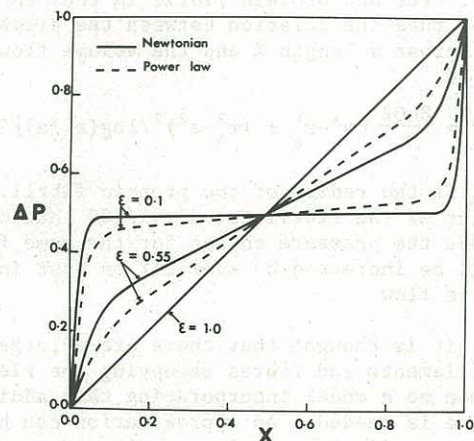
b

Figure 3(a) Ratio of volume flow rates in central cavity to that in desmotubule (Q/Q^1) as a function of the non-dimensional gap thickness ε for both a Newtonian (—) and a power-law ($\gamma = \frac{1}{2}$, ---) fluid. (b) Pressure changes across the plasmodesma as a function of length and gap thickness; again for both fluids

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volume flow rate with decreasing gap thickness ε being the prominent feature of both curves. For ε less than about 0.15 the volume flow rate is larger in the desmotubule in both examples. To understand the physics of flow in the central cavity it is illuminating to look at the pressure changes along its length. In Figure 3(b), the pressure changes are illustrated for the ideal symmetric plasmodesma used in this paper. Values of ε are indicated on the figure. For narrow neck gap thicknesses most of the pressure change across the central cavity of the plasmodesma occurs in the neck region: for example in the case of $\varepsilon = 0.1$, 95% and 99% of the pressure change for the power-law and Newtonian fluids respectively. In the rigid central desmotubule the pressure change follows the straight line given by $\varepsilon = 1.0$. From this graph it is apparent that the desmotubule membrane may have a pressure change across it equal to almost half the neck gap thicknesses. If this membrane is sufficiently permeable another pathway using both the desmotubule and central cavity may be possible.

5 CONCLUSIONS

In this paper we have looked at several aspects of flow in sieve tubes and plasmodesmata within plants. Our theory would indicate that the presence of fibrils within the sieve tubes may significantly decrease the volume flow rate for a given pressure change. Clearly this effect needs to be included in any future models of sucrose translocation, possibly by using a lower value of the permeability. It is apparent from the mathematical model of flow in the plasmodesma that the single most important feature affecting volume flow rates is the constriction (the neck) at each end of the central cavity. Geometry also has an important influence on the pressure distribution within the plasmodesma, opening up other possible transport paths. These will be investigated in more detail in a later paper (Blake 1978). Overall, these theoretical analyses produce much lower estimates for the hydraulic conductivity than have been used previously. This may indicate that other mechanisms need to be considered for transport in plants instead of the standard pressure difference – bulk flow models.

6 ACKNOWLEDGEMENTS

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