Fluid Dynamics of Phloem Flow: An Axisymmetric Model

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ABSTRACT

FLOW through sieve tubes with sieve plates in the phloem of plants is studied by using an idealized single-pore, axisymmetrical model. The sap is modeled by the steady creeping motion of an incompressible viscous fluid. Numerical results are presented for the associated pressure drop and comparison is made with the simplified resistance formula currently in use in the plant physiology literature.

INTRODUCTION

Sugars manufactured in the leaves of plants during photosynthesis are translocated to other parts of the plant through the phloem. The flow takes place chiefly through cells called sieve tubes which are arranged end to end and are joined by perforated cell walls called sieve plates (see Fig. 1).

Recent mathematical models of the process of translocation in the phloem have dealt with the pressure drop encountered by a viscous fluid moving through a series of sieve tubes and sieve plates (Crafts and Crisp, 1971; Christy and Ferrier, 1973; Young, Evert and Eschrich, 1973; Tyree, Christy and Ferrier, 1974). This question is of physiological importance in determining the validity of various hypothesis for the mechanism of translocation (Housley and Fisher, 1977; Aronoff, 1975).

The currently used expression for this pressure drop is derived by applying Poiseuille's law to both the sieve tubes and to the individual pores of the sieve plate, with the following result:

$$\Delta p = \frac{8}{\pi} \frac{Q\eta}{R^4} \left[L + \frac{\ell}{N} \left(\frac{R}{r} \right)^4 \right] \quad [1]$$

where

- Δp = pressure drop due to one sieve tube and one sieve plate
- Q = flow rate
- η = viscosity
- N = no. of pores in sieve plate
- r = pore radius (Fig. 2)
- R = sieve tube radius (Fig. 2)
- ℓ = sieve plate thickness (Fig. 2)
- L = sieve tube length (Fig. 2)

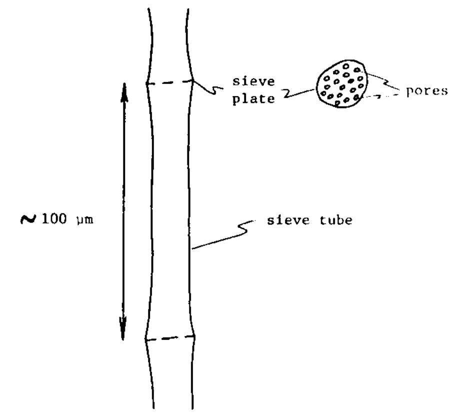

FIG. 1 Sieve tubes with sieve plates.

We refer to equation [1] as the resistance formula since it can be derived (by analogy with Ohm's law) by placing the sieve tube resistance in series with the set of N parallel sieve plate pore resistances.

The resistance formula neglects some additional pressure drop that occurs as the streamlines in the sieve tube bend to pass through the pores in the sieve plate. For example, consider the limiting case $\ell \rightarrow 0$ in which the sieve plate is taken as having arbitrarily small but nonzero) thickness. Here the resistance formula predicts a pressure drop equal to that of simple Poiseuille flow in a

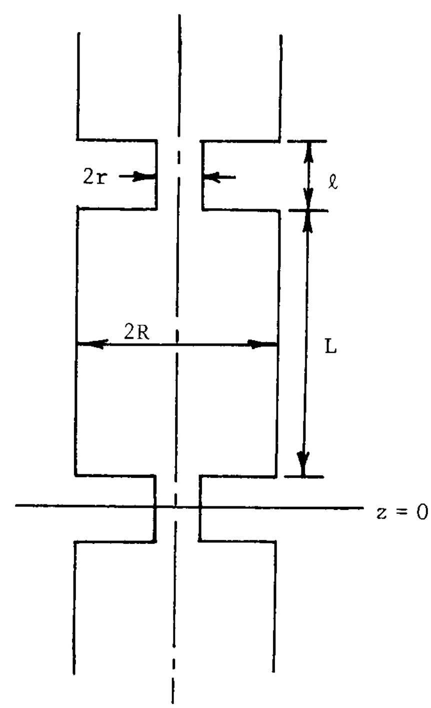

FIG. 2 Geometry of idealized axisymmetric model.

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uniform circular tube (without sieve plates). This value of Δp is obviously smaller than that which would be predicted by the Navier-Stokes equations.

The purpose of this paper is to offer an estimate of the accuracy of the widely used resistance formula, equation [1], in the special (mathematically simpler) case in which each sieve plate contains a single axisymmetrically placed circular pore ($N = 1$). It is to be emphasized that this axisymmetric study is not intended to be either a realistic model or a definitive treatment of phloem flow. The more realistic N pore case is more difficult analytically and may be better handled numerically (e.g. by finite element methods.) Our strategy is to explore the simplest case ($N = 1$) before the more general. Moreover, this paper is concerned only with the fluid dynamics of phloem flow and does not consider the physiological factors which drive the flow.

Since the Reynolds number for phloem flow had been estimated to be about 10^{-3} (Horwitz, 1958), we ignore inertia terms in the Navier-Stokes equations and consider an incompressible viscous fluid undergoing steady creeping motion (Happel and Brenner, 1965).

Lew, Fung and Lowenstein, (1971) studied this problem for the limiting case $\ell \to 0$. Although they presented an analytic solution, all their numerical results pertained to the case of a moving sieve plate (modeling peristalsis).

Wang and Skalak, 1969, presented an analytic solution for the problem of creeping flow around a line of spheres placed periodically along the axis of a circular tube (modeling the microcirculation). Although their problem is very different from the one considered in this paper (both physically and biologically), the mathematical treatments are similar.

BOUNDARY VALUE PROBLEM

The steady creeping motion of an incompressible fluid is governed by the differential equations (Happel and Brenner, 1965).

$$\nabla p = \eta \nabla^2 \overline{V} \qquad [2]$$

$$\nabla \cdot \overline{V} = 0 \qquad [3]$$

where $\overline{V}$ = velocity vector. These equations are supplemented by the no slip condition, $\overline{V} = 0$ on the boundary (Fig. 2), as well as by the requirement that the flow rate Q be given.

For axisymmetric flows, the problem can be simplified by introducing a stream funciton ψ (Happel and Brenner, 1965). In cylindrical coordinates, ρ, Θ, z, the velocities V_ρ and V_z are related to ψ as follows: ($V_\Theta = 0$ for axisymmetric flows)

$$V_\rho = \frac{1}{\rho}\frac{\partial \psi}{\partial z}, \quad V_z = -\frac{1}{\rho}\frac{\partial \psi}{\partial \rho} \qquad [4]$$

Equation [4] automatically satisfies the incompressibility condition [3].

Now since $\nabla \times \nabla p = 0$, taking the curl of equation [2] gives

$$\nabla \times (\nabla^2 \overline{V}) = 0 \qquad [5]$$

Equations [4], [5] together yield a fourth order partial differential equation on ψ,

$$\left(\frac{\partial^2}{\partial z^2} + \frac{\partial^2}{\partial \rho^2} - \frac{1}{\rho}\frac{\partial}{\partial \rho}\right)^2 \psi = 0 \qquad [6]$$

Wang and Skalak (1969) give the following expression for solutions to equation [6] which are even, periodic in z with period $L + \ell = 2\pi/k$, and which are bounded at $\rho = 0$,

$$\psi(\rho,z) = \sum_{m=0}^{\infty} C_m(\rho)\cos mkz \qquad [7]$$

where

$$C_o(\rho) = A_o\rho^4 + B_o\rho^2$$

$$C_m(\rho) = A_m\rho I_1(mk\rho) + B_m\rho^2 I_o(mk\rho), \quad m > 0$$

and where A_m, B_m are arbitrary constants and I_o, I_1 are modified Bessel functions of the first kind.

From equations [4], [7] the velocities V_ρ, V_z become

$$V_\rho(\rho,z) = \sum_{m=1}^{\infty} D_m(\rho)\sin mkz \qquad [8]$$

$$V_z(\rho,z) = \sum_{m=0}^{\infty} K_m(\rho)\cos mkz \qquad [9]$$

where

$$D_m(\rho) = -mk[A_m I_1(mk\rho) + B_m\rho I_o(mk\rho)]$$

$$K_o(\rho) = -4\rho^2 A_o - 2B_o$$

$$K_m(\rho) = -mkA_m I_o(mk\rho) - B_m[mk\rho I_1(mk\rho) + 2I_o(mk\rho)], \quad m > 0$$

Substitution of equations [8], [9] into equation [2] gives the following expression for pressure p:

$$p(\rho,z) = p_o - 16\eta A_o z + \sum_{m=1}^{\infty} S_m(\rho)\sin mkz \qquad [10]$$

where $S_m(\rho) = -2\eta mkB_m I_o(mk\rho)$
and where ρ_o is an arbitrary constant.

In this work we are interested in the pressure drop Δp occurring over one period of length $L+\ell$ (see Fig. 2). From equation [10], find

$$\Delta p = 16\eta(L+\ell)A_o = 16\eta\frac{Q}{R^4}(L+\ell)\overline{A}_o \qquad [11]$$

where $\overline{A}_0 = R^4A_0/Q$ is a dimensionless form of the coefficient A_0. Here $\overline{A}_0$ depends only on the geometrical ratios r/R, ℓ/R, L/R. We are therefore interested only in the coefficient $\overline{A}_0$. Equation [11] will be compared to the predictions of the resistance formula [1].

It remains for us to choose the constants A_m, B_m so as to satisfy the boundary conditions. For a general shaped boundary B: $\rho = \rho(z)$ we require that $\psi = -Q/2\pi$ (for the

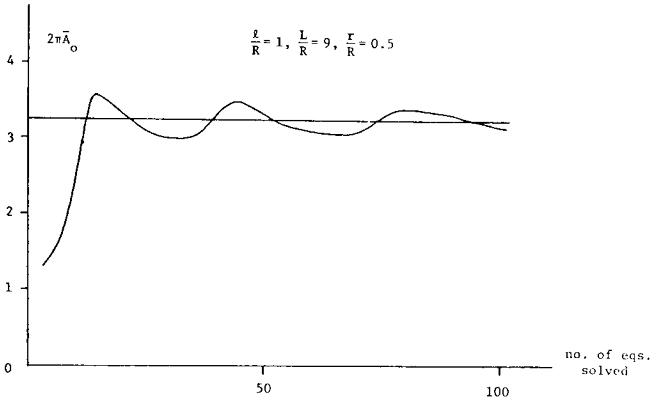

FIG. 3 Behavior of successive approximations of coefficient $\overline{A}_o$ obtained by solving truncated system of algebraic equations.

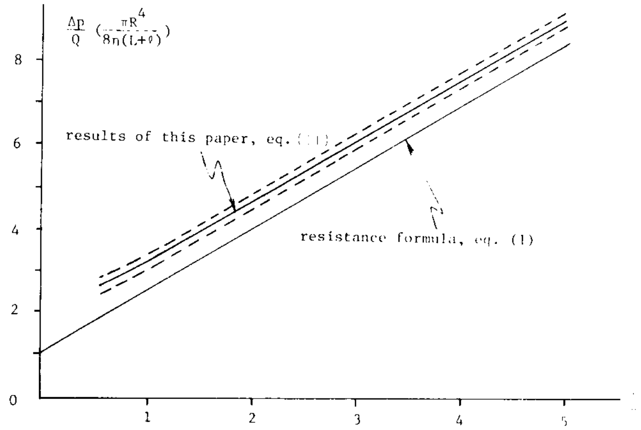

FIG. 4 Dimensionless resistance displayed as a function of ℓ/R for fixed values of $r/R = 0.5$, $\ell + L = 10R$. Dotted lines show the extent of numerical oscillation [cf. Fig. 3].

flow rate to equal Q) and $V_t = 0$ on B (for no slip), where V_t is the velocity in the direction tangent to B. (The velocity normal to B is automatically zero since ψ = constant on B implies that B is a streamline).

For this problem we therefore require that

$$\psi = -\frac{Q}{2\pi} \text{ and } V_z = 0 \qquad [12]$$

$$\text{on B: } \rho = \rho(z) = \begin{cases} r, & 0 < z < \dfrac{\ell}{2} \\ R, & \dfrac{\ell}{2} < z < \dfrac{\ell}{2} + \dfrac{L}{2} \end{cases} \qquad [13]$$

where ψ and V_z are given by equations [7], [9]. Only $0 < z < (\ell+L)/2$ need be considered here due to the even, periodic form of equations[7], [9].

Multiplying both of equations [12] by cos mkz and integrating from $z = 0$ to $(\ell+L)/2$, obtain an infinite system of linear algebraic equations on A_m, B_m:

$$\sum_{m=o}^{\infty} E_{mn}A_m + F_{mn}B_m = \begin{cases} -Q, & n = 0 \\ 0, & n = 1,2,3,\ldots \end{cases} \qquad [14]$$

$$\sum_{m=o}^{\infty} G_{mn}A_m + H_{mn}B_m = 0, \quad n = 0,1,2,3,\ldots$$

where

$$\begin{aligned}
E_{on} &= r^4\alpha_{on} + R^4\beta_{on} \\
E_{mn} &= rI_1(mkr)\alpha_{mn} + RI_1(mkR)\beta_{mn}, \; m > 0 \\
F_{on} &= r^2\alpha_{on} + R^2\beta_{on} \\
F_{mn} &= r^2 I_o(mkr)\alpha_{mn} + R^2 I_o(mkR)\beta_{mn}, \; m > 0 \\
G_{on} &= 4F_{on} \\
G_{mn} &= mkI_o(mkr)\alpha_{mn} + mkI_o(mkR)\beta_{mn}, \; m > 0 \\
H_{on} &= \begin{cases} 4\pi, & n = 0 \\ 0, & n > 0 \end{cases} \\
H_{mn} &= [mkrI_1(mkr) + 2I_o(mkr)]\alpha_{mn} \\
&\quad + [mkRI_1(mkR) + 2I_o(mkR)]\beta_{mn}, \; m > 0
\end{aligned}$$

$$\alpha_{mn} = \begin{cases} \dfrac{\sin(m+n)\pi\lambda}{m+n} \quad \dfrac{\sin(m-n)\pi\lambda}{m-n}, & m \neq n \\ \dfrac{\sin 2n\pi\lambda}{2n} + \pi\lambda, & m = n \neq 0 \\ 2\pi\lambda, & m = n = 0 \end{cases}$$

$$\beta_{mn} = \begin{cases} -\alpha_{mn}, & m \neq n \\ \pi-\alpha_{nn}, & m = n \neq 0 \\ 2\pi-\alpha_{oo}, & m = n = 0 \end{cases}$$

$$\lambda = \frac{1}{1 + \dfrac{L}{\ell}}$$

Since the eigenfunctions involved in this problem are not orthogonal, the system of algebraic equations [14] is not diagonal.

NUMERICAL RESULTS

Although the above analytical solution is formally exact, it is necessary to truncate the infinite series [7] and the corresponding system of algebraic equations [14] in order to evaluate them numerically.

We obtained successive approximations to the coefficient $\overline{A}_o$ by truncating equation [7] at $m = M$ and solving $2(M+1)$ simultaneous equations [14], for $M = 1$ to about 50. Fig. 3 contains an example of the graph of the resulting sequence of values of $\overline{A}_o$. The convergence was very slow and even after solving 100 non-banded simultaneous equations, the sequence was still oscillating as in Fig. 3.

In order to obtain an approximate value for $\overline{A}_o$, we averaged the successive maxima and minima of the graph of the $\overline{A}_o$ sequence (Fig. 3). The values of each of these extrema were approximated by passing a parabola through three neighboring points on the graph of the sequence.

Equation [11] is displayed in Fig. 4 using the values of $\overline{A}_o$ obtained in this way. The parameter values were taken as $r = R/2$, $L + \ell = 10R$ while ℓ/R was varied between 0.5 and 5.0. Although values of $\ell/R < 0.5$ are of interest, slow convergence would have required far more than 100 simultaneous equations to be solved for such values of ℓ/R. The average amplitude of the oscillation is characterized in Fig. 4 by dotted lines which show how far the graph of the sequence deviates from the computed value of $\overline{A}_o$. Fig. 4 also displays the resistance formula, equation [1], with $N = 1$ pore.

The validity of our numerical procedure was tested

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by comparing these results with those independently obtained by Professor S. F. Shen and his colleagues. They used the finite element method to study this same problem (in a totally different physical context).

CONCLUSION

Fig. 4 shows that, as suggested in the introduction, the resistance formula gives too small a value for Δp. The largest error occurs for small ℓ/R.

Although dimensions of sieve elements vary considerably, a typical value for ℓ/R is 0.1. In this range of values, Fig. 4 suggests that the resistance formula is off by a factor of about 2.

Of course these results are limited to $r = R/2$; smaller values of r/R will lead to larger errors in the predictions of the resistance formula.

The biologist who uses the resistance formula, equation [1], should beware that it contains an assumption regarding the fluid flow pattern. Consideration of the error in equation [1], which is a consequence of this assumption, has been the subject of this paper. Our analysis has revealed that in the highly idealized axisymmetric case ($N = 1$) with the particular geometry considered, equation [1] underestimates the resistance ($\Delta p/Q$) by a factor of about 2. In a more realistic non-axisymmetric case with $N(> 1)$ pores, the resistance formula would also give a smaller value for resistance than a more exact analysis comparable to that presented in this paper. Such a non-axisymmetric study would be of interest.

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