Fluid Dynamics of Phloem Flow: Part II
An Approximate Formula

R. H. Rand, S. K. Upadhyaya, J. R. Cooke
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ABSTRACT

AN approximate formula is derived for the pressure drop encountered by a viscous fluid as it flows through a series of sieve tubes with sieve plates. The derivation is based upon the known solution for low Reynolds number conical flow. Our treatment offers an improvement to the resistance formula currently used in the plant physiology literature.

INTRODUCTION

The study of the fluid dynamics of flow in the phloem tissue of plants is closely related to the largely unanswered question of the mechanism of translocation. In order to evaluate a particular translocation mechanism, the biologist must be able to determine whether the mechanism can generate, from physiological considerations, enough of a pressure difference to drive the fluid through the phloem tissue against pressure losses due to viscous effects. Thus the biologist needs to know the pressure drop encountered by fluid flowing through a series of sieve tubes with periodically placed sieve plates with pores (Fig. 1).

The approach which is usually taken in computing this pressure drop is to apply Poiseuille's law to the sieve tube in series with N pores of the sieve plate in parallel. We will call the resulting expression the resistance equation:

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

where

- Δp = pressure drop due to flow past one sieve tube and one sieve plate, dyne/cm²
- η = viscosity, g/cm-s
- Q = flow rate, cm³/s
- N = number of pores in sieve plate
- R = sieve tube radius, cm
- r = sieve pore radius, cm
- L = sieve tube length, cm
- ℓ = sieve plate thickness, cm

(See, e.g., Crafts and Crisp, 1971; Christy and Ferrier, 1973; Young, Evert and Eschrich, 1973; Tyree et al., 1974; Aronoff, 1975; Housley and Fisher, 1977).

Equation [1] neglects some additional pressure drop which occurs as the streamlines in the flow bend in the region near the sieve tube-sieve plate interface (Tryee et al., 1974). See Figs. 2a, 2b.

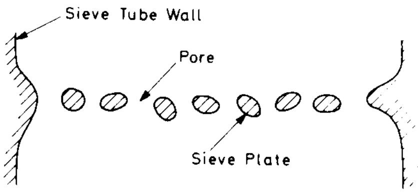

FIG. 1 Longitudinal section of a sieve tube in the neighborhood of a sieve plate showing pores. (After Esau, 1965, p. 669).

In a previous paper (Rand and Cooke, 1978) we developed a procedure for estimating the accuracy of the resistance equation in the special (mathematically simpler) case of a single axisymmetric circular pore (N = 1). We presented an analytical solution to the Navier-Stokes equations for creeping flows which involved solving at least a hundred simultaneous algebraic equations. Although this work was formally exact, its usefulness was limited both by the complexity of the computational algorithm as well as by the inapplicability of the model (the N = 1 case is anatomically unrealistic).

The purpose of the present work is to supplement our previous paper by providing a simple (though approximate) equation which estimates the error involved in the resistance equation [1]. The improved equation will be shown to have the form

$$\Delta p = \frac{8}{\pi} \frac{\eta Q}{R^4} \left[L + \frac{\ell}{N} \left(\frac{R}{r}\right)^4\right] + 2\,(\Delta p') \quad [1a]$$

where $\Delta p'$ will be given later. Although the approximate equation [1a] to be derived in this work has been verified only for the axisymmetric N = 1 case, we believe it represents an improvement over the resistance equation [1] in the general N-pore case as well.

In addition to the technical papers referenced in our previous work (Rand and Cooke, 1978) we wish to add

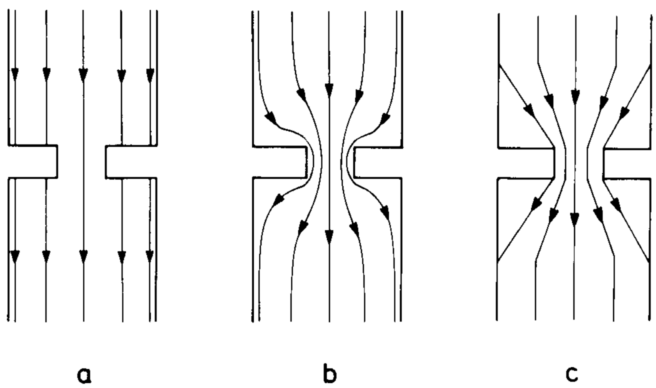

FIG. 2 Sketch of streamlines as assumed by various theories in the case of a single pore: (a) resistance formula; (b) exact solution of Navier-Stokes equations; (c) approximate formula of this paper.

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The authors are: R. H. RAND, S. K. UPADHYAYA and J. R. COOKE, Departments of Theoretical and Applied Mechanics and Agricultural Engineering, Cornell University, Ithaca, NY.

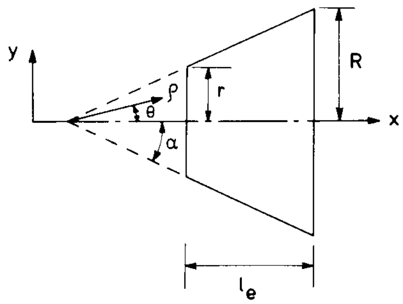

FIG. 3 The geometry of conical flow.

the paper of Lew and Fung (1971) who studied the N = 1 case in the limit $\ell \rightarrow 0$. They presented an analytical solution upon which they based their numerical computations which involved solving 20 simultaneous algebraic equations. Their work was involved with modeling the flow of blood in valved veins.

It is to be noted that we assume in this paper that the sieve plate pores are open (i.e., they are not occluded by P-protein filaments, cf. Spanner, 1978). Furthermore all results presented are based on theoretical considerations rather than experimental data.

The Model

In order to derive an approximation for the additional pressure drop over the resistance equation [1] we will assume the simplified flow pattern of Fig. 2c. That is, we will replace the bending of the streamlines in the realistic situation, Fig. 2b, by a region of conical flow. This assumption represents a compromise between the mathematically difficult situation of the Navier-Stokes equations (Fig. 2b) and the more unrealistic flow associated with the resistance equation (Fig. 2a). We restrict discussion in this section to the single pore (N = 1) case, but return to consider the general N pore problem later.

After deriving an expression for the pressure drop associated with the flow of Fig. 2c, we will compare our results with the more exact (and more computationally cumbersome) analysis presented in our previous paper (Rand and Cooke, 1978).

We begin by computing the pressure drop in a region of conical flow. The basic fluid dynamics for low Reynolds number (creeping) conical flow has been presented in Happel and Brenner (1965), pp. 138-141. They give the pressure distribution associated with Fig. 3 as

$$p = -\frac{\eta Q}{\pi \rho^3}\,\frac{1-3\xi^2}{(1+2\xi_o)(1-\xi_o)^2} \quad \text{[2]}$$

where

- p = pressure at (p,θ)
- p,θ = spherical polar coordinates
- ξ = $\cos\theta$
- ξ_o = $\cos\alpha$, where α = cone angle (Fig. 3)

and where the (arbitrary) pressure at infinity has been set to zero.

Using equation [2] we compute the average pressure $\bar{p}$ on the end cross-sections perpendicular to the cone axis (of radii r, R respectively). On the radius R cross-section,

$$\bar{p} = \frac{1}{\pi R^2}\int_0^R \frac{-\eta Q}{\pi \rho^3}\,\frac{(1-3\xi^2)}{(1+2\xi_o)(1-\xi_o)^2}\,2\pi y\,dy \quad \text{[3]}$$

where

$y = p\sin\theta$ = distance from cone axis (Fig. 3)
$x = p\cos\theta$ = distance along cone axis from vertex (Fig. 3)

On the end cross-section of radius R, the distance x is a constant:

$$x = R\cot\alpha \quad \text{[4]}$$

Also,

$$y = R\cot\alpha\tan\theta \quad \text{[5]}$$

Substituting equations [4], [5] into [3], we obtain

$$\bar{p} = \frac{2\eta Q\tan\alpha}{\pi R^3(1+2\xi_o)(1-\xi_o)^2}\int_o^{\xi_o}(1-3\xi^2)d\xi \quad \text{[6]}$$

Performing the integration and using $\xi_o = \cos\alpha$,

$$\bar{p} = \frac{2\eta Q}{\pi R^3}\,\frac{\sin\alpha(1+\cos\alpha)}{(1+2\cos\alpha)(1-\cos\alpha)} \quad \text{[7]}$$

A similar computation on the other end cross-section of radius r gives the following expression for the additional pressure drop over Poiseuille flow, $\Delta p'$, due to the flow in the conical region:

$$\Delta p' = \frac{8\eta Q}{\pi R^3}\left\{\frac{\sin\alpha(1+\cos\alpha)}{4(1+2\cos\alpha)(1-\cos\alpha)}\left[\left(\frac{R}{r}\right)^3-1\right]-\frac{\ell e}{R}\right\} \quad \text{[8]}$$

where the pressure drop due to Poiseuille flow over a length ℓe has been subtracted from the pressure drop due to the conical flow. Here

$$\ell e = (R-r)\tan\alpha = \text{entrance length (Fig. 3)} \quad \text{[9]}$$

For a given problem it remains to choose ℓe (or equivalently, α). From our previous work (Rand and Cooke, 1978), we found that the resistance formula was low by an amount that did not depend on the lengths ℓ (of the sieve plate) or L (of the sieve tube). (See e.g. Fig. 4 of Rand and Cooke, 1978). From similitude considerations we therefore expect that

$$\frac{\ell e}{R} = f\left(\frac{r}{R}\right) \quad \text{[10]}$$

Although we do not know the form of the function f in equation [10], we must have no additional pressure drop as $r \rightarrow R$:

$$f(1) = 0 \quad \text{[11]}$$

Expanding f(r/R) in a Taylor series about r = R, and using equation [11], we find

$$f(r/R) = f'(1)\left(\frac{r}{R}-1\right) + \ldots \quad \text{[12]}$$

Neglecting higher order terms and setting $\lambda = -f'(1)$, we are led to assume

$$\frac{\ell e}{R} = \lambda\left(1-\frac{r}{R}\right) \quad \text{[13]}$$

TABLE 1. COMPARISON OF PRESSURE DROPS DUE TO ONE SIEVE TUBE AND ONE SIEVE PLATE AS PREDICTED BY VARIOUS THEORIES
Values given are nondimensional pressure drops defined by $(\Delta p)(\pi R^4)/[8\eta Q(L+\ell)]$. All cases are for $\ell = L = 5R$. Note that in column 4, $\Delta p'$ of equation [8] has been doubled since there is an entrance region on each side of the sieve plate.

r/R	"exact" solution (Rand and Cooke)	Resistance formula equation [1]	Equation [8] with $\lambda = 1.5$ in equation [13]	Improved approximation (cols. 3+4)
0.5	9.15	8.50	0.65	9.15
0.6	4.69	4.36	0.29	4.65
0.7	2.72	2.58	0.13	2.71
0.8	1.775	1.721	0.049	1.770
0.9	1.275	1.262	0.012	1.274

where λ is a constant independent of the other model parameters. The cone angle α may be expressed in terms of λ by equation [9].

$$\tan\alpha = 1/\lambda \quad \ldots\ldots \quad [14]$$

The problem now reduces to finding a suitable value for λ. We accomplished this by comparison with more exact results obtained by the method of our previous paper (Rand and Cooke, 1978). We found that $\lambda = 1.5$ gave good results. See Table 1 where we list values of nondimensional pressure drops obtained by both methods for several geometries. In fact the value of $\Delta p'$ of equation [8] is not very sensitive to the choice of λ. We found that values of λ between about 1.4 and 1.6 gave reasonable results. In their study of the $\ell \to 0$ case, Lew and Fung (1971) (p. 89) found that there was an entrance region about 1.3 times the tube radius R. (Note however that (a) they did not use a conical flow, and (b) our equation [13] gives ℓe as $\lambda(1\text{-}r/R)$ times the tube radiius R, or with $\lambda = 1.5$, $\ell e/R$ is smaller than 1.5 by a factor depending on the pore size).

DISCUSSION

The approximate solution of the previous section may be rewritten in a more useful form. Substituting $\lambda = 1.5$ into equation [14] we find

$$\alpha = \arctan(1/\lambda) = 33.7 \text{ deg} \quad \ldots\ldots \quad [15]$$

Utilizing equation [13] in [8] we find

$$\Delta p' = \frac{8\eta Q}{\pi R^3}\left\{0.57[(\frac{R}{r})^3 - 1] - 1.5(1 - \frac{r}{R})\right\} \quad \ldots\ldots \quad [16]$$

Equation [16] permits us to write an improved approximate equation based on the resistance equation [1]. We find that in the single pore case (N = 1), the pressure drop across one sieve tube and one sieve plate is well approximated by the expression

$$\Delta p = \frac{8\eta Q}{\pi R^4}[L + \frac{\ell}{N}(\frac{R}{r})^4] + 2(\Delta p') \quad \ldots\ldots \quad [17]$$

where $\Delta p'$ is given by equation [16] for N = 1. Note that $\Delta p'$ must be counted twice since there is an entrance region on each side of the sieve plate.

Now let us consider the more realistic N pore case. If we assume that each pore is fed by a portion of the sieve tube and if we taken each of the N pores to have an average radius r, then the "effective tube radius" R_e associated with each pore may be defined by the relation

$$\pi R^2 = N\pi R_e^2 \quad \ldots\ldots \quad [18]$$

or

$$R_e = R/\sqrt{N} \quad \ldots\ldots \quad [19]$$

where once again R is the sieve tube radius. In order to obtain an approximate expression for $\Delta p'$ in the N pore case, we replace R in equation [7] by R_e and proceed with the derivation as in the N = 1 case, dividing the resulting expression for the pressure drop in the conical flow region by N (for N pores in parallel). Taking $\ell e = 1.5(R_e\text{-}r)$ (cf. equation [13]), we find

$$\Delta p' = \frac{8\eta Q}{\pi R^3}(\frac{R_e}{R})\left\{0.57N[(\frac{R_e}{r})^3 - 1] - 1.5(1 - \frac{r}{R_e})\right\} \quad \ldots \quad [20]$$

equation [17] still holds in the general N pore case, but now $\Delta p'$ is given by equation [20].

Although equations [17] and [20] have been checked against a more exact solution in the single pore (N = 1) case, there is no easy way to check their accuracy in the general $N > 1$ case. For $N > 1$ the problem is non axisymmetric and therefore is more difficult mathematically than the N = 1 case: no exact solution is available for $N > 1$. Nevertheless the $N > 1$ case could be checked against a numerical solution obtained, e.g., by finite elements or finite differences. Alternately, an experimental simulation involving a physical model of a sieve tube with a sieve plate could be used to check the $N > 1$ case. However, since the approximate equations [17] and [20] give good agreement with a more exact solution in the case of a single pore (N = 1) we believe they offer an improvement to the resistance equation [1] in the $N > 1$ case.

The ratio E of the additional pressure drop predicted by the conical flow analysis of equation [20], $2\,\Delta p'$, to the pressure drop predicted by the resistance equation [1] gives a measure of the improvement offered by our theory.

$$D = \frac{\Delta p_{additional}}{\Delta p_{resistance}} \times 100 \text{ percent} = \frac{2\,\Delta p'}{\Delta p_{resistance}} \times 100 \text{ percent} \quad \ldots\ldots \quad [21]$$

Table 2 displays evaluations of equation [21] for various biological parameters taken from the literature.

The value of E was found to vary from 15 percent to 76 percent. This suggests that while the resistance equation may be sufficiently accurate for certain applications, the

TABLE 2. NUMERICAL EVALUATION OF EQUATION [21]

Species	R μm	r μm	L μm	ℓ μm	N§	E(%) (equation [21])	Reference
Cucurbita melopepo	40	2.4	250	5	120	36	Crafts and Crisp, 1971 (p. 399)
Glycine max (stem)	6.5	0.60	156	1.2	53	26	Housley and Fisher, 1977 (p. 705)
Beta vulgaris	5	0.1	200	0.4	1250	17	Tyree et al., 1974 (p. 592)
Sabal palmetto	18	0.95	700	0.5	287	15	"
Robina pseudo-acacia	10	0.5	125	0.5	133	76	"
Gossypium bardadense	11	0.5	210	1.0	161	40	"

§N is calculated from percent pore area (ρ) using the relation $N = \frac{\rho}{100}(\frac{R}{r})^2$.

approximate equation [17] may provide a significant improvement for quantitative studies requiring greater precision.

CONCLUSION

We have derived an expression for the pressure drop in phloem flow, equation [17], which improves the much used resistance equation [1]. The new approximation offers a compromise between the mathematically intricate but more exact solution of our previous paper (Rand and Cooke, 1978) and the straightforward but questionably accurate resistance equation [1].

We have checked our approximate equation [17] against our previous work in the axisymmetric single pore case ($N = 1$). We have provided a logical extension of this approximate formula to the more realistic $N > 1$ pore case, but it has not been checked against a more exact solution. A study involving a more exact solution in the $N > 1$ pore case would be of interest.

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