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ESTIMATING VOLUME FLOW RATES THROUGH XYLEM CONDUITS[1]

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We discuss the errors in common approximations of the volume flow rate for laminar flow through conduits with noncircular transverse sections. Before calculating flow rates, ideal geometric shapes are chosen to represent the noncircular transverse sections. The Hagen–Poiseuille equation used with hydraulic diameter underestimates the volume flow rate for laminar flow through conduits even with such ideal shapes. Correction factors that have been proposed for the Hagen–Poiseuille equation also lead to underestimates of the volume flow rate for those shapes. The exact solutions are sometimes difficult to attain, but rates calculated using the exact solutions for the ideal shapes may be as much as five times higher than the approximated rates for common transversely elongated shapes. Either the exact solutions or the approximations may be used to calculate volume flow rates through the xylem of plants. Both of these methods actually approximate flow through the original conduits because the shapes used are approximations of the conduits' transverse sections. We recommend using the exact solutions whenever possible; they should be closer to the real solution than other approximations. We give tables of correction factors for use in the cases where calculating volume flow rate from the approximate solution, the Hagen–Poiseuille equation, is more feasible. Obtaining theoretical volume flow rates that are larger than previously thought highlights the need to clarify the causes of differences between the theoretical rates and the smaller measured volume flow rates in plant xylem.

As part of an ongoing project to understand the dynamics of water flow through the xylem we discuss exact equations to calculate water flow through noncircular ideal capillaries and investigate the errors in frequently used approximations. In determining theoretical volume flow rates through the xylem of plants, the Hagen–Poiseuille equation for laminar flow through conduits is often used. The Hagen–Poiseuille equation provides the exact solution for laminar flow in individual ideal capillaries with circular transverse sections, but the application of this equation to conduits with noncircular transverse sections using the hydraulic diameter results in errors in the calculated volume flow rates. Exact solutions for the determination of volume flow rate through capillaries with some common noncircular transverse sections have recently been published in English (White, 1991). In general, errors in calculated flow rates may result from anatomical deviations of the xylem conduits from ideal capillaries, or from methods used to calculate the volume flow rate. This paper investigates the latter more completely than previous botanical literature (e.g., Leyton, 1975; Nonweiler, 1975; Petty, 1978; Pickard, 1981; Zimmermann, 1983; Calkin, Gibson, and Nobel, 1986; Lewis, 1992), discusses some exact solutions for volume flow rates through some common noncircular conduits, and recommends methods for the calculation of theoretical volume flow rates based on desired accuracy, speed, and ease of calculation.

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SOURCES OF ERROR

Potentially large errors in the calculated volume flow rate (J_v) may result from errors in the measurement of the conduit transverse-sectional axes, from the approximation of the conduit transverse section by a simple geometric shape, or from the application of the volume flow equations for that shape. Tracheids and vessels with circular transverse sections are the easiest to measure, and the calculation of J_v is straightforward. However, even in such conduits, errors in diameter measurements are magnified to the fourth power in the Hagen–Poiseuille equation (see Lewis, 1992). For conduits with noncircular transverse sections, additional errors may result from the calculation of J_v, or from the calculation of the hydraulic diameter (D_h), where D_h is used as an intermediate step in calculating J_v. For such conduits, the formulas used to arrive at D_h and/or J_v may be approximations. Determination of D_h for elliptical transverse sections (most common shape in angiosperms; Figs. 2, 3) and of J_v for rectangular transverse sections (most common shape in conifers, Fig. 1, and frequent at vessel junctions of some species; Fig. 2) are the most problematic of the simple shapes likely to be encountered in xylem. Triangular transverse sections (occasional in conifers, not shown, and frequent at vessel junctions; Figs. 2, 3) are another shape that may be found in xylem; fortunately, their computations are straightforward. Calculations of D_h and J_v for elliptical, rectangular, and triangular transverse sections are discussed in the next sections.

Calculating hydraulic diameter (D_h)—Hydraulic diameter (D_h) is defined to be four times the conduit's transverse-sectional area, A, divided by its wetted perimeter, P (see Appendix), or

$$D_h = 4A/P \tag{1}$$

In turbulent flow, the volume flow rate through a conduit with hydraulic diameter D_h equals the volume flow rate through a circular conduit with diameter D_h, at the same pressure gradient. Methods for the calculation of D_h are often based on approximating an actual conduit by a simple geometric shape, and (in many cases) applying approximate formulas for D_h. Lewis (1992) has a discussion of the errors in determining D_h and the error inherent in using D_h to calculate J_v under conditions of laminar flow. Of the transverse-sectional shapes described here, the exact solution for D_h of elliptically shaped conduits is particularly difficult to obtain.

Elliptical transverse sections—The area of an ellipse is

$$A = \pi ab/4, \tag{2}$$

where a is the short axis and b is the long axis. The perimeter of an ellipse is approximated as

$$P \cong \pi \sqrt{\frac{a^2 + b^2}{2}}. \tag{3}$$

The exact solution for an ellipse's perimeter is

$$P = 2b \int_0^{\pi/2} \sqrt{1 - e^2 \sin^2\Phi}\, d\Phi, \tag{4}$$

where e, the eccentricity, is given by

$$e = \frac{\sqrt{b^2 - a^2}}{b}. \tag{5}$$

Beyer (1981) has tables for the solution of the elliptic integral in Eq. 4. A circle may be considered an ellipse where $a = b$, and $e = 0$. Because the exact solution for P is not readily attained, the approximate solution is frequently used but gives results that overestimate P by 5% for $b/a = 3$ and by 10% for $b/a = 10$, even though it is exact for $b/a = 1$ (Table 1). Using Eq. 3 for the perimeter of the conduit yields an approximate value for D_h,

$$D_h \cong \sqrt{\frac{2a^2b^2}{a^2 + b^2}}. \tag{6}$$

The numbers reported for the actual hydraulic diameters in Table 1 of Lewis (1992) are approximations using Eq. 6.

Rectangular transverse sections—The D_h of a conduit with a rectangular transverse section is exactly and simply

$$D_h = \frac{2ab}{a + b}, \tag{7}$$

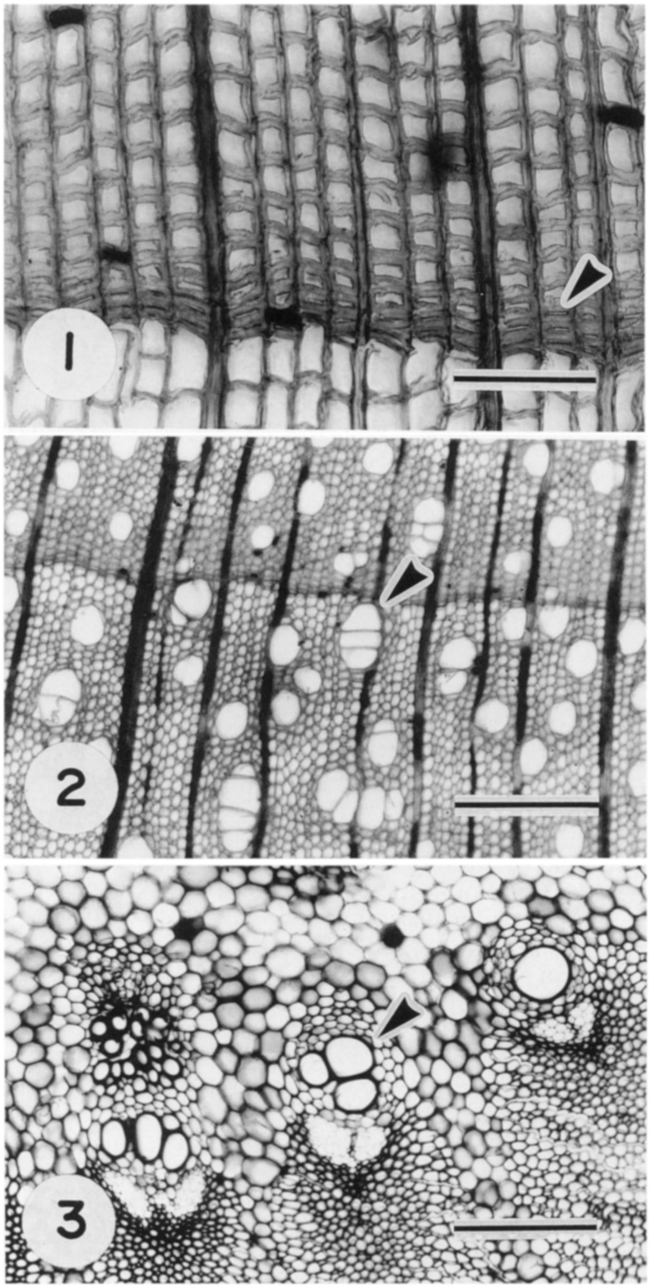
where a and b are the short and long sides, respectively.

Equilateral-triangular transverse sections—The D_h of a conduit with a transverse section in the shape of an equilateral triangle is exactly and simply

$$D_h = \frac{a}{\sqrt{3}}, \tag{8}$$

where a is a side.

Calculating volume flow rate (J_v)—Because many of the exact equations for calculating volume flow rate in noncircular conduits under conditions of laminar flow are not easily solved without a calculator or computer, two methods of approximating flow rate have been developed: 1) using D_h in the Hagen–Poiseuille equation and 2) applying a correction factor to the equation when D_h is used. These methods and the exact solutions are detailed in this section. Tables 1–3 show the errors in the approximations



Figs. 1–3. Transverse sections of typical tree stems showing a range of xylem conduit transverse-sectional shapes. **1.** *Thuja occidentalis.* Most of the tracheids may be approximated by rectangles. The latewood has tracheids with highly elongated lumens (arrow). Bar = 100 μm. **2.** *Acer rubrum.* The transverse-sectional shapes may be approximated by circles, ellipses, or rectangles. Occasionally, a shape may be approximated by an equilateral triangle (arrow). Bar = 200 μm. **3.** *Rhapis excelsa.* The vessels are best approximated by circles or ellipses, although one (arrow) might be interpreted as an equilateral triangle. Bar = 200 μm.

TABLE 1. Correction factors for estimating laminar volume flow rates in elliptical conduits. a = short axis, b = long axis, e = eccentricity (Eq. 5), P = exact perimeter (Eq. 4), P_1 = approx. perimeter (Eq. 3), D_h = exact hydraulic diameter (Eqs. 1, 2, and 4), D_{h1} = approx. hydraulic diameter (Eq. 6), J_v = exact volume flow rate (Eq. 13), J_{v1} = Nonweiler's equation (Eq. 10) using D_h, J_{v2} = Nonweiler's equation using D_{h1}, J_{v3} = Hagen–Poiseuille equation (Eq. 9) using D_h, and J_{v4} = Hagen–Poiseuille equation using D_{h1}.

b/a	e	P/P_1	D_h/D_{h1}	J_v/J_{v1}	J_v/J_{v2}	J_v/J_{v3}	J_v/J_{v4}
1.0	0.000	1.000	1.00	1.00	1.00	1.00	1.00
1.1	0.417	0.999	1.00	1.01	1.01	1.00	1.00
1.2	0.553	0.998	1.00	1.02	1.02	1.01	1.02
1.3	0.639	0.996	1.00	1.04	1.05	1.02	1.03
1.4	0.700	0.993	1.01	1.05	1.07	1.03	1.06
1.5	0.745	0.990	1.01	1.07	1.09	1.04	1.08
1.6	0.781	0.987	1.01	1.09	1.12	1.06	1.11
1.7	0.809	0.984	1.02	1.10	1.14	1.07	1.14
1.8	0.832	0.981	1.02	1.12	1.16	1.09	1.18
1.9	0.850	0.978	1.02	1.13	1.18	1.11	1.21
2	0.866	0.975	1.03	1.14	1.20	1.13	1.25
3	0.943	0.951	1.05	1.24	1.37	1.36	1.67
4	0.968	0.937	1.07	1.30	1.48	1.64	2.13
5	0.980	0.927	1.08	1.34	1.56	1.92	2.60
6	0.986	0.921	1.09	1.38	1.62	2.22	3.08
7	0.990	0.917	1.09	1.40	1.67	2.53	3.57
8	0.992	0.914	1.09	1.42	1.70	2.84	4.06
9	0.994	0.912	1.10	1.44	1.73	3.15	4.56
10	0.995	0.910	1.10	1.45	1.75	3.47	5.05
20	0.999	0.904	1.11	1.53	1.87	6.68	10.03
40	1.000	0.901	1.11	1.57	1.93	13.21	20.01
60	1.000	0.901	1.11	1.59	1.95	19.76	30.01
80	1.000	0.901	1.11	1.59	1.97	26.33	40.01
100	1.000	0.901	1.11	1.60	1.97	32.89	50.01

TABLE 2. Correction factors for estimating laminar volume flow rates in rectangular conduits. a = short side, b = long side, J_v = exact volume flow rate (Eq. 14), J_{v1} = Hagen–Poiseuille equation (Eq. 9) using hydraulic diameter (D_h, Eq. 7).

b/a	J_v/J_{v1}
1.0	1.43
1.1	1.43
1.2	1.43
1.3	1.44
1.4	1.44
1.5	1.44
1.6	1.45
1.7	1.45
1.8	1.46
1.9	1.47
2	1.47
3	1.59
4	1.75
5	1.92
6	2.11
7	2.31
8	2.51
9	2.71
10	2.91
20	5.00
40	9.22
60	13.46
80	17.70
100	21.94

in comparison with the volume flow rates from the exact solutions. Of the transverse-sectional shapes described here, the exact solution for flow through rectangularly shaped conduits is particularly difficult to solve.

Hydraulic diameter and the Hagen–Poiseuille equation—The Hagen–Poiseuille equation is the exact solution for the volume flow rate (J_v) through circular conduits under laminar flow conditions:

$$J_v = -\frac{\pi D^4}{128\mu}\frac{\Delta p}{\Delta x}, \tag{9}$$

where D is the diameter of a circular conduit, μ is the viscosity (dynamic or Newtonian) of water, and $\Delta p/\Delta x$ is the pressure gradient. The minus sign shows the direction of flow; flow moves in the direction of decreasing pressure. Because D_h was developed for turbulent flow, substituting D_h for D in the Hagen–Poiseuille equation results in errors in the calculation of volume flow rate for noncircular conduits with laminar flow. For example, for an elliptical conduit, using D_h in the Hagen–Poiseuille equation yields 60% of the exact value (see Exact solutions below) for b/a = 3 and 20% of the exact value for b/a = 10. See Tables 1–3 for a more complete listing of errors. Note that any error in D or D_h is magnified to the fourth power in the Hagen–Poiseuille equation.

Correcting the Hagen–Poiseuille equation—Corrections to the Hagen–Poiseuille equation have been proposed for calculating laminar flow in noncircular conduits (Leyton, 1975; Nonweiler, 1975; Pickard, 1981). The correction factors vary with the shape of the conduit and with the eccentricity, or ratio of the axes. Both Nonweiler and Pickard give a few constants, showing the derivations for some. Nonweiler (1975) generalizes the Hagen–Poiseuille equation as

$$J_v = -A\frac{D_h^2}{16k\mu}\frac{\Delta p}{\Delta x}, \tag{10}$$

where J_v is the volume flow rate; A is the area of the conduit's transverse section; D_h is the hydraulic diameter; k is a correction factor, which is determined by the shape and eccentricity of the transverse-sectional area; μ is the dynamic viscosity; and $\Delta p/\Delta x$ is the pressure gradient. Flow is in the direction of decreasing pressure.

Nonweiler (1975) gives k for an ellipse as

$$k = \frac{4}{1 + \sqrt{1 - e^4}}, \tag{11}$$

where e is the eccentricity as described in Eq. 5. Because in Lewis (1992), P, used to calculate D_h, is approximated for ellipses using Eq. 3, the correction factor reported in Lewis is itself an approximation. Nonweiler (1975) lists $k = 2$ for a circular transverse section ($e = 0$), $k = 4$ for a completely flatted ellipse ($e = 1$), $k = 2.03$ for an ellipse with $e = 0.5$, $k = 1.78$ for a square, and $k = 3$ for a narrow slit.

Pickard (1981) uses a slightly different form of the Hagen–Poiseuille equation:

$$J_v = -\kappa\frac{\pi D_h^4}{128\mu}\frac{\Delta p}{\Delta x}, \tag{12}$$

where J_v is the volume flow rate; κ is a correction factor dependent on the conduit shape and eccentricity; D_h is the hydraulic diameter; μ is the dynamic viscosity; and $\Delta p/\Delta x$ is the pressure gradient. Flow is in the direction of decreasing pressure. Pickard gives $\kappa = 1$ for a conduit with a circular transverse section, $\kappa \cong 1$ for mildly circular ellipses, $\kappa = 1.43$ for a square, and $\kappa = 1.98$ for an equilateral triangle. Pickard's corrections indicate that even for the least elongated rectangle (a square) and triangle (an equilateral triangle) the difference between the exact solution and the Hagen–Poiseuille solution using D_h is significant (see Tables 2, 3).

Exact solutions—Berker (1963) presents exact solutions for laminar flow in conduits with noncircular transverse sections. White (1991) has more accessible exact solutions:

Elliptical transverse sections—Volume flow in a conduit with elliptical transverse section is

$$J_v = -\frac{\pi}{64\mu}\frac{a^3b^3}{a^2+b^2}\frac{\Delta p}{\Delta x}, \tag{13}$$

where J_v is the volume flow rate; μ is the viscosity; a and b are the short and long axes, respectively; and $\Delta p/\Delta x$ is the pressure gradient. The pressure decreases downstream.

Rectangular transverse sections—Volume flow in a conduit with rectangular transverse section is

$$J_v = -\frac{ab^3}{12\mu}\left[1 - \frac{192b}{\pi^5 a}\sum_{j=1,3,5,\ldots}^{\infty}\frac{\tanh\left[\frac{j\pi a}{2b}\right]}{j^5}\right]\frac{\Delta p}{\Delta x}, \tag{14}$$

where J_v is the volume flow rate; μ is the viscosity; a and b are the short and long sides of the rectangle, respectively; and $\Delta p/\Delta x$ is the pressure gradient. The pressure decreases downstream.

Triangular transverse sections—Volume flow in a conduit with an equilateral triangle for its transverse section is

$$J_v = -\frac{\sqrt{3}a^4}{320\mu}\frac{\Delta p}{\Delta x}, \tag{15}$$

where J_v is the volume flow rate; μ is the viscosity; a is the triangle's side; and $\Delta p/\Delta x$ is the pressure gradient. The pressure decreases downstream.

RECOMMENDATIONS FOR CALCULATING VOLUME FLOW RATE (J_v)

Ideally, the exact solutions should be used to calculate J_v in xylem conduits, but the equations are difficult to solve without the aid of computers, and it is not always practical to measure both axes precisely. Note that flow rate in a stem is the sum of the individual conduit flow rates. The following are recommendations for calculating J_v of individual conduits in practical applications.

TABLE 3. Correction factor for estimating laminar volume flow rates in conduits with transverse sections in the shape of equilateral triangles. a = side, J_v = exact volume flow rate (Eq. 15), J_{v1} = Hagen–Poiseuille equation (Eq. 9) using hydraulic diameter (D_h, Eq. 8).

a	J_v/J_{v1}
1	1.98

Elliptical transverse sections—With elliptically shaped conduits, determining the exact D_h is more complex than determining the exact J_v. Use the exact solution to determine J_v in conduits with elliptical transverse sections after measuring both axes. If only one axis is measured, recommendations in Lewis (1992) can be used to calculate and correct D_h, and the correction factor for J_v/J_{v4} in Table 1 of this paper with the Hagen–Poiseuille equation can be used to calculate J_v.

Rectangular transverse sections—With rectangularly shaped conduits, determining D_h is straightforward, but determining J_v is difficult. When calculating J_v for a large number of conduits, we recommend using the exact solution if a computer or programmable calculator is available. Otherwise the Hagen–Poiseuille equation can be used with D_h, applying the correction factor from Table 2. Follow the recommendations in Lewis (1992) to determine D_h.

Triangular transverse sections—Conduits with equilateral triangles as their transverse sections have simple solutions for both D_h and J_v. In order to calculate J_v use the exact solution.

DISCUSSION

For accuracy, it is best to use the exact solutions for J_v through xylem conduits with noncircular transverse sections. The exact solutions are simple to attain for conduits having transverse sections in the shapes of ellipses or equilateral triangles. Rectangular transverse-sectional conduits have exact solutions that are not easily attained. In this case, researchers may choose to use the Hagen–Poiseuille equation with the simple solution for D_h. The practical constraint of the time required to measure two axes for elliptically and rectangularly shaped conduits may also affect whether the exact solution or the Hagen–Poiseuille equation is used (cf. Lewis, 1992).

Actual volume flow rates measured in xylem have been consistently lower than the theoretical rates. The approximate ratios of theoretical to measured volume flow rates in tree axes range from 1:1 to 4:1 (Zimmermann, 1983, p. 15). In general, the ratio increases as the xylem conduit diameter decreases. The error is often attributed to the fact that xylem elements have finite length, so that perforation plates, wall sculpturing, and pit fields interrupt fluid flow through the otherwise ideal capillaries. The error should be more extreme in the more narrow elements because they tend to be shorter with more obstructions to water flow, such as perforation plates and pit fields, in a given distance (see Petty, 1978; Zimmermann, 1983, pp. 14–15; Calkin, Gibson, and Nobel, 1986). Another source of error that has been largely overlooked is the possibility that the small diameter of xylem conduits affects the fluid dynamics. The volume flow equations discussed here are based on systems $\approx 10^{-2}$ m in diameter, while xylem conduits are $\approx 10^{-5}$ m in diameter. At this smaller scale, the forces between water molecules, solutes, suspended particles, and the cell walls may be sufficient to increase the viscosity of the xylem sap and reduce the volume flow rate (see Leyton, 1975, pp. 27–28). Interestingly, Canny (1991) indicates that very small diameter xylem conduits may have flow in the radial direction, with little to no longitudinal flow.

Using the exact solutions for D_h and J_v gives volume flow rates that are even greater than those previously reported, increasing the difference between the theoretical and the measured flow rates (see Zimmermann, 1983, p. 15). At present not enough is known about xylem transport to fully account for the effects of scale and the anatomical variations of xylem conduits from ideal capillaries. We will be more capable of reconciling the differences between theoretical and measured volume flow rates as we improve measurements of xylem anatomy and the field parameters: volume flow rate, viscosity, and pressure gradient.

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APPENDIX 1

Hydraulic radius—In texts concerned with fluid flow, the term hydraulic radius (r_h) is often used. Hydraulic radius is defined in different texts variously as $m = A/P$, where a circle's r_h equals half the radius ($r_h = r/2$) (e.g., Nonweiler, 1975); or as $r_h = 2A/P$, where a circle's hydraulic radius equals the radius ($r_h = r$) (e.g., Pickard, 1981). The first definition is a matter of convenience in fluid dynamics; the second definition makes more sense to the rest of us and lessens confusion. Fortunately, the definition for hydraulic diameter (D_h, as defined in Eq. 1) does not vary!