Flow and Pressure Distributions in Vascular Networks Consisting of Distensible Vessels

Gary S. Krenz \(^1,3,\dagger\) and Christopher A. Dawson\(^2,3,4\)

\(^1\)Department of Mathematics, Statistics and Computer Science, 
\(^2\)Department of Biomedical Engineering, Marquette University, 
PO 1881, Milwaukee, WI, USA 53201-1881 
\(^3\)Research Service, Zablocki Veterans Affairs Medical Center 
Milwaukee, WI, USA 53295 
\(^4\)Department of Physiology, Medical College of Wisconsin 
Milwaukee, WI, USA 53226 

\(^\dagger\)To whom correspondence should be addressed; e-mail: gary.krenz@marquette.edu

Abstract

We examine the influence of vessel distensibility on the fraction of the total network flow passing through each vessel of a model vascular network. An exact computational methodology is developed yielding an analytical proof that, for a class of structurally heterogeneous asymmetrical vascular networks, if all the individual vessels share a common distensibility relationship, when the total network flow is changed, each vessel will continue to receive the same fraction of the total network flow. This constant flow partitioning occurs despite a redistribution of pressures, which may result in a decrease in the diameter of one and an increase in diameter of the other of two vessels having a common diameter at a common pressure. This theoretical observation taken along with published experimental observations on pulmonary vessel distensibilities suggests that vessel diameter independent distensibility in the pulmonary vasculature may be an evolutionary adaptation for preserving the spatial distribution of pulmonary blood flow in the face of large variations in cardiac output.

Keywords: flow partitioning, heterogeneity, mathematical models, nonlinear, pulmonary circulation, vascular networks.

Introduction. Pulmonary capillary perfusion and alveolar ventilation are adequately matched for efficient gas exchange over a wide range of cardiac output from rest to heavy exercise. Normally, this matching is achieved in a largely passive manner despite the fact that the heterogeneous and asymmetrical vascular geometry (9) results in a wide distribution of local flows

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The pulmonary arteries are also quite distensible as required to provide the appropriate impedance for the right ventricle output. Even though the pulmonary arterial wall structure varies considerably from the main pulmonary artery to the precapillary terminal arteries (8, 44), the distensibility, defined as the fractional change in vessel diameter per unit change in pressure, is essentially constant and vessel diameter and vessel wall composition independent (1, 8, 29). The same is true for the veins (2). We have made the observation that in model arterial (diverging flow) or venous (converging flow) tree-like structures having one common outflow or inflow pressure, respectively, common distensibility results in the fraction of the total flow passing through each vessel segment of the heterogeneous asymmetrical tree being constant regardless of the total flow or the pressure at the inlet(s). This is true despite the fact that in such a tree the distending pressures and therefore the diameters of individual vessels of identical unstressed diameter may diverge substantially when the total flow or inflow pressure is changed. In fact, depending on the functional relationship between pressure and diameter, given two identical vessels located in different parts of the tree, the diameter of one may increase while the diameter of the other decreases in response to a given change in total flow, and yet the ratio of flows passing through the two vessels will remain the same. Thus, the flow distribution, normalized to total flow, will be the same as if the vessel walls were rigid. This perhaps counter intuitive observation led us to the conclusion that the vessel diameter independent distensibility of the pulmonary blood vessels may be an adaptation that helps fix the pulmonary flow distribution in the face of the large variations in total pulmonary blood flow (31). This conclusion was met with some skepticism at least in part because of the stipulation of a common terminal outlet pressure (for an arterial tree) or inlet pressure (for a venous tree). Thus, since the capillary inlet pressure distribution is not known, it is not clear to what extent this stipulation might affect the degree to which the idealized model might reflect the behavior of the real system. In the present study, we extend the theoretical analysis to the more general case of an entire vascular network diverging from a single inlet and then converging to a single outlet, with some additional observations on multiple inlet-outlet networks.
Model Vascular Network. The model vascular networks which we consider first are those with a single arterial inlet and a single venous outlet. To simplify the notation, intravascular pressure at a point in the network will be taken to be the same as transmural pressure at the point, which we will refer to jointly as the pressure \( P \). We employ the standard development for relating pressure to flow within distensible vessels (5, 10, 14, 29, 31, 37, 53).

First, consider a single distensible vessel subjected to constant, nonpulsatile flow. For ease of exposition, assume Poiseuille flow within the vessel (14). Modeling a vessel segment as a distensible right circular cylinder and ignoring entrance effects, the local frictional pressure drop per unit length from inlet to outlet of a single vessel is represented as

\[
\frac{dP}{dL} = -\frac{128\mu}{\pi D^4} F
\]

where \( P \) denotes pressure, \( L \) vessel length, \( \mu \) blood viscosity, \( F \) vascular flow, and \( D \) denotes the vessel diameter (14). The model vessels share a common diameter-pressure relationship given by

\[
\frac{D}{D_0} = f(P).
\]

We refer to expression Eq. 2 as the vessel distensibility relationship. Example \( f(P) \) which have been discussed in the pulmonary circulation literature include \( f(P) = 1 + \alpha P \) and \( f(P) = b + (1 - b) \exp(-cP) \) (1, 2, 14, 53).

Throughout, we assume:

1. \( f(P) \) is sufficiently smooth so when \( D = D_0f(P) \) is used in Eq. 1, the differential equation has a unique solution,

2. \( f(0) = 1 \) and \( f(P) > 0 \) for all \( P \), and

3. distensibility is constant throughout the vascular network, that is, the \( f(P) \) in Eq. 2 applies to each vessel within the vascular network.

No additional restrictions are placed upon \( f(P) \). Under the above assumptions, it follows, \textit{c.f.}, (14), (31) or (37), that:
Lemma 1 If $\Psi(P)$ denotes an antiderivative of the fourth power of $f(P)$, then

$$\Psi(P_{in}) - \Psi(P_{out}) = r_0 F$$

where $P_{in}$ and $P_{out}$ are the inlet pressure and outlet pressures of the vessel, respectively, and $r_0$ is the vascular resistance that would exist at the zero pressure diameter, $D_0$.

Remark 2 In the above lemma, individual vessel blood viscosity is part of $r_0$, rather than part of $\Psi$. Thus, blood viscosity, $\mu$, appears as a multiplicative constant separated from $\Psi$. This separation allows us to view $\mu$ as possibly being different from vessel to vessel, and $\mu$ affects only the vessel’s $r_0$.

Remark 3 As pointed out in (31), Lemma 1 is not the most general result possible since any resistance per unit length formula which allows the separation of $D_0$ and $f(P)$ could be employed, giving rise to an appropriate $\Psi$. An example of a separable local resistance per unit length relationship which describes how pressure, $P$, changes with length, $L$, would be $dP/dL = -C\mu D^{-\gamma}F$, where $F$ is the flow in a particular vessel segment, $D$ is vessel segment diameter, $\gamma > 0$ is fixed and $C, \mu > 0$ are constant within an individual vessel, but might change from vessel to vessel; however they do not change with diameter or flow. With a distensibility relationship, $f(P)$, such that

$$\frac{dP}{dL} = -\frac{C\mu}{(D_0 f(\phi(L)))\gamma} F$$

has a unique solution $P = \phi(L)$, then, as shown in (31),

$$\phi'(L) = -\frac{C\mu}{(D_0 f(\phi(L)))\gamma} F$$

or

$$\int_0^{L_0} (f(\phi(L)))^\gamma \phi'(L) dL = \int_0^{L_0} -\frac{C\mu}{D_0^2} F dL$$

$$\int_{P_{in}}^{P_{out}} (f(P))^\gamma dP = -r_0 F$$

$$\Psi(P_{out}) - \Psi(P_{in}) = -r_0 F$$
where \( P_{\text{in}} \) and \( P_{\text{out}} \) are the inlet and outlet pressures of the vessel segment, respectively, and both \( \Psi \) and \( r_0 \) are modified from their Poiseuille flow derived formula.

In what follows, the key observation is not dependent on whether one uses a Poiseuille flow assumption to model vascular resistance, or selects an affine versus an exponential relationship between diameter and pressure to model vessel distensibility. The key observation is instead that \( \Psi \) should be viewed as the abstraction of pressure in a distensible vessel, rather than dealing with actual pressure, \( P \). With this observation in mind, Eq. 3 can be viewed as a hemodynamic equivalent of Ohm’s Law which accommodates distensibility of vessel segments, relating resistance and flow to a pressure drop:

\[
\Delta \Psi \equiv \Psi(P_{\text{in}}) - \Psi(P_{\text{out}}) = r_0 F \tag{6}
\]

where \( r_0 \) is a fixed vessel resistance, \( F \) is flow in the vessel, and \( \Delta \Psi \) represents the nonlinear transformed pressure drop across the vessel segment. Notice that rather than the usual vessel segment pressure drop, \( \Delta P = P_{\text{in}} - P_{\text{out}} \), this “Ohm’s Law” relates the drop in nonlinear transformed pressure, \( \Delta \Psi \), from inlet to outlet, of the vessel segment to a fixed reference resistance (i.e., the resistance that would exist at the zero pressure diameter) and actual vessel flow. By ascending a single inlet-single outlet vascular network using both the standard electrical circuit analogy and Eq. 6, one can write equations which calculate flow fractions and nonlinear pressures for a vascular network containing distensible vessels. Then, nonlinear pressures, \( \Psi \), can be inverted to obtain actual pressures, \( P \).

To illustrate the computational methodology proposed above, consider the vascular network in Fig. 1. We first examine the reference case, where reference inlet flow is one, the reference outlet pressure is zero, and reference resistances, \( r_1, \ldots, r_{22} \). For this reference setting, vessel segment \( i \) would have flow \( f_i \), \( i = 1, \ldots, 22 \) and the vascular network would experience pressures \( p_2, \ldots, p_{18}, e.g., p_2 \) is the pressure at node 2, \( \ldots \), \( p_{18} \) is the pressure at node 18. Then, in the reference case, conservation of flow at node 18 in Fig. 1 would imply \( f_1 = 1 \), while at node 17, conservation of flow would yield \( f_1 = f_2 + f_5 \), or equivalently, \( -f_1 + f_2 + f_5 = 0 \). Similarly, at
Fig. 1. Example vascular network comprised of 22 vessel segments. Each vessel is assigned a unique vessel segment number, \( i \), ranging from 1 to 22. Filled circles, enumerated using digits 1–18, denote the 18 locations or nodes, \( n_1 \) to \( n_{18} \), where pressures are determined. Vessel 1 is the inlet vessel.

\[ f_{12} + f_{13} = f_{18} \]

At node 7, \(-f_6 + f_{12} = 0\).

The upstream pressure at node 2 is \( p_2 = f_{22}r_{22} \), or \( f_{22}r_{22} - p_2 = 0 \). The two distinct pathways to node 15 would yield \( f_{10}r_{10} + p_{11} - p_{15} = 0 \), as well as, \( f_{11}r_{11} + p_{12} - p_{15} = 0 \), etc. Overall, the 17 (conservation of) flow equations and 22 upstream pressure equations in the reference setting result in a system

\[ A\mathbf{x} = \mathbf{b} \quad (7) \]

where \( \mathbf{x} = [f_1 f_2 \cdots f_{22} p_2 p_3 \cdots p_{18}]’ \), \( \mathbf{b} = [1 0 0 \cdots 0]’ \), the symbol ‘ denotes vector transpose and the matrix \( A \) (given in Appendix I) captures the left hand sides of the equations corresponding to conservation of flow and pressure calculations.

We now turn to the distensible vessel flow and pressure calculations for the vascular network depicted in Fig. 1. Throughout, lowercase subscripted variables refer to the previous reference setting calculation, \( i.e., f_i, r_i \) and \( p_{n_j} \) are reference flow (fraction), reference resistance, and
reference pressure, respectively, while corresponding uppercase variables denote the distensible vessel value.

Remark 4 Because antiderivatives differ by at most an additive constant, we may select $\Psi$ such that $\Psi(P_{n_1}) = 0$ at pressure $P_{n_1}$. This is equivalent to selecting the nonlinear outlet pressure to be the zero baseline, simplifying notation and computations without affecting the generality of the results. We do not require $P_{n_1}$ to be zero.

For any nonzero total inlet flow $F$, the flow in the $i^{th}$ distensible vessel segment will be denoted by $F_i$. Suppose the $i^{th}$ distensible vessel segment is between nodes $n_k$ and $n_j$. We will show that:

1. $F_i = Ff_i$ and

2. the pressure, $P_{n_j}$, at node $n_j$ is obtained from the nonlinear equation

$$\Psi_{n_j} \equiv \Psi(P_{n_j}) = Fp_{n_j} \tag{8}$$

Similarly, for $P_{n_k}$.

To see this, one uses Eq. 6 as an equivalent Ohm’s Law. The matrix equation arising from conservation of flow and nonlinear transformed pressure drop is

$$\Lambda \mathbf{y} = F \mathbf{b} \tag{9}$$

where $\mathbf{y} = [F_1, F_2, \ldots, F_{22}, \Psi_2, \Psi_3, \ldots, \Psi_{18}]'$. The matrix $\Lambda$ is exactly the matrix obtained in the reference calculation. Uniqueness of the solution of Eq. 7 implies the system of equations which determines the flows, $F_i$, and nonlinear pressures, $\Psi_{n_j}$, is equivalent to

$$\Lambda (F \mathbf{x}) = (F \mathbf{b}). \tag{10}$$

where $\mathbf{y} = F \mathbf{x}$ are related through $F_i = Ff_i$, $i = 1, \ldots, 22$ and $\Psi_{n_j}$, $n_j = 2, \ldots, 18$ are given by Eq. 8.

With this example of calculation methodology in mind, we can now state the main result. Throughout, suppose each vessel segment in a vascular network is assigned a unique number $i$. 

**Theorem 5** Suppose that in an arbitrary single inlet-single outlet vascular network

1. every vessel segment has the same distensibility relationship, \( \frac{D}{D_0} = f(P) \), (each vessel segment, however, may have a different \( D_0 \)),

2. blood viscosity, \( \mu \), although it may be different in each vessel segment, remains constant within a vessel segment as flow or diameter changes, and

3. up to a multiplicative constant, every vessel segment has the same separable local resistance per unit length relationship.

Then, for each vessel segment \( i \) in the vascular network, there exists a unique constant, \( f_i \), independent of \( F \), such that

\[
\frac{F_i}{F} = f_i
\]  

relating the flow in the vessel, \( F_i \), to the nonzero total inlet flow, \( F \).

This result follows directly from the calculation methodology using conservation of flow, non-linear pressure \( P \) and relating the reference calculations to the distensible vessel calculations. As a corollary, we have

**Corollary 6** Under the same suppositions as for Theorem 5, if \( F_R \) denotes the flow in one daughter vessel at a bifurcation and \( F_L \) denotes the flow in the other daughter vessel, then \( F_R/F_L \) is the same for every nonzero total inlet flow, \( F \), through the vascular network.

To provide a concrete numerical example, we employ a \( f(P) \) which exhibits autoregulatory-like behavior to the vascular network in Fig. 1. The reason for choosing this example, despite the focus of the introduction on the pulmonary circulation in which passive mechanics dominates, is because the example tends to be a rather severe challenge to one’s intuition. In a network experiencing autoregulatory behavior, it is easy to see that for two vessels having the same \( D_0 \), a change in total flow can result in an increase in diameter of one and a decrease in diameter of the other, but perhaps not so obvious is that the fraction of flow through each vessel will remain
the same. One such autoregulatory distensibility relationship is 
\[ f(P) = a_1 + b_1 P^{b_2} e^{-c_1 P} + (1 - a_1) e^{-c_2 P}, \]
where \( a_1 = 0.9, b_1 = 0.25, b_2 = 1, c_1 = 0.25, \) and \( c_2 = 0.25 \) (31). A graph of \( f(P) \) versus \( P \) is given in Fig. 2. This \( f(P) \) provides a maximum diameter of 131\% \( D_0 \) but falls to only 90\% \( D_0 \) as pressure increases.

The autoregulatory \( f(P) \) was applied to the 22 vessel vascular network in Fig. 1, where vessels in the network are numbered \( i = 1, \ldots, 22 \), nodes denoted \( n_1, \ldots, n_{18} \) and vascular network outlet pressure, \( P_{n_1} \), was set to zero. Employing the vessel numbering scheme, \( r_i \) denotes the reference resistance which would result at the diameter corresponding to zero pressure in vessel segment \( i \). Assuming Poiseuille flow, \( \Psi(P) \) would be an antiderivative of the fourth power of \( f(P) \). Figure 3 is one such antiderivative, with the appropriate additive constant such that \( \Psi(0) = 0 \). For the vascular network in Fig. 1, we set \( r_1 = 1/8, r_2 = r_{21} = 1/2, r_3 = r_4 = r_5 = r_{18} = r_{19} = r_{20} = 1, r_6 = r_8 = r_{10} = r_{12} = r_{13} = r_{15} = r_{16} = r_{17} = 2, r_7 = r_9 = r_{11} = r_{14} = 3, \) and \( r_{22} = 1/16 \). Particular reference resistances would correspond to a known vessel geometry at zero pressure. However, since flow division depends solely upon the

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Fig. 2. An autoregulatory-like distensibility relationship. Vertical axis is distensibility \( D/D_0 = f(P) \), horizontal axis is pressure \( P \). Peak distension occurs at approximately \( P = 3.6 \).
Fig. 3. An antiderivative $Ψ$ for the fourth power the $f(P)$ given in Fig. 2. Vertical axis is the abstraction of the concept of pressure in distensible vessels, $Ψ(P)$, horizontal axis is the actual pressure, $P$.

reference resistances, selecting the resistances suffices.

Solving the reference case Eq. 7 and numerically inverting the nonlinear expression Eq. 8 provides the pressures $P_{n_j}$ at the nodes (filled circles locations) of Fig. 1. The pressures, as a function of total vascular network flow, are given in Fig. 4. At any fixed total vascular network flow, a vertical line would cut through the various pressure curves, which along with the zero outlet pressure, would depict the complete nodal pressure distribution in the network. At a total network flow of 20, the pressure at node 3 is $P_3 = 4.90$, at node 4 the pressure is $P_4 = 2.82$, and, in regards to further increases in flow and therefore in the pressures, vessel 1 has become a rigid tube with diameter approximately 90% of its $D_0$ value. In Fig. 5, we have plotted the pressure drop across each individual vessel in Fig. 1 as a function of individual vessel flow. If the vessels were rigid, each plot would be a straight line. Although each vessel has the same distensibility relationship, the nonlinear interaction of distensibility, pressure, and vascular network connective structure is readily apparent both in the nonlinear appearance of
Fig. 4. Pressure flow relationship for individual vessels for the vascular network in Fig. 1. Horizontal axis is total vascular network flow, $F$. Individual vessel flow is a constant fraction of total vascular network flow. Vertical axis is pressure, $P$, at nodes.

Fig. 5. Individual pressure drop versus flow for each vessel in the Fig. 1 network. Horizontal axis is individual vessel flow. Vertical axis is pressure difference between nodes at each end of the vessel segment. Numbers indicate which vessel segment corresponds to the plot: 1, ..., 22.
the curves, and more importantly, in the differences in concavities of the curves, and yet every vessel segment in the vascular network is receiving a constant fraction of the total vascular network flow over the entire range of total network flow.

To demonstrate the alternative condition, that is, the effect of changing total flow on individual vessel flows in networks with varying vessel distensibility, we carried out the simulations depicted in Fig. 6. The vertical columns in Fig. 6 exemplify the impact of diameter dependent distensibility for the network in Fig. 1. For Fig. 6 the vessel distensibility relationship was taken as $D/D_0 = 1 + \alpha P$, which is more consistent with pulmonary vessels (1, 2, 14, 53). With vessel segments having a fixed length to diameter ratio, Poiseuille flow, and constant $\mu$ for each vessel, the reference resistances translate into an initial $P = 0$ geometry. Starting with the same $P = 0$ resistances as in the Fig. 4 example, and hence an implied $P = 0$ geometry, the leftmost column of Fig. 6 shows the hemodynamic consequences of a particular choice of $\alpha$ increasing with decreasing vessel size [as an illustrative example, $\alpha$ for each vessel was taken to be proportional to its $D_0^{-3}$, with $\alpha$ ranging from 0.0625 to 3]. While for the rightmost column of Fig. 6, $\alpha$ decreases with decreasing vessel size [$\alpha$ for each vessel was taken to be proportional to its $D_0^3$ with the same diameters as for the left column, $\alpha$ ranging from 16 to 0.33]. The center column is the results with a constant $\alpha = 0.57$, chosen to provide overall network pressure drops in the same range as the left and rightmost columns. The individual segment flow reversal upon increasing total flow in the left column is the result of inversion of the order of the pressures at nodes 6, 10 and 14, i.e., $P_6 > P_{10} > P_{14}$, which occurs at a total network flow of 11.3.

Discussion. The primary observation of this study is that if a heterogeneous asymmetrical vascular network (having the stated properties) is comprised of blood vessels each of which has the same distensibility relationship, despite potentially wide variations in pressures within vessels that have a common diameter at a given pressure, the flow distribution within the network will be unaffected by changes in total network flow and the accompanying redistribution of pressures. A similar observation was made previously for diverging (arterial) and converging (venous) trees.
Fig. 6. Hemodynamic calculations for network topology in Fig. 1 using distensibility relationship $D/D_0 = 1 + \alpha P$. Each vertical column represents a different choice of $\alpha$. Left column: $\alpha$ increases with decreasing vessel size. Middle column: $\alpha$ the same for all vessels. Right column: $\alpha$ decreases with decreasing vessel size. From top to bottom: Pressure at the 18 nodes as a function of total network flow, vessel segment flow as a function of total network flow, fraction of total flow in a vessel segment as a function of total network flow, pressure drop across a vessel segment as a function of vessel segment flow. Negative values indicate retrograde flow.

with the restriction that there was, respectively, a common outlet or inlet pressure. What little experimental information is available on capillary pressure distributions (24) raises the
Fig. 7. Left: Pulmonary arterial distensibilities ($\alpha$) from six species obtained in 26 studies of vessels of various internal diameters ($D$), where $\alpha$ is defined by $D(P) = D(0) + \alpha P/D(0)$. The values were either reported as such in the cited reference or estimated from data provided in the reference. The pressure ($P$) range was generally within 0 to 30 mmHg. The dashed line, representing $\alpha = 0.02$/mmHg, appears to reflect the central tendency of the data reasonably well. Right: Sources of data represented on graph.

question as to how damaging that restriction might be to the relevance of the theorem to any real vascular system. Extension to the single inlet-single outlet network helps to address this question to the extent that an arterial (or venous) tree can now be thought of as being a part of a network for which there is somewhere downstream (or upstream) a common pressure, and in which distributed arterial outlet or venous inlet pressures would be the normal condition for a heterogeneous asymmetrical network.

As indicated in the introduction, this study was motivated by an attempt to understand the significance of observations indicating that the distensibility of the pulmonary arteries (Fig. 7) and veins (2) are virtually independent of vessel size. The network model does not completely resolve the question because the specific assumption invoked is that the arteries, capillaries and veins all have the same distensibility relationship. Over the physiological range of pulmonary pressures, that assumption appears to be reasonable for the pulmonary arteries and veins (1, 2, 26). Whether the same can be said for the capillaries is not so clear, in part dependent on
whether the capillaries are viewed as cylinders (21, 48), which distend with a uniform increase in diameter, or a punctuated sheet, wherein distension is only orthogonal to the alveolar surface (13, 14, 48), or somewhere in between. For a cylindrical capillary, the geometric component of the resistance would involve the fifth power of the diameter, as in the cylindrical arteries and veins, whereas, the sheet resistance involves the fourth power of the dimension orthogonal to the alveolar surface (14). On the other hand, the available data suggest that the capillary distensibility is at least within the same order of magnitude as the arteries and veins, with values of capillary distensibility (defined as the fractional change in the vessel dimension orthogonal to the alveolar surface per unit change in pressure), obtainable from the literature, ranging from about 0.023/mmHg in the dog lung (40) to about 0.07/mmHg for the cat and dog lungs (14, 15).

Cox (8) was apparently the first to point out that the mechanical properties of the pulmonary arterial vessel walls are essentially independent of both vessel diameter and the composition of the individual vessel walls defined by relative amounts of connective tissue and smooth muscle. This is reiterated by the compilation of data in Fig. 7, updated from (1), wherein the vessel diameter independence of the distensibility coefficient $\alpha$ is reflected by the fact that the data from several studies obtained using various methods can be correlated by a virtually constant value of $\alpha$ over several orders of magnitude in $D_0$ from the main pulmonary artery to terminal arterioles, and representing many more orders of magnitude in individual vessel segment resistances. Despite the diameter independence, there is in fact variability in the individual values within a given diameter range even between studies on the same species. The reasons for this are not clear, but may reflect sensitivity to some aspect(s) of study conditions that have not been systematically identified. Thus, it seems probable that the variability within a given diameter range in Fig. 7 is greater than would be expected within any particular individual lung. However, the objective of the analysis is not to provide an argument that the distensibility is constant. Rather it points out that limits on the distribution of individual vessel distensibilities would be a logical result of evolutionary pressure to maintain gas exchange efficiency (i.e., the ventilation:perfusion distribution) over a wide range of cardiac output.
The question as to the impact of the various obvious differences between the model and the real system (including pulsatile flow, gravity effects, etc.) will probably require numerical simulations beyond the scope of present study. Thus, even having generalized the model to encompass an entire network, it remains idealized. This allows for the analytical approach to understanding the model behavior, and we think that the observations provide a reference point for understanding the implications of vascular network design in a sense similar to other idealizations, including “Poiseuille’s law,” “sheet flow,” the “fifth power law” (14, 53), “Murray’s law” (32), and others (30, 37, 43, 49).

It may also be useful to reiterate that the theorem presented herein is not dependent on the assumption of Poiseuille flow. Rather, in the deviation of Eq. 9, the existence of a Ψ and the reference $r_0$’s is what is needed, where the reference $r_0$ might be thought of as the resistance that would exist if the vessel diameters were fixed at their zero pressure values. This is accomplished if, up to a multiplicative constant, each vessel in the vascular network has the same local normalized resistance per unit length expression. Although the results allow for blood viscosity being different in each vessel, the restriction of constant viscosity within a vessel may be viewed as more limiting. However, changes in viscosity within any single vessel segment, due to physiologically reasonable flow or diameter changes, is small (28).

Although our primary goal was to examine the potential for fixed flow partitioning within a heterogeneous asymmetric vascular network, the methodology can be employed to determine flows within multiple input-multiple outlet vascular networks where each vessel experiences the same distensibility relationship (see Appendix II). It is further clear that reference flow distribution calculations apply to the distensible vessel case when any of the following hold:

1. Multiple inlet-single outlet vascular network, where the inlet flows may increase or decrease, but inlet flows are delivered in a fixed ratio.

2. A single inlet-multiple outlet vascular network, where all outlet pressures are fixed at the same value.
3. Multiple inlet-multiple outlet vascular network, where the inlet flows may increase or decrease, but the inlet flows are delivered in a fixed ratio and all outlet pressures are fixed at the same value.

In each case, the individual vessel segment flows throughout the network would follow the constant partitioning results above.

The observation that distensibility of the pulmonary arteries and veins is diameter independent over the several orders of magnitude range in vessel diameter may reflect a design feature that takes advantage of the observations made above. Providing a structure with vessels sharing a common distensibility should result in a stabilizing effect on the impact of changing cardiac output on the pulmonary capillary flow distribution without requiring an elaborate controlling mechanism (29). When the distensibility is not constant throughout the network, in particular, when it is diameter-dependent, the fraction of total flow within any one branch of the network may diverge from the initial flow distribution and even reversal of flow in some segments is possible (Fig 6). Some observations made on the effects of changing cardiac output on the pulmonary flow distribution (4, 23, 46) appear to be generally consistent with a nearly constant flow distribution.

These observations may have implications for the function of diseased lungs somewhat analogous to the effect of the distribution of airway mechanics on the breathing frequency dependence of the distribution of ventilation. That is, in diseased lungs having an abnormally broad distribution of time constants among respiratory units, the increase in breathing frequency generally accompanying an increase in total ventilation results in a redistribution of the fraction of the total ventilation received by a given respiratory unit (41). Likewise, increasing cardiac output in a lung with a disease extended distribution in individual vessel distensibilities would tend to result in a redistribution of blood flow. At present, little information is available regarding any changes in the longitudinal or parallel distributions of distensibilities of vessels that might occur as the result of pulmonary vascular remodeling in pulmonary diseases.
### Glossary

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
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<tbody>
<tr>
<td>( \alpha )</td>
<td>Distensibility parameter defined by ( \frac{D}{D_0} = f(P) = 1 + \alpha P ), see for example Fig. 7</td>
</tr>
<tr>
<td>( \gamma )</td>
<td>Parameter in a general vessel segment resistance per unit length formula</td>
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<tr>
<td>( \phi )</td>
<td>Used to denote pressure as a function of length, ( P = \phi(L) )</td>
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<tr>
<td>( \mu )</td>
<td>Individual vessel blood viscosity. Viscosity may be different in each vessel but assumed constant within a vessel as flow or diameter is changed</td>
</tr>
<tr>
<td>( \mathbf{b} )</td>
<td>Used to denote a vector in linear system of equations: ( A\mathbf{x} = \mathbf{b} )</td>
</tr>
<tr>
<td>( b, c )</td>
<td>Distensibility parameters defined by ( \frac{D}{D_0} = f(P) = b + (1 - b)e^{-cP} )</td>
</tr>
<tr>
<td>( f_i )</td>
<td>Reference flow in vessel segment ( i ) in a vascular network, e.g., Fig. 1. If the vessels were rigid having diameters fixed at geometry given at zero pressure, ( f_i ) would be the flow in vessel segment ( i ) when the total network inlet flow is 1 and outlet pressure is 0</td>
</tr>
<tr>
<td>( i, j )</td>
<td>Subscripts used to denote a vessel segment (flow through, or the resistance of, a vessel segment) or a node (the pressure, or the nonlinearly transformed pressure, at the inlet or outlet of a vessel segment)</td>
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<tr>
<td>( f(P) )</td>
<td>Vessel diameter distensibility relationship</td>
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<tr>
<td>( p_i )</td>
<td>Reference pressure at node ( i ) in a vascular network, e.g., Fig. 1. If the vessels were rigid having diameters fixed at geometry given at zero pressure, ( p_i ) would be the pressure at node ( i ) when total network inlet flow is 1 and outlet pressure is 0</td>
</tr>
<tr>
<td>( n_j )</td>
<td>Occasionally, ( n_j ) is used to emphasize that subscripting refers to node number, rather than vessel segment number</td>
</tr>
<tr>
<td>( r_0 )</td>
<td>Used in general discussion, denotes the resistance that would exist in a vessel segment if the vessel diameter were fixed at geometry given at zero pressure</td>
</tr>
<tr>
<td>( r_i )</td>
<td>Denotes the ( r_0 ) for vessel segment ( i ) in a vascular network</td>
</tr>
<tr>
<td>( \mathbf{x} )</td>
<td>Solution to a linear system of equations: ( A\mathbf{x} = \mathbf{b} )</td>
</tr>
<tr>
<td>( \mathbf{y} )</td>
<td>Solution to a linear system of equations: ( A\mathbf{y} = F\mathbf{b} )</td>
</tr>
</tbody>
</table>
Matrix containing conservation of flow and vessel segment pressure drop using either the usual Ohm’s Law (reference calculation) or the nonlinarly transformed pressure Ohm’s Law, Eq. 6

Parameter in a general vessel segment resistance per unit length formula

Vessel diameter, changes with pressure, \( P \), according to model \( D(P) = D_0 f(P) \)

Vessel diameter at zero pressure, \( D(0) = D_0 \)

Flow, either in a single vessel segment or the total network flow

At a bifurcation, the flow in, respectively, the “right” \( R \) and “left” \( L \) daughter vessels

Flow in distensible vessel segment \( i \)

Length variable

For simplicity, transmural and vascular pressures are taken as equal in the analysis and denoted by \( P \)

Pressure at node \( i \)

Pressure at the inlet of a vessel segment

Pressure at the outlet of a vessel segment

Upstream downstream pressure drop across a vessel segment \( \Delta P = P_{in} - P_{out} \)

Uppercase \( P \), in script font, denotes a nonlinear transformation of pressure \( P \), e.g., for Poiseuille flow and \( f(P) = 1 + \alpha P \), \( \Psi(P) = \int (f(P))^4 dP = \int (1 + \alpha P)^4 dP = (1 + \alpha P)^5 / (5\alpha) \). \( \Psi \) enables use of an equivalent Ohm’s Law for distensible vessels wherein the upstream downstream “pressure” drop for a single vessel \( \Psi(P_{in}) - \Psi(P_{out}) \) is directly proportional to the flow through the vessel segment. The constant of proportionality is the resistance that would exist if the vessel diameter were fixed at its zero pressure value

Nonlinear transformed pressure \( \Psi_{n_j} = \Psi(P_{n_j}) \) at node \( n_j \)

Nonlinear transformed upstream downstream pressure drop for distensible vessels, \( \Delta \Psi = \Psi(P_{in}) - \Psi(P_{out}) \)

Vector transpose

Bibliography


2. al-Tinawi A., Clough A.V., Harder D.R., Linehan J.H., Rickaby D.A., Dawson


**Appendix I.** The connective structure of the single inlet-single outlet vascular network and the explicit choice of the separable local resistance per unit length relationship determines the matrix $\mathbf{A}$ in *Eq. 7*. For the example vascular network in Fig. 1, $\mathbf{A}$ is given by

$$\mathbf{A} = \begin{bmatrix} A_{1,1} & A_{2,1} \\ A_{2,1} & A_{2,2} \end{bmatrix}$$

where

$$A_{1,1} = \begin{bmatrix} f_1 & f_2 & f_3 & f_4 & f_5 & f_6 & f_7 & f_8 & f_9 & f_{10} & f_{11} & f_{12} & f_{13} & f_{14} & f_{15} & f_{16} & f_{17} & f_{18} & f_{19} & f_{20} \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ -1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -1 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -1 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -1 & 0 & 0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$
\[
A_{1,2} = \begin{bmatrix}
 f_{21} & f_{22} & p_2 & p_3 & p_4 & p_5 & p_6 & p_7 & p_8 & p_9 & p_{10} & p_{11} & p_{12} & p_{13} & p_{14} & p_{15} & p_{16} & p_{17} & p_{18} \\
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 r_{21} & 0 & 1 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\end{bmatrix}
\]

\[
A_{2,1} = \begin{bmatrix}
 f_1 & f_2 & f_3 & f_4 & f_5 & f_6 & f_7 & f_8 & f_9 & f_{10} & f_{11} & f_{12} & f_{13} & f_{14} & f_{15} & f_{16} & f_{17} & f_{18} & f_{19} & f_{20} \\
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 0 & r_6 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & r_7 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & r_8 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & r_9 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
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 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
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 0 & 0 & 0 & 0 & 0 & r_5 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 r_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\end{bmatrix}
\]
and

\[
A_{2,2} = \begin{bmatrix}
    f_{21} & f_{22} & p_2 & p_3 & p_4 & p_5 & p_6 & p_7 & p_8 & p_9 & p_{10} & p_{11} & p_{12} & p_{13} & p_{14} & p_{15} & p_{16} & p_{17} & p_{18} \\
    0 & 0 & 0 & 1 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
    0 & 0 & 0 & 1 & 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
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    0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & -1
\end{bmatrix}
\]

**Appendix II.** Provided sufficient, and appropriate, boundary conditions are given so they uniquely specify the reference calculation, a linear system of equations can be created to determine the resulting flows and pressure throughout the vascular network which contains distensible vessels. For example, consider the vascular network in Fig. 8, wherein each vessel has the same distensibility relationship \( f(P) \) and, up to a multiplicative constant, each vessel has the same separable local resistance per unit length relationship, which gives rise to some \( \Psi \).

We denote the direction of individual vessel flow in Fig. 8 to be from a higher node number to a lower node number, *e.g.*, the flow in vessel 4, \( F_4 \), is considered directed from \( n_3 \) to \( n_2 \). Further, suppose we set pressures at \( n_1, n_4 \) and \( n_6 \) such that \( \Psi(P_{n_1}) \) is the smallest of the terminal pressures. Then, we define \( \Delta\Psi_{n_j} \) as \( \Delta\Psi_{n_j} = \Psi(P_{n_j}) - \Psi(P_{n_1}) \), for \( j = 1, \ldots, 6 \).
Conservation of flow and calculation of nonlinear pressures, using Eq. 6, gives

1. \( F_1 = F_2 + F_3 \)
2. \( F_4 = F_3 + F_6 \)
3. \( F_5 = F_2 + F_4 \)
4. \( \Delta \Psi_1 = 0 \)
5. \( \Delta \Psi_2 - \Delta \Psi_1 = F_5 r_5 \)
6. \( \Delta \Psi_3 - \Delta \Psi_2 = F_4 r_4 \)
7. \( \Delta \Psi_4 = V_1 \)
8. \( \Delta \Psi_4 - \Delta \Psi_3 = F_6 r_6 \)
9. \( \Delta \Psi_5 - \Delta \Psi_3 = F_3 r_3 \)
10. \( \Delta \Psi_5 - \Delta \Psi_2 = F_2 r_2 \)
11. \( \Delta \Psi_6 = V_2 \)
12. \( \Delta \Psi_6 - \Delta \Psi_5 = F_1 r_1 \)

which is a system of linear equations \( \mathbf{A} \mathbf{y} = \mathbf{b} \) with \( \mathbf{A} \) a 12 by 12 matrix, \( \mathbf{y} = [F_1 \cdots F_6 \Delta \Psi_1 \cdots \Delta \Psi_6]^T \), \( \mathbf{b} = [0 0 0 0 0 0 V_1 0 0 0 V_2 0]^T \), \( V_1 \) and \( V_2 \) denote known values from the vascular network pressure boundary conditions and the \( r_i \) denote fixed reference resistances. Although the flows can repartition as pressures are changed, flow calculation, as well as the nonlinear pressures \( \Delta \Psi \), is linear problem. Nonlinearity comes into play only for (a) setting \( V_1 \) and \( V_2 \) and (b) if one needs to invert \( \Delta \Psi \) to obtain the actual pressures. This example also illustrates the necessary modifications if one does not select \( \Psi \) to have a zero baseline.

In this setting, if, say, \( V_2 \) is always a fixed constant multiple of \( V_1 \), then each vessel in the network in Fig. 8 will experience fixed fraction of the total network flow.
Figure Legends

1. Example vascular network comprised of 22 vessel segments. Each vessel is assigned a unique vessel segment number, $i$, ranging from 1 to 22. Filled circles, enumerated using digits 1–18, denote the 18 locations or nodes, $n_1$ to $n_{18}$, where pressures are determined. Vessel 1 is the inlet vessel.

2. An autoregulatory-like distensibility relationship. Vertical axis is distensibility $D/D_0 = f(P)$, horizontal axis is pressure $P$. Peak distension occurs at approximately $P = 3.6$.

3. An antiderivative $\Psi$ for the fourth power the $f(P)$ given in Fig. 2. Vertical axis is the abstraction of the concept of pressure in distensible vessels, $\Psi(P)$, horizontal axis is the actual pressure, $P$.

4. Pressure flow relationship for individual vessels for the vascular network in Fig. 1. Horizontal axis is total vascular network flow, $F$. Individual vessel flow is a constant fraction of total vascular network flow. Vertical axis is pressure, $P$, at nodes.

5. Individual pressure drop versus flow for each vessel in the Fig. 1 network. Horizontal axis is individual vessel flow. Vertical axis is pressure difference between nodes at each end of the vessel segment. Numbers indicate which vessel segment corresponds to the plot: 1, \ldots, 22.

6. Hemodynamic calculations for network topology in Fig. 1 using distensibility relationship $D/D_0 = 1 + \alpha P$. Each vertical column represents a different choice of $\alpha$. Left column: $\alpha$ increases with decreasing vessel size. Middle column: $\alpha$ the same for all vessels. Right column: $\alpha$ decreases with decreasing vessel size. From top to bottom: Pressure at the 18 nodes as a function of total network flow, vessel segment flow as a function of total network flow, fraction of total flow in a vessel segment as a function of total network flow, pressure drop across a vessel
segment as a function of vessel segment flow. Negative values indicate retrograde flow.

7. Left: Pulmonary arterial distensibilities ($\alpha$) from six species obtained in 26 studies of vessels of various internal diameters ($D$), where $\alpha$ is defined by $D(P) = D(0) + \alpha P/D(0)$. The values were either reported as such in the cited reference or estimated from data provided in the reference. The transmural pressure ($P$) range was generally within 0 to 30 mmHg. The dashed line, representing $\alpha = 0.02/$mmHg, appears to reflect the central tendency of the data reasonably well. Right: Sources of data represented on graph.

8. Vessel network with several inputs. Each vessel is assigned a unique vessel segment number, 1 to 6. Filled circles, numbered using white numerals, denote the 6 locations or nodes, $n_1$ to $n_6$, where pressures are determined.
Fig. 1. Example vascular network comprised of 22 vessel segments. Each vessel is assigned a unique vessel segment number, $i$, ranging from 1 to 22. Filled circles, enumerated using digits 1–18, denote the 18 locations or nodes, $n_1$ to $n_{18}$, where pressures are determined. Vessel 1 is the inlet vessel.

Fig. 2. An autoregulatory-like distensibility relationship. Vertical axis is distensibility $D/D_0 = f(P)$, horizontal axis is pressure $P$. Peak distension occurs at approximately $P = 3.6$. 

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Fig. 3. An antiderivative $\mathfrak{P}$ for the fourth power the $f(P)$ given in Fig. 2. Vertical axis is the abstraction of the concept of pressure in distensible vessels, $\mathfrak{P}(P)$, horizontal axis is the actual pressure, $P$.

Fig. 4. Pressure flow relationship for individual vessels for the vascular network in Fig. 1. Horizontal axis is total vascular network flow, $F$. Individual vessel flow is a constant fraction of total vascular network flow. Vertical axis is pressure, $P$, at nodes.
Fig. 5. Individual pressure drop versus flow for each vessel in the Fig. 1 network. Horizontal axis is individual vessel flow. Vertical axis is pressure difference between nodes at each end of the vessel segment. Numbers indicate which vessel segment corresponds to the plot: 1, ..., 22.
Fig. 6. Hemodynamic calculations for network topology in Fig. 1 using distensibility relationship $D/D_0 = 1 + \alpha P$. Each vertical column represents a different choice of $\alpha$. Left column: $\alpha$ increases with decreasing vessel size. Middle column: $\alpha$ the same for all vessels. Right column: $\alpha$ decreases with decreasing vessel size. From top to bottom: Pressure at the 18 nodes as a function of total network flow, vessel segment flow as a function of total network flow, fraction of total flow in a vessel segment as a function of total network flow, pressure drop across a vessel segment as a function of vessel segment flow. Negative values indicate retrograde flow.
Fig. 7. Left: Pulmonary arterial distensibilities ($\alpha$) from six species obtained in 26 studies of vessels of various internal diameters ($D$), where $\alpha$ is defined by $D(P) = D(0) + \alpha P / D(0)$. The values were either reported as such in the cited reference or estimated from data provided in the reference. The transmural pressure ($P$) range was generally within 0 to 30 mmHg. The dashed line, representing $\alpha = 0.02$ mmHg, appears to reflect the central tendency of the data reasonably well. Right: Sources of data represented on graph.

Fig. 8. Vessel network with several inputs. Each vessel is assigned a unique vessel segment number, 1 to 6. Filled circles, numbered using white numerals, denote the 6 locations or nodes, $n_1$ to $n_6$, where pressures are determined.