A model of glomerular ultrafiltration in the rat

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The rate of glomerular ultrafiltration is governed by the same driving force that causes fluid movement across other capillary membranes, the imbalance between transmembrane hydrostatic and osmotic pressures. At any point in the glomerulus, the net driving pressure (PuF) is given by

\[ PuF = \Delta P - \Delta w = (P_{GC} - P_T) - (\pi_{GC} - \pi_T) \] (1)

where \( P_{GC} \) and \( P_T \) are the hydrostatic pressures in the glomerular capillary and Bowman’s space, respectively, and \( \pi_{GC} \) and \( \pi_T \) are the corresponding colloid osmotic pressures.

Using a strain of Wistar rats in which glomeruli are frequently present as surface structures and thus accessible to micropuncture, Brenner and co-workers (2, 3) have recently made direct measurements of \( P_{GC} \) and \( P_T \) and have estimated colloid osmotic pressures in pre- and postglomerular blood (\( \pi_{AA} \) and \( \pi_{EA} \), respectively). Among their findings is the discovery that \( PuF \) declines to essentially zero before glomerular capillary blood enters the efferent arteriole.

In the present study we have developed a mathematical model of glomerular filtration which allows us to predict the variation in \( PuF \) with distance along the capillary under a variety of experimental conditions. This model is a useful tool for examining the effects of changes in membrane hydraulic permeability (\( k \)), mean driving pressure \( (PuF) \), initial glomerular capillary plasma flow \( (Q_0) \), systemic plasma protein concentration \( (C_{AA}) \) on single-nephron glomerular filtration rate (SNGFR).

The model finally adopted here is based primarily on conservation of mass and equation 1 and appears to provide the simplest means for predicting realistic \( PuF \) profiles and of understanding variations in SNGFR. In order to justify the inclusion of certain features in this model, two simpler approaches will also be considered. The first of these involves the use of arithmetic average osmotic pressures, equivalent to assuming the \( \Delta \pi \) profile to be linear, an assumption employed earlier by Brenner et al. (2). The second approach predicts nonlinear \( \Delta \pi \) profiles, but assumes no hydrostatic pressure drop in the direction of flow in the capillary. The final model, adopted as being most useful, differs from the second approach only in that it includes a small, but finite, axial pressure drop.

Assumption of a linear \( \Delta \pi \) profile. Let \( x \) be the distance along a glomerular capillary measured from the point at which filtration begins. Assuming that \( P_T \) does not vary with \( x \) and neglecting \( \pi _T \), the mean ultrafiltration pressure is given by

\[ (PuF) = ((P_{GC}) - P_T) - (\pi_{GC}) \] (2)

The most convenient way to treat the available micropuncture data is to assume that \( \pi_{GC} \) rises linearly along the capillary segment, allowing one to compute \( (\pi_{GC}) \) as an arithmetic mean of the beginning and end-point values, as in equation 3.

\[ (\pi_{GC}) = \frac{\pi_{EA} + \pi_{AA}}{2} \] (3)

The rate of production of ultrafiltrate is related to the mean driving pressure according to

\[ SNGFR = K_t(PuF) \] (4)

where \( K_t \) is a filtration coefficient viewed most simply as the product of the membrane hydraulic permeability (\( k \)) and the available filtering surface area (S). Given measurements of SNGFR and \( (PuF) \), \( K_t \) can be found readily from equation 4. The assumption of a linear osmotic pressure profile is represented by the solid line, \( \Delta \pi \) (linear), in Fig. 1, in which it is also assumed that the axial pressure drop is small compared to \( \Delta P \), so that \( \Delta P \) is shown to be constant.

Although mathematically convenient, the assumption of

\[ \pi_{AA} \] is assumed to be the same as \( \pi_{EA} \), calculated from femoral arterial protein concentration.
a linear \( \Delta \pi \) profile can be questioned on physical grounds. Since the local rate of filtration is proportional to \( P_{UF} \), the protein in the capillary lumen should be concentrated most rapidly near \( x = 0 \). This in turn should produce a relatively rapid initial rise in \( \Delta \pi \), with the slope of the \( \Delta \pi \) curve gradually declining as \( \Delta \pi \) becomes more nearly equal to \( \Delta P \). According to this reasoning, the broken line in Fig. 1, \( \Delta \pi \) (nonlinear), ought to be a more realistic representation of \( \Delta \pi \). Since \( (P_{UF}) \) is proportional to the area between the \( \Delta \pi \) and \( \Delta P \) curves of Fig. 1, the linear \( \Delta \pi \) profile will overestimate \( (P_{UF}) \) and underestimate \( K_f \).

**Development of model.** This study was undertaken to develop a model that would provide more reasonable pressure profiles and more accurate values of \( (P_{UF}) \) and \( K_f \) than could be obtained from the use of equation 3. For simplicity, the glomerular capillary bed has been idealized as a single tube of equivalent surface area and of length \( L \). The tube radius \( r \) and hydraulic permeability of the membrane \( k \) are both assumed to be constant. Since glomerular capillaries are freely permeable to small solutes, the osmotic contributions of which are assumed to be negligible, the system is considered to have only two components, water and plasma protein. The tube wall is considered to be impermeable to protein (reflection coefficient, \( \sigma = 1 \)), only the steady state is considered, and flow rates and concentrations are taken to depend only on the axial distance coordinate \( x \). This idealized capillary bed is shown in Fig. 2.

The equation of Landis and Pappenheimer (4), which expresses \( \pi \) as a cubic function of protein concentration, is approximated in this study by a quadratic equation:

\[
\pi = a_1 C + a_2 C^2
\]

where \( C \) is the plasma protein concentration and \( a_1 \) and \( a_2 \) are constants found from a least-squares fit to the Landis-Pappenheimer results over the range \( 4 \leq C \leq 10 \, \text{g/100 ml} \). *Equation 5* differed from the Landis-Pappenheimer equation by less than 1% for plasma protein concentrations encountered in this study and considerably simplified the solutions to several of the equations.

Referring now to Fig. 2, a material balance over the disk bounded by \( x \) and \( x + \Delta x \) gives the expression for conservation of mass as

\[
\frac{dQ}{dx} = -\left(\frac{kS}{L}\right) P_{UF}, \quad Q(0) = Q_0
\]

where \( Q \) is the volumetric flow rate of plasma in the lumen and \( S \) is the total surface area of the tube. It is more convenient to work directly with protein concentration, which is related to the volume flow rate according to

\[
C = \frac{m}{Q}, \quad \frac{dQ}{dx} = -\frac{m}{C^2} \frac{dC}{dx}
\]

where \( m \) is the mass flow rate of protein, a constant. Substituting *equation 7* into *equation 6* and nondimensionalizing with \( L, C_0, \) and a reference pressure \( \Delta P_R \) (to be defined later) gives

\[
\frac{dC^*}{dx^*} = \frac{kS\Delta P_R}{Q_0} C^* - \frac{P_{UF}}{\Delta P_R}, \quad C^*(0) = 1
\]

where \( C^* \) and \( x^* \) are dimensionless protein concentration and distance, respectively, and \( Q_0 \) is the initial glomerular capillary plasma flow. The product \( kS \) is equivalent to the filtration coefficient, \( K_f \), used in *equation 4*. Substituting the dimensionless expression for \( P_{UF} \) into *equation 8* yields

\[
\frac{dC^*}{dx^*} = \frac{F C^* \Delta P}{\Delta P_R} - A_1 C^* - A_2 C^* \]

where

\[
F = \frac{kS\Delta P_R}{Q_0}, \quad \frac{K_f \Delta P R}{Q_0}
\]

\[
A_1 = \frac{a_1 C_0}{\Delta P_R}
\]

\[
A_2 = \frac{a_2 C_0}{\Delta P_R}
\]

A knowledge of \( \Delta P(x) \) and values of the parameters \( F, A_1, \) and \( A_2 \) are all that are needed to obtain the concentration profile from *equation 9*.

Measurements of \( P_{OC} \) reported by Brenner et al. (2, 3) were made at unidentified sites within the glomerular capillaries, so that it has not yet been possible to determine a complete hydrostatic pressure profile, \( \Delta P(x) \). However, the use of these values of \( P_{OC} \) in computing the ratio \( \pi_{BA}/(P_{OC} - P_f) \) yielded an average result very close to unity, suggesting to these authors, in view of the presumably random distribution of puncture sites, that \( P_{OC} \) changes little with \( x \). Since flow through the capillaries requires the presence of at least a small axial pressure drop, and since \( P_f \) is assumed to be independent of \( x \), \( \Delta P \) must decrease with \( x \). We will assume here that the drop in \( \Delta P \) is sufficiently small that \( \Delta P \) may be approximated by a constant minus

![Fig. 1. Comparison of linear and nonlinear \( \Delta \pi \) profiles.](image)
a small linear correction term. Let

\[ \Delta P = \Delta P_R (1 - \epsilon (x^* - \frac{1}{2} \epsilon)) \]  

where \( \epsilon \) is a small positive number. According to equation 11, the pressure drop along the length of the tube is equal to \( \epsilon \Delta P_R \). The reference pressure may now be chosen as

\[ \Delta P_R = \langle \Delta P \rangle = \langle P_{GC} \rangle - P_T \]  

Substituting equation 11 for \( \Delta P \) in equation 9 yields the final form of the equation for \( C^* \),

\[ \frac{dC^*}{dx^*} = F C^* (1 - A_1 C^* - A_2 C^2) \]  

\[ - \epsilon (x^* - \frac{1}{2} \epsilon), \quad C^*(0) = 1 \]  

The parameters \( A_1 \) and \( A_2 \) can be determined directly from the available data, and in subsequent discussions these will be considered as known quantities. The pressure drop \( \epsilon \) is known only to be small and will be assumed to take on various values between 0 and 0.10. \( F \) contains the unknown filtration coefficient, \( K_f \), and given \( A_1, A_2, \epsilon, \) and \( C^*_{EA}, F \) and thus \( K_f \) can, in principle, be calculated. However, as shown below, a unique value of \( K_f \) cannot be computed from present measured quantities when filtration pressure equilibrium occurs.

**Profiles for constant \( \Delta P \).** As we have already discussed, \( \Delta P \) in the rat glomerulus appears to be relatively constant. It must be supposed that, if the change in \( \Delta P \) were small enough, its effect on the concentration and osmotic pressure profiles would be negligible. This turns out not to be the case, but it is still informative to solve equation 13 with \( \epsilon = 0 \) before considering the more realistic case of \( \epsilon > 0 \).

Setting \( \epsilon = 0 \) in equation 13, one obtains

\[ \frac{dC^*}{dx^*} = F C^* (1 - A_1 C^* - A_2 C^2), \quad C^*(0) = 1 \]  

The quantity in parentheses in equation 14 is the dimensionless form of \( P_{UF} \), which approaches zero as \( \Delta P \) approaches \( \Delta P \). Inspection of the equation shows that the slope of the concentration curve will start out at a maximally positive value and gradually decrease, resulting in a \( \Delta P \) profile similar to the broken line in Fig. 1. An important consequence of this equation is that in a finite length of capillary, \( C^* \) can never reach a value such that \( A_1 C^* + A_2 C^2 > 0 \), the resultant \( \Delta P \) curve can closely approach the \( \Delta P \) curve, but the two cannot intersect.

The solution to equation 14 is

\[ \frac{A_1}{2} \ln \left| \frac{C^*}{1 - A_1 C^* - A_2 C^2} \right| - \frac{1}{C^*} + \left( \frac{A_1^2 + 2 A_2}{2 \sqrt{A_1^2 + 4 A_2}} \right) \frac{\ln \sqrt{A_1^2 + 4 A_2} + A_1 + 2 A_2 C^*}{\sqrt{A_1^2 + 4 A_2} - A_1 - A_2 C^*} = F x^* + I \]  

where \( I \) is an integration constant found from the initial condition to be equal to the left side of the equation with \( C^* = 1 \).

\[ A_1, A_2, \text{ and } C^*_{EA} \text{ were calculated for five of the animals studied in ref. 2, and equations 4, 10a, and 15 were used to compute } K_f \text{ and } (P_{UF}) \text{ for these animals. These results are compared in Table 1 to the corresponding values obtained using linear } \Delta P \text{ profiles. Assuming the results from equation 15 to be exact, the linear } \Delta P \text{ profiles overestimate } (P_{UF}) \text{ by an average of 21% and underestimate } K_f \text{ by an average of 33%. In one animal the estimates are identical, whereas in two others they differ by a factor of 2.} \]

If we define an "equilibration ratio" \( R \) as an index of the relative magnitudes of \( \Delta P \) and \( \Delta \sigma \) in the blood leaving the glomerulus,

\[ R = \frac{\Delta \sigma}{\Delta P} \]  

then the assumptions on which equation 15 is based limit its usefulness to cases where \( R < 1 \). This is clearly unsatisfactory, as 20 of 43 animals studied in refs. 2 and 3 show \( R > 1 \). However, by incorporating a small but nonzero axial pressure drop in the model, it is possible to account for both classes of observations and satisfy the hydrodynamic conditions for forward blood flow.

**Profiles for small axial pressure drop.** The assumption of constant \( \Delta P \) combined either with a linear or nonlinear \( \Delta P \) profile does not adequately simulate a capillary in which \( P_{UF} \) declines to zero. The linear \( \Delta P \) profile is not consistent with the expectation of more rapid filtration at the beginning of the capillary, while the \( \Delta P \) profile obtained from equation 15 fails to account for the observation of filtration pressure equilibrium, \( R \geq 1 \). The change in \( \Delta P \) evidently cannot be neglected.

Before solving equation 13 with \( \epsilon > 0 \) we can state with some confidence that a glomerular capillary with nonzero axial pressure drop may be expected to have certain properties: (a) If at some point along the capillary \( \Delta \sigma = \Delta P \), then \( \Delta \sigma = 0 \) at that point. This can be seen from equation 8, where it is clear that \( \Delta \sigma = 0 \) when \( P_{UF} = 0 \), an equivalent statement. (b) After intersection of the \( \Delta \sigma \) and \( \Delta P \) curves, \( \Delta \sigma \) cannot greatly exceed \( \Delta P \), since the resultant water flow back into the capillary would dilute the protein and thus \( \Delta \sigma \) greatly lower \( \Delta P \). (c) The \( \Delta \sigma \) and \( \Delta P \) curves can intersect only once. A second intersection would require that

\[ \Delta \sigma_{(\text{max})} < \Delta P \]  

where \( \Delta \sigma_{(\text{max})} \) is the maximum value of \( \Delta \sigma \) that can be achieved.
Fluid to the capillary when the average filtration rate limited only by the return of approximately the same small amount at the distal end. These curves verify that solutions to properties discussed at the beginning of this section.

Pressure and protein concentration profiles were calculated for a number of choices of $A_1$, $A_2$, $F$, and $\epsilon$. Since $F$ and $\epsilon$ are the parameters that cannot be obtained directly from the available data, the most interesting results were the sets of profiles obtained by varying $F$ or $\epsilon$ with the other three parameters held constant. Figure 3, A and B, illustrates the dependence of the osmotic pressure profiles on $F$ for an axial pressure drop of 0.7 mm Hg ($\epsilon = 0.02$, $\Delta P_R = 35.3$ mm Hg) and osmotic coefficients $A_1$ and $A_2$ representative of rats in normal hydropenia (3). The $\Delta \pi$ curves approach $\Delta P$ more rapidly for higher values of $F$, with exact equilibration of the opposing pressures first occurring at some critical value of $F$ between 2 and 3. Increasing $F$ above this value causes the curves to intersect earlier in the capillary, but in all of these cases $\Delta \pi$ was predicted to remain greater than $\Delta P$ by approximately the same amount at the distal end. These curves verify that solutions to equation 13 have the properties discussed at the beginning of this section.

For small values of $F$ in Fig. 3, corresponding to end points far removed from filtration pressure equilibrium, the $\Delta \pi$ profiles are essentially linear. The $\Delta \pi$ profiles depart more from linearity as $F$ is increased and the predictions for $\pi_{EA}$ converge to a value slightly greater than $\Delta P$. In this extreme the capillary may be thought of as being very leaky, with the average filtration rate limited only by the return of fluid to the capillary when $\Delta \pi > \Delta P$.

The average driving pressures for ultrafiltration are proportional to the areas between the $\Delta P$ and $\Delta \pi$ curves in Fig. 3A, and $\langle P_{TF} \rangle$ can be seen to decrease with increasing $F$. Reference to equation 10a shows that for a given $\Delta P_R$, $\langle P_{TF} \rangle$ decreases with increasing hydraulic permeability or surface area ($K_f$) and increases with initial glomerular capillary plasma flow ($Q_p$). In those cases where the system closely approaches equilibration (and the values for $\pi_{EA}$ converge), $\langle P_{TF} \rangle$ may vary substantially without any noticeable change in $\pi_{AA}$, $\pi_{EA}$, or $\langle \Delta P \rangle$.

Table 2 gives the equilibration ratio $R$, the point of equilibrium ($x^*_{EQ}$), and the final protein concentration ($C_{EA}^\epsilon$) for each of the profiles shown in Fig. 3. The extent of equilibration increases with $F$ until it reaches a plateau value of 1.002 for $F \geq 3.0$. The three lowest values of $F$ result in distinctly different values of $C_{EA}$, but for $F \geq 1.5$ the predicted values of $C_{EA}$ differ by only 2%, approximately the same as the uncertainty in current techniques for measuring protein concentrations (2, 3). This convergence of concentrations makes it impossible with current techniques to distinguish, for example, between $F = 1.50$ and $F = 6.00$ (or higher), even if $\epsilon$, $A_1$, and $A_2$ were known precisely. While in principle it was possible to determine $F$ using equation 13, small uncertainties in $C_{EA}$ prevent the estimation of anything more than minimum values. The mean values of the ratio $\pi_{EA}/(\langle P_{OC} \rangle - P_T)$ calculated from four sets of data in refs. 2, 3 are 0.96, 1.04, 1.02, and 1.00, indicating that equilibrium is the rule rather than the exception and underlining the futility of attempting to determine values of $K_f$ from equation 13 under these conditions.

Table 3 shows the effects of varying $\epsilon$ from 0 to 0.10, the latter value corresponding to an axial pressure drop of 3.5 mm Hg. Higher values of $\epsilon$ promote equilibration by causing $\Delta P$ to decrease more rapidly, and the inability to determine

| Table 2. Degree of equilibration as a function of $F$ ($\epsilon = 0.02, A_1 = 0.268, A_2 = 0.280$) |
|---|---|---|---|---|
| $F$ | $R$ | $x^*_{EQ}$ | $C_{EA}^\epsilon$ | $C_{EA}^\epsilon$ |
| 0.20 | 0.631 | 1.090 | 6.32 |
| 0.50 | 0.747 | 1.216 | 7.05 |
| 1.00 | 0.895 | 1.363 | 7.91 |
| 1.50 | 0.966 | 1.430 | 8.29 |
| 2.00 | 0.992 | 1.454 | 8.43 |
| 3.00 | 1.002 | 0.88 | 1.464 | 8.49 |
| 4.00 | 1.002 | 0.69 | 1.464 | 8.49 |
| 5.00 | 1.002 | 0.57 | 1.465 | 8.49 |
| 6.00 | 1.001 | 0.48 | 1.463 | 8.49 |

*Assumes $\Delta P_R = 35.3$ mm Hg and $C_{AA} = 5.80$ g/100 ml. * The value of $x^*$ at which $\Delta P = \Delta \pi$, the point of filtration pressure equilibrium. * $C_{EA}^\epsilon = 5.80$ C_{EA} g/100 ml.

| Table 3. Degree of equilibration as a function of $\epsilon$ ($F = 2.00, A_1 = 0.268, A_2 = 0.280$) |
|---|---|---|---|
| $\epsilon$ | $R$ | $x^*_{EQ}$ | $C_{EA}^\epsilon$ | $C_{EA}^\epsilon$ |
| 0.00 | 0.987 | 1.459 | 8.46 |
| 0.02 | 0.992 | 1.454 | 8.43 |
| 0.05 | 0.998 | 1.446 | 8.39 |
| 0.10 | 1.010 | 0.88 | 1.433 | 8.31 |

See footnotes of Table 2.
DISCUSSION

We have considered three methods of characterizing glomerular capillary osmotic and hydrostatic pressure profiles in the rat. The first of these assumes the Δτ profile to be linear, the mean glomerular capillary osmotic pressure being taken as the arithmetic average of \( \pi_{AA} \) and \( \pi_{EA} \). The other two methods are based on an idealized capillary bed in which concentrations and pressures vary only in the axial direction. Of these, one assumes \( \Delta P \) to be constant, while the other assumes \( \Delta P \) to decrease linearly with distance.

The model with axial pressure drop is the only one of the three approaches that predicts physically reasonable pressure profiles and is fully consistent with experimental observations of filtration pressure equilibrium (2, 3). The assumption of constant \( \Delta P \) provides adequate pressure profiles only when \( \Delta \tau \) is always less than \( \Delta P \). Both of these models predict essentially linear \( \Delta \tau \) profiles when the end points are far from equilibrium, but this condition appears not to be the case for the normal rat (1–3). The model with axial pressure drop is valid for all values of \( R \) far from observed (2, 3), whereas the model with constant \( \Delta P \) is applicable only when \( R < 1 \), and the linear \( \Delta \tau \) approach is valid only for \( R \) less than approximately 0.8. In the normal hypertensive rat, it is most often the case that \( R > 0.95 \) (2, 3).

The assumption that \( \Delta \tau \) is linear provides convenient estimates of the minimum value of \( K_i \) and the maximum value of \( (P_{UF}) \). While in principle the axial pressure drop model could be used to find more precise estimates of \( K_i \) and \( (P_{UF}) \), these are extremely sensitive to small errors in the measurement of \( (C)_{AA} \) and \( (C)_{EA} \) when \( R \) is close to unity. The uncertain magnitude of the axial pressure drop compounds this problem.

When \( R \) is near unity, the \( \Delta \tau \) profiles for different values of \( F \) have end points that are identical within the uncertainty of available protein concentration measurements. Values of \( (P_{UF}) \) calculated from \( \pi_{AA} \) and \( \pi_{EA} \) using, for example, the linear \( \Delta \tau \) approach, would also be identical, even though the true values of \( (P_{UF}) \) vary markedly with \( F \). Thus, with \( R \) close to unity, measurements of \( \pi_{AA} \) and \( \pi_{EA} \) cannot be taken as evidence that \( (P_{UF}) \) remained constant throughout a series of experiments. It is clear that \( (P_{UF}) \) depends not only on \( \pi_{AA} \), \( \pi_{EA} \), and \( \Delta P \), but on \( K_i \) and \( Q_0 \) as well.

The single-nephron glomerular filtration rate is related to glomerular capillary plasma flow and afferent and efferent arteriolar protein concentrations by the equation

\[
\text{SNGFR} = Q_o \left( 1 - \frac{1}{(C)_{EA}} \right)
\]  

(17)

As can be seen from Table 2 and equation 10a, when \( R \) is near unity (as in the normal rat), \( Q_o \) may be doubled or halved with almost no change in \( (C)_{EA} \). In this regime changes in SNGFR should be proportional to changes in plasma flow rate. For \( R \) not close to unity an increase in \( Q_o \) will cause a noticeable decrease in \( (C)_{EA} \), and SNGFR will depend less strongly on \( Q_o \). The same conclusion applies when \( Q_o \) is decreased.

We have emphasized the need for including an axial pressure drop in a satisfactory model of glomerular ultrafiltration. This pressure drop was assumed to be small compared to \( \Delta P \) and linear in \( x \), although properties \( a-e \) discussed previously require only that \( \Delta P \) decreases monotonically. Glomerular hydrostatic pressures are known to be pulsatile (2), but the three properties should be applicable at any instant in time provided that \( \Delta P \) and \( \Delta \tau \) are in phase. The pressures calculated with this model should be regarded as averaged over a period of time encompassing several cardiac cycles.

GLOSSARY OF SYMBOLS

\[
\begin{align*}
\text{Values in angular parentheses are mean values.} \\
\theta, \phi \quad \text{osmotic pressure coefficients in equation 5, mm Hg/(g/ml)} \\
\theta_1, \phi_2 \quad \text{dimensionless osmotic pressure coefficients, equation 10, } b \text{ and } c \\
C \quad \text{plasma protein concentration, g/100 ml} \\
C^* \quad \text{dimensionless protein concentration, C/C_0} \\
F \quad \text{K/F, permeability and plasma flow rate parameter, equation 10a} \\
I \quad \text{integration constant in equation 15} \\
k \quad \text{membrane hydraulic permeability, nl/(sec-mm Hg cm^2)} \\
K_i \quad \text{ultrafiltration coefficient, nl/(sec-mm Hg), equation 4} \\
L \quad \text{length of capillary, cm} \\
m \quad \text{mass flow rate of protein, g/sec.} \\
P \quad \text{hydrostatic pressure, mm Hg} \\
(P_{UF}) \quad \text{net ultrafiltration pressure, mm Hg, equation 1} \\
\Delta P \quad \text{F, reference pressure, mm Hg, equation 12} \\
Q \quad \text{volumetric flow rate in capillary lumen, nl/sec.} \\
Q_0 \quad \text{glomerular capillary plasma flow rate, Q(0)} \\
Technology \text{radius of idealized capillary, cm} \\
R \quad \text{ratio of osmotic to hydrostatic pressure differences at end of capillary, equation 16} \\
S \quad \text{surface area available for filtration, cm^2} \\
\text{SNGFR, single-nephron glomerular filtration rate, nl/min or ml/} \text{sec.} \\
\Delta \tau \quad \text{x point at which } (P_{UF}) \text{ and } \Delta P = \Delta \tau \text{, transmembrane osmotic pressure difference, mm Hg} \\
C^*_{EA} \quad \text{dimensionless variable} \\
\text{Super/subscript} \\
^* \quad \text{dimensionless variable} \\
\AA \quad \text{afferent arteriole} \\
EA \quad \text{efferent arteriole} \\
GC \quad \text{glomerular capillary} \\
T \quad \text{Bowman's space, or beginning or proximal tubule}
\end{align*}
\]
REFERENCES


