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INFLUENCE OF THE PERICAPILLARY PLASMA ON CHEMICAL EXCHANGE FROM BLOOD TO TISSUE

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16. Abstract

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If permeabilities are reassigned so that the endothelium is very leaky and the blood-tissue interface is the chemical barrier (low permeability), the species concentration in the tissue is increased again. The reason is that the blood velocity in the endothelium is much larger than that of the annulus. Thus the high rate of supply of species in the leaky endothelium is available to the annulus, and although the permeability of the blood-tissue interface is low, its large surface area is bathed by a high chemical concentration. The result is an increase in the species flux to the tissues and an increase in concentration. The effect increases with capillary radius (lower capillary hematocrit).

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SUMMARY

The transport of chemical species from blood to tissues is studied for capillaries that have an extra annulus of plasma outside the endothelium. The equations of flow and diffusive transport are solved in closed form in the blood compatible with transport into the surrounding tissue, which consumes the species according to first order kinetics. Results show that the plasma annulus increases the supply of species and thus the rate of chemical exchange between blood and tissues, raising the concentration (and the consumption rate) in tissue spaces.

If permeabilities are reassigned so that the endothelium is very leaky and the blood-tissue interface is the chemical barrier (low permeability), the species concentration in the tissue is increased again. The reason is that the blood velocity in the endothelium is much larger than that of the annulus. Thus the high rate of supply of species in the leaky endothelium is available to the annulus, and although the permeability of the blood-tissue interface is low, its large surface area is bathed by a high chemical concentration. The result is an increase in the species flux to the tissues and an increase in concentration. The effect increases with capillary radius (lower capillary hematocrit).

INTRODUCTION

It is known (refs. 1-3) that an annulus of fluid exists outside the endothelial wall of some capillaries. Sapirstein (ref. 4) has argued that the fluid is blood plasma rather than lymph (as first supposed by Heimberger (ref. 1). Howe and Sheaffer (refs. 5, 6) have shown several hydrodynamic reasons why the fluid should be plasma: Many experimental observations can be readily explained hydrodynamically with a plasma annulus (on the basis of flow in a "typical" capillary) - but not without one. They have shown a number of characteristics of such capillaries; for example, for low ratios of capillary to large blood vessel hematocrits, the plasma velocity along the annulus can be much less than that within the endothelium tube.

The function of the annulus has not been explained (ref. 3). The question remains whether there is an advantage of the extra plasma annulus other than that it simply provides a plasma reservoir. A second question is

which of the two capillary membranes is the true barrier to chemical exchange between blood and tissues. It has long been assumed that the endothelium is the barrier. But Sapirstein (ref. 4) has suggested that the outer wall is the "true hematolymph barrier." This paper investigates both of these questions.

SYMBOLS

a_1, a_2	defined by equations (A17) and (A18)
b	defined by equation (A19)
c	concentration of a chemical species in blood by mass fraction
$\bar{c}$	$\frac{c}{c_{2_o}}$
C_1, C_2	defined by equations (A26) and (A27)
D	diffusion coefficient
h	membrane permeability
I_o, I_1	modified Bessel function of order 0 and 1 of first kind
j_3	defined by equation (A13)
K_o, K_1	modified Bessel function of order 0 and 1 of second kind
k	metabolic rate coefficient
L	capillary length
m_1, m_2	defined by equations (A24) and (A25)
p	pressure
q	defined by equation (A21)
Q	rate of consumption per unit mass of tissue (eq. (A4))
r	radius from capillary axis
$\bar{r}$	$\frac{r}{L}$
R	radius of tissue supplied by capillary
$\bar{R}$	$\frac{R}{L}$

s	defined by equation (A22)
u	blood velocity in axial direction
z	axial distance from capillary entrance
$\bar{z}$	$\frac{z}{L}$
β	defined by equation (A14)
γ	defined by equation (A6)
η	coefficient of viscosity for plasma
μ	length in microns

Subscripts (except as noted above)

o	property at z = 0
1	red cells
2	either the blood in the endothelial tube or the properties of the endothelium
3	either the plasma in the annulus or the properties of the outer wall of the annulus
4	properties of the tissue space
r	radial
z	axial

ANALYSIS

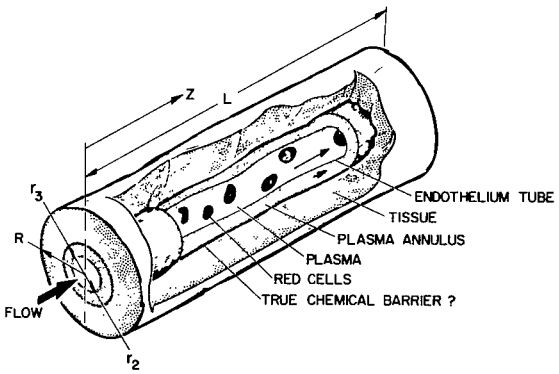

Figure 1.- Capillary - tissue model.

The bi-walled capillary model is shown in figure 1, where r_1, r_2, r_3, and R are, respectively, the radii of the red cells, the endothelium, the outer wall of the plasma annulus, and the outer boundary of the tissue supplied by the capillary of length L.

The model is described by a set of differential equations that describes blood laden with a chemical species entering and moving along the capillary

at a steady rate. The blood travels along the endothelium and the annulus at different velocities (u_2 and u_3). During the passage of blood along the capillary, some of the chemical substance is transported across the endothelium membrane to the blood in the annulus and from there across the outer membrane to the tissue space. As the species diffuses outward in the tissue space, it is also being consumed locally according to first-order kinetics.

The mathematical details are straightforward and appear in the appendix. Blum's results (ref. 7), for a single-walled capillary, are included as a special case of the present result.

RESULTS AND DISCUSSION

Input Quantities

The solutions of the differential equations that describe the exchange of chemical species between the blood and tissues were obtained in the manner described in the appendix. The numerous input quantities for these solutions are listed by example number in the following table. The example number is also shown in brackets for each curve in the figures.

Input Quantities for Solutions*

Example	r_2 (μ)	r_3 (μ)	R (μ)	L (μ)	u_2 (μ/sec)	u_3 (μ/sec)	h_2 (μ/sec)	h_3 (μ/sec)	Comment
1	8	---	30	500	500	---	4	---	No annulus
2	8	10	30	500	500	20	4	100	Inner barrier
3	8	10	30	500	500	20	100	4	Outer barrier
4	4.8	---	20	500	500	---	4	---	No annulus
5	4.8	5.6	20	500	500	20	4	100	Inner barrier
6	4.8	5.6	20	500	500	20	100	4	Outer barrier
7	8	10	30	1000	500	20	100	4	Double length
8	8	10	30	500	500	20	100	12	Triple permeability
9	8	10	30	500	1000	40	100	4	Double velocity
10	8	10	30	500	500	0	100	4	Annulus at rest

*Other input common to all examples: $k_4 = 0.40\ \text{sec}^{-1}$, $D_r = 40\ \mu^2/\text{sec}$

Since the plasma annulus is of concern here, the main input variation will be the radii of its boundaries - the endothelium and outer wall (r_2 and r_3) - and their permeabilities (h_2 and h_3). The blood velocity in the annulus (u_3) has been specified to vary with the radii r_2 and r_3 approximately as shown in the hydrodynamic analysis of Howe and Sheaffer (ref. 5) (their fig. 8).

Other input common to all examples is as follows. The blood velocity (u_2) in the endothelium was 500 μ/sec (except for example 9 where it was doubled) and the capillary length (L) was 500 μ (except for example 7 where it was doubled), so that transit time in the endothelium was 1 sec. The red cell radius was 4 μ. The diffusion coefficient (D_r) in the tissues was 40 μ^2/sec, which corresponds to a molecule the size of oxygen (ref. 8, p. 44). The tissue consumption rate coefficient (k_4) of 0.40 sec^{-1} corresponds to $\gamma = 0.1\ \mu^{-1}$ (eq. (A6)) which is within the range that Blum (ref. 7) used. The outer radius (R) of the tissue supplied by the capillary was either 20 or 30 μ, which is compatible with Blum's work and is the right order of magnitude (Hill, ref. 9, estimated that each capillary supplies about 12 times its volume of tissue).

Typical Chemical Distribution

The solutions give the variation of concentration of the chemical species in the blood and in the tissues in both the axial and radial directions as shown in figures 2 through 4. In these isometric plots the viewer is looking upstream from the capillary exit. Local chemical concentration is given by the height of the surface above the base plane.

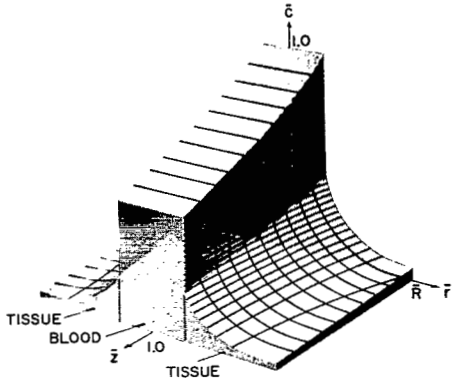

Figure 2.- Concentration surface - no plasma annulus (example 1).

Figure 2 corresponds to tissue supplied by a capillary with no plasma annulus outside the endothelium. The flat center portion of each radial profile is the chemical concentration in the blood in the endothelium. The curved portion is the concentration in the tissue space. The abrupt drop between blood and tissue concentrations is the effect of the permeability of the endothelium wall. The permeability is 4 μ/sec, which seems to be the right order of magnitude for molecular weights under 100 (ref. 10).

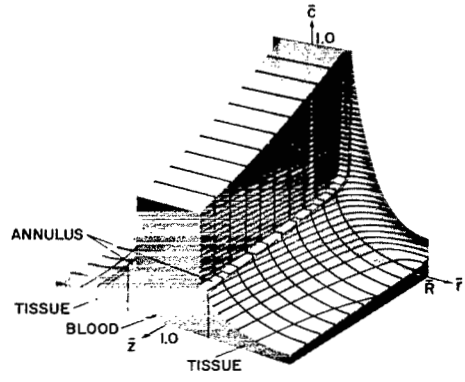

Figure 3.- Concentration surface - plasma annulus with inner barrier (example 2).

In figure 3 there is an annulus of plasma between the endothelium and the tissue space. The concentration in the annulus is shown by the outer notch on the flat portion of each profile. The interface separating the annular blood from the tissue has been assigned a high permeability, 100 μ/sec (i.e., it is a very leaky interface).

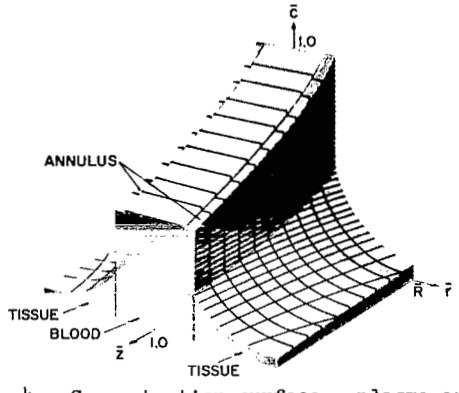

Figure 4.- Concentration surface - plasma annulus with outer barrier (example 3).

The conditions in figure 4 differ from those in figure 3 only in that the membrane permeabilities have been switched. That is, the endothelium is now very leaky, and the outer wall is the resistance to chemical exchange. This represents Sapirstein's (ref. 4) suggestion that the outer wall is the true hematolymph barrier.

The capillary dimensions and blood velocities of figures 3 and 4 correspond approximately to the curve labeled $k/h_c = 6$ in figure 8(a) of reference 5 (where the ratio of capillary to large vessel hematocrit was about 0.4). The capillary is large:

r_3 = 10 μ and r_2 = 8 μ, and the plasma velocity in the annulus (20 μ/sec) is small compared with the velocity in the endothelium (500 μ/sec).

COMPARISON OF RESULTS

Large Capillaries

The results of the previous three figures are compared in figures 5 and 6. The three curves in figure 5 show the axial variation of chemical concention within the endothelium for the previous three figures. The upper two lines correspond to the first two examples in which the endothelium was the main chemical barrier. The lowest curve corresponds to figure 4 - the leaky endothelium. As expected, chemical exchange from the leaky endothelial tube is greater, resulting in a lower concentration in the blood. Examples of a leaky endothelium have slightly lower concentration in the plasma annulus than in the endothelium blood, while examples in which the endothelium is the chemical barrier have significantly lower concentrations in the plasma annulus.

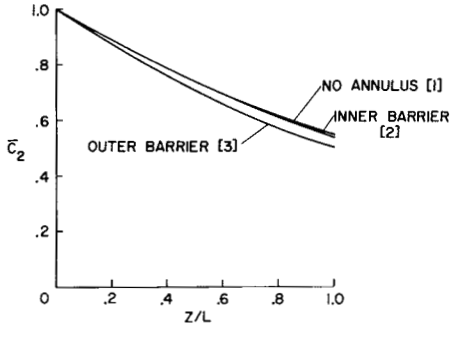

Figure 5.- Concentration in blood in endothelium (r_2 = 8μ, r_3 = 10μ).

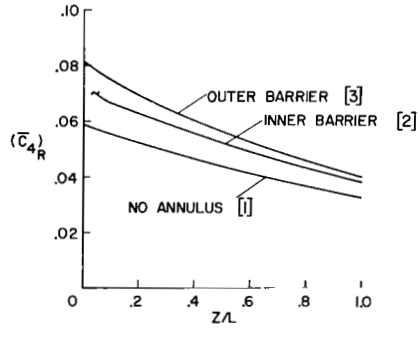

Figure 6.- Tissue concentration of outermost cell (r_2 = 8μ, r_3 = 10μ).

The solid lines of figure 6 show the corresponding axial concentration profiles in the outermost cells (at r = R) served by the capillary. The profiles are also a measure of the rate of consumption which is proportional to the concentration for first-order kinetics. The bottom curve corresponds to figure 2 - no plasma annulus. The middle curve has the annulus, with the endothelium as the chemical barrier (i.e., fig. 3). The concentration increase over the no annulus result was supplied by the blood in the annulus (since the two examples had almost identical profiles within the endothelium). The upper curve corresponds to figure 4 in which the outer wall was the true barrier. Thus, we see that Sapirstein's model of the double-walled capillary with the outer wall as the true hematolymph barrier is more efficient for chemical exchange and produces higher tissue concentrations than the double-walled model with the inner barrier, and is still more efficient than the model without the annulus (by 25 to 30 percent). The outer barrier provides a higher species concentration in the tissue space than the inner barrier because the blood velocity in the endothelium is much greater than that in the annulus ($u_2 >> u_3$). Thus, the high rate of supply of species in the leaky endothelium

is available to the annulus, and although the permeability of the blood-tissue interface is low, its large surface area is bathed by a high chemical concentration. The result is an increase in the species flux to the tissues.

If u_3 were sufficiently large, the reverse would be true - the inner barrier would provide the higher tissue concentration. This is illustrated by the dashed lines in figure 6 for which u_3 has (unrealistically) been set equal to u_2 (500 μ/sec). Now there is a high rate of supply of species along the annulus adjacent to the blood-tissue interface. Consequently, if that interface (rather than the endothelium) were leaky, chemical transfer to the tissue space would be enhanced. Realistically, however, the hydrodynamics of this configuration requires a low velocity in the annulus (ref. 5), which leads to the previous result.

Small Capillaries

Figures 7 and 8 compare results of solutions for which $r_3 = 5.6$ μ and $r_2 = 4.8$ μ. These correspond approximately to the curve labeled $k/h_c = 2$ in figure 8(b) of reference 5 (where the ratio of capillary to large vessel hematocrit was about 0.625). For these conditions, u_3 is again estimated to be about 20 μ/sec. The result for $r_2 = 4.8$ μ without an annulus is also shown.

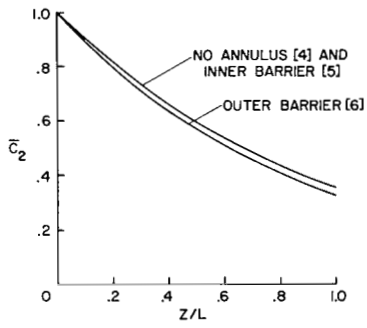

Figure 7.- Concentration in blood in endothelium ($r_2 = 4.8\mu$, $r_3 = 5.6\mu$).

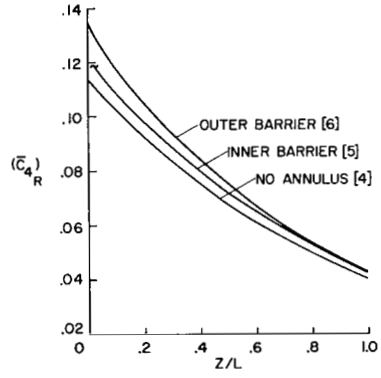

Figure 8.- Tissue concentration of outermost cell ($r_2 = 4.8\mu$, $r_3 = 5.6\mu$).

Generally, the results follow the same pattern as before (figs. 5 and 6) but to a lesser extent; that is, the annulus still provides better chemical exchange and higher tissue concentration; and Sapirstein's outer barrier is still superior to the inner barrier, but the advantages have diminished.

Other Comparisons for Large Capillaries

For the larger capillaries, it is of interest to examine the effects of varying some of the input parameters. The example of figure 4 is a standard for this comparison.

Figure 5 shows that the concentration in the blood in the endothelium at the capillary exit is more than half its value at the entrance. Intuitively,

this residual concentration seems high, which suggests that such capillaries may have additional features that would improve the overall chemical exchange between blood and tissues. Two such features are higher permeability or greater length. Figure 9 shows that tripling the permeability (h_3 = 12 μ/sec) or doubling the length would give exit plane residuals of 0.33 or 0.25, respectively. The corresponding tissue concentration curves are presented in figure 10 which shows that the high permeability increases the consumption rate of the outermost cells between 5 and 60 percent over the upper solid curve of figure 6. The first half of the double length capillary is actually identical to the upper solid curve of figure 6 (it is simply shifted to the left by the z/L scale of fig. 10). Thus the second half of the longer capillary shows a diminished tissue concentration for those cells served by the additional length. But, even at that the cell concentration for the second half is the same order of magnitude as the first half.

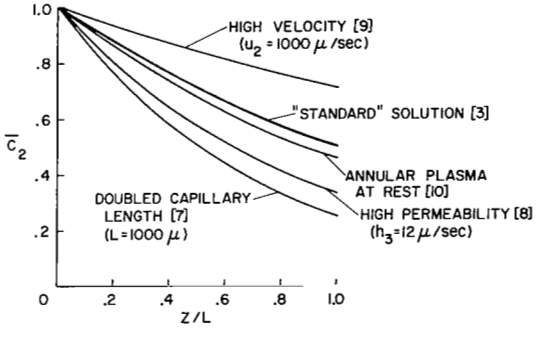

Figure 9.- Effects of various parameters on the concentration in endothelial blood (r_2 = 8μ, r_3 = 10μ).

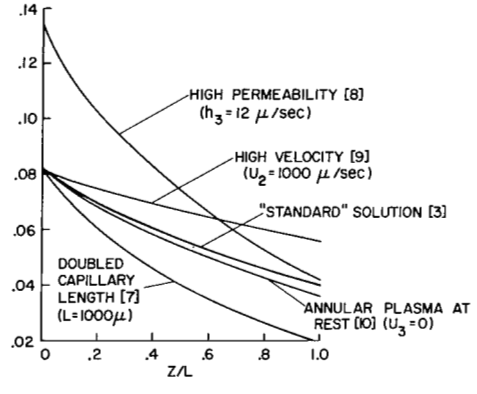

Figure 10.- Effects of various parameters on tissue concentration of outermost cell (r_2 = 8μ, r_3 = 10μ).

From these results, we may speculate that larger capillaries (r_2, r_3) are also characterized by either high permeability or greater length (either to provide high local tissue concentration or to supply more tissue). Interestingly, the photomicrographs of nailfold capillary loops by Bosley (ref. 11) and by Gibson, Bosley, and Griffiths (ref. 2) show both the large radius of the pericapillary "halo space" (r_3) and the greater length (L ≈ 1500 μ).

For hydrodynamic reasons, also, the greater length may be associated with the larger capillary radius. From reference 5 (eq. (A5)), the pressure gradient is related to the cell speed and endothelium radius by

$$u_c = -\frac{1}{4\eta}\frac{dp}{dz}(r_2^2 - r_1^2) \tag{1}$$

where the pressure gradient is

$$\frac{dp}{dz} = \frac{p_{venule} - p_{arteriole}}{L} \tag{2}$$

Combining these gives

$$u_c = - \frac{(p_{venule} - p_{arteriole})}{4\eta} \frac{(r_2^2 - r_1^2)}{L} \qquad (3)$$

If the venule and arteriole pressure are fixed and if the cell speed should be approximately constant (for efficient chemical exchange), then large capillaries (large r_2) should have correspondingly greater lengths (eq. (3)).

Alternatively, if the large radius capillary is not longer, the cell speed would be larger according to equation (3). A result for doubled cell speed is also shown in figures 9 and 10. The efficiency of chemical transfer is lower for this high velocity; the endothelial blood gives up less than 30 percent of its load on a single pass through the capillary. However, the cell concentration is enhanced very significantly as shown in figure 10 because the tissue-blood interface is bathed by a supply of high chemical concentration.

As a matter of interest, the result for stationary plasma in the annulus is also shown in figures 9 and 10. In an analysis of the microcirculation of the liver, Goresky (ref. 12) assumed the plasma in the extravascular space to be at rest. As shown in figure 9 the rest condition leads to a concentration profile in the endothelium a little lower than the corresponding profile for the moving plasma in the annulus. Figure 10 shows that the tissue concentration is also diminished if the annular plasma is at rest.

Ames Research Center
National Aeronautics and Space Administration
Moffett Field, Calif., 94035 Aug. 4, 1967
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APPENDIX A

MATHEMATICAL ANALYSIS

A general description of the model (fig. 1) was presented previously, where it was noted that Blum (ref. 7) has solved the problem of chemical exchange between blood and tissue across one membrane - the endothelium. In the present study, the effect of an extra annulus of plasma (region 3) and a second membrane (the outer wall characterized by permeability h_3) is examined. Like Blum, we neglect the details within the red cells in the endothelium, as well as the details of the velocity profile in the capillary. As noted previously, we allow the axial velocity, u_2, in the endothelium to differ from that in the annulus, u_3, to retain the character of the results of reference 5. Chemical reactions are allowed only in the tissue space (region 4).

The concentration (mass fraction), c_2, of some chemical species in a volume element of blood of axial length dz in the endothelium (region 2) is depleted by leakage across the endothelium and replenished by fresh blood entering the element so that, for the steady state,

$$\frac{dc_2}{dz} = -\frac{2h_2}{u_2 r_2}(c_2 - c_3) \tag{A1}$$

Similarly, in the annulus (region 3)

$$\frac{dc_3}{dz} = -\frac{2}{u_3(r_3^2 - r_2^2)}\{r_2 h_2(c_3 - c_2) + r_3 h_3[c_3 - (c_4)_{r_3}]\} \tag{A2}$$

In the tissue space, the usual diffusive transport equation applies

$$D_z \frac{\partial^2 c_4}{\partial z^2} + D_r\left(\frac{\partial^2 c_4}{\partial r^2} + \frac{1}{r}\frac{\partial c_4}{\partial r}\right) = Q \tag{A3}$$

where Q is the rate of consumption per unit mass of tissue, which for first-order kinetics is

$$Q = k_r c_4 \tag{A4}$$

In the tissue space diffusion in the axial direction is neglected in favor of that in the radial direction because distances are small and gradients are large in the radial direction compared with the axial direction. Thus, equation (A3) becomes

$$\frac{\partial^2 c_4}{\partial r^2} + \frac{1}{r}\frac{\partial c_4}{\partial r} - \gamma^2 c_4 = 0 \tag{A5}$$

where

$$\gamma^2 = \frac{k_4}{D_r} \tag{A6}$$

The boundary conditions for equations (A1), (A2), and (A5) are, at $z = 0$:

$$c_2 = c_{2_o} \tag{A7}$$

$$c_3 = c_{3_o} \tag{A8}$$

at $r = r_3$:

$$-D_r \left(\frac{\partial c_4}{\partial r}\right)_{r_3} = h_3[c_3 - (c_4)_{r_3}] \tag{A9}$$

and at $r = R$:

$$\frac{\partial c_4}{\partial r} = 0 \tag{A10}$$

The solution of equation (A5) is readily found to be (7)

$$\bar{c}_4 \equiv \frac{c_4}{c_{2_o}} = (\bar{c}_4)_{r_3} \left[\frac{K_1(\gamma R)I_o(\gamma r) + K_o(\gamma r)I_1(\gamma R)}{K_1(\gamma R)I_o(\gamma r_3) + K_o(\gamma r_3)I_1(\gamma R)}\right] \tag{A11}$$

where $(\bar{c}_4)_{r_3}$ has yet to be determined.

If h_3 from equation (A9) is substituted into equation (A2), and $(\partial c_4/\partial r)_{r_3}$ is used (from eq. (A11) differentiated), one obtains

$$\frac{dc_3}{dz} = -\frac{2}{u_3(r_3^2 - r_2^2)} [c_3(r_2h_2 + r_3h_3j_3) - c_2r_2h_2] \tag{A12}$$

where

$$j_3 = \frac{1}{1 + \frac{h_3}{D_r\gamma\beta}} \tag{A13}$$

and

$$\beta = \frac{-K_1(\gamma R)I_1(\gamma r_3) + K_1(\gamma r_3)I_1(\gamma R)}{K_1(\gamma R)I_o(\gamma r_3) + K_o(\gamma r_3)I_1(\gamma R)} \tag{A14}$$

Equations (A1) and (A12) can be written as

$$\frac{dc_2}{dz} = a_1c_2 - a_1c_3 \tag{A15}$$

and

$$\frac{dc_3}{dz} = a_2c_3 + bc_2 \tag{A16}$$

respectively, where

$$a_1 = -\frac{2h_2}{u_2 r_2} \tag{A17}$$

$$a_2 = -\frac{2}{u_3(r_3^2 - r_2^2)}(r_2 h_2 + r_3 h_3 j_3) \tag{A18}$$

$$b = \frac{2r_2 h_2}{u_3(r_3^2 - r_2^2)} \tag{A19}$$

Differentiate (A15) with respect to z and combine with equation (A16) to obtain

$$\frac{d^2 c_2}{dz^2} + q\frac{dc_2}{dz} + sc_2 = 0 \tag{A20}$$

where

$$q = -(a_2 + a_1) \tag{A21}$$

$$s = a_1(a_2 + b) \tag{A22}$$

The solution of equation (A20) is[1]

$$\bar{c}_2 \equiv \frac{c_2}{c_{2_0}} = C_1 e^{m_1 z} + C_2 e^{m_2 z} \tag{A23}$$

where

$$m_1 = \frac{-q + \sqrt{q^2 - 4s}}{2} \tag{A24}$$

$$m_2 = \frac{-q - \sqrt{q^2 - 4s}}{2} \tag{A25}$$

The coefficients C_1 and C_2 can be evaluated from boundary condition (A7) and equation (A15) applied at $z = 0$ with the results:

$$C_1 = \frac{a_1\left[\left(\frac{c_{3_0}}{c_{2_0}}\right) - 1\right] + m_2}{m_2 - m_1} \tag{A26}$$

[1]The solution is valid for $q^2 - 4s > 0$ and for the present examples.

and

$$C_2 = \frac{-\left\{a_1\left[\left(\frac{c_{3_0}}{c_{2_0}}\right) - 1\right] + m_1\right\}}{m_2 - m_1} \tag{A27}$$

Equation (A16) can be integrated directly by use of equation (A23) and boundary condition (A8) to obtain

$$\bar{c}_3 \equiv \frac{c_3}{c_{2_0}} = \left[\frac{c_{3_0}}{c_{2_0}} - b\left(\frac{C_1}{m_1 - a_2} + \frac{C_2}{m_2 - a_2}\right)\right] e^{a_2 z} + b\left(\frac{C_1 e^{m_1 z}}{m_1 - a_2} + \frac{C_2 e^{m_2 z}}{m_2 - a_2}\right) \tag{A28}$$

By differentiating equation (A28) with respect to z, using the result in equation (A2), and solving for $(c_4)_{r_3}$, we obtain

$$\begin{aligned}(\bar{c}_4)_{r_3} \equiv \frac{(c_4)_{r_3}}{c_{2_0}} &= (1 - j_3)\bar{c}_{3_0} e^{a_2 z} \\ &+ \frac{C_1}{m_1 - a_2}\left\{\left[\left(\frac{r_2 h_2}{r_3 h_3}\right)(b + a_2) + b\right] e^{m_1 z} - (1 - j_3) b e^{a_2 z}\right\} \\ &+ \frac{C_2}{m_2 - a_2}\left\{\left[\left(\frac{r_2 h_2}{r_3 h_3}\right)(b + a_2) + b\right] e^{m_2 z} - (1 - j_3) b e^{a_2 z}\right\}\end{aligned} \tag{A29}$$

Thus, the concentration in regions 2, 3, and 4 is given by equations (A23), (A28), and (A11), respectively, with $(\bar{c}_4)_{r_3}$ in equation (A11) given by equation (A29).

The equations for the solutions can be rewritten in terms of dimensionless parameters. The resulting equations are not particularly interesting and will not be shown. But the corresponding parameters are important and so are listed: h_2/u_2, h_3/u_3, u_2/u_3, r_2/r_3, j_3, r_2/L, R/L, γL, z/L, and c_{3_0}/c_{2_0}. A given set of these parameters completely determines a solution. Of particular importance are the ratios h_2/u_2 and h_3/u_3 - that is, the ratio of the wall permeability to the adjacent blood velocity is significant rather than the permeability alone.

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