

A Theoretical Analysis of CO₂ Absorption in Sun Versus Shade Leaves

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A one-dimensional, steady-state, constant temperature model of diffusion and absorption of CO₂ in the intercellular air spaces of a leaf is presented. The model includes two geometrically distinct regions of the leaf interior, corresponding to palisade and spongy mesophyll tissue, respectively. Sun, shade, and intermediate light leaves are modeled by varying the thicknesses of these two regions. Values of the geometric model parameters are obtained by comparing geometric properties of the model with experimental data of other investigators found from dissection of real leaves. The model provides a quantitative estimate of the extent to which the concentration of gaseous CO₂ varies locally within the leaf interior.

Introduction

When leaves develop it has been observed that their size and form are dependent upon the quantity of light which they have been exposed to during differentiation [1-5].¹ Leaves which develop in the presence of relatively large quantities of light (sun leaves) have been found to be thicker than leaves which develop in the presence of relatively small quantities of light (shade leaves). The mesophyll region of sun leaves typically contains a higher ratio of number of palisade cells to spongy cells than the mesophyll region of shade leaves. (See Figs. 1 and 2.)

It is the purpose of this work to consider how these variations in thickness and type of mesophyll cell structure influence the absorption and diffusion of CO₂ inside the leaf.

The first mathematical model of gaseous diffusion in leaves was presented in 1900 by Brown and Escombe [10]. They gave an approximate solution for the steady-state diffusion through a plane septum with a single circular pore. Bange [11] extended their work by modeling the substomatal cavity as a spherical region. Elliptical pores were considered analytically by Cooke [12], who also investigated interactions between neighboring pores.

A model based on the electrical circuit analogy was successfully applied to the leaf diffusion problem by Penman and Schofield [13]. This "resistance" model was extended by Monteith [6] and an up-to-date summary may be found in Nobel's text [7]. The resistance model represents one-dimensional steady-state diffusion without distributed sources or sinks. The model presented in this paper extends previous work by including sinks

for CO₂ distributed along the walls of the intercellular air space in the leaf interior.

The effect of morphological differences between leaves of the same plant species was considered in the context of resistance models by de Wit [14], by El-Sharkawy and Hesketh [15], and more recently by Nobel and his coworkers [2, 3]. Although these resistance models have been shown to be successful in predicting overall leaf CO₂ flux, these models do not indicate how the concentration C of CO₂ in the intercellular air spaces varies from point of point within the leaf, nor how this variation is influenced by changes in internal leaf geometry.

Qualitative considerations suggest that as CO₂ diffuses into the leaf's intercellular air spaces, being absorbed into the wet mesophyll cell walls for photosynthesis in the chloroplasts in the cell interiors, the values of C in the deep interior of the leaf will

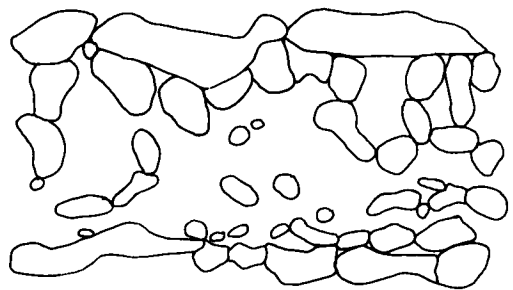


Fig. 1 Transverse section of *Fragaria vesca* shade leaf (after [4]). Bar equals 50 μ m. Note absence of palisade cells, cf., Fig. 2.

¹Numbers in brackets designate References at end of paper.

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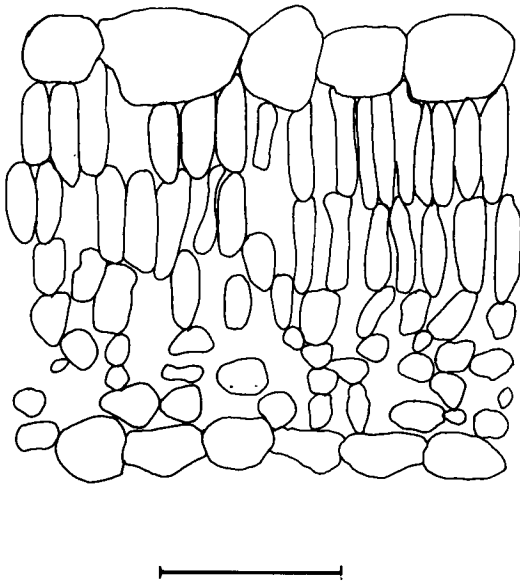


Fig. 2 Transverse section of *Fragaria vesca* sun leaf (after [4]). Bar equals 50 μ m. Note presence of several layers of palisade cells.

be lower than those in the substomatal cavity adjacent to the stomatal pore. (This is because CO₂ is being "used up", i.e., absorbed, as it diffuses inward.) It follows that the thicker the leaf and the greater the surface area of mesophyll cells per unit leaf area, A^{mes}/A , the smaller will be the expected concentration of CO₂ in the deep interior of the intercellular air spaces. Thus sun leaves should achieve smaller values of C in their deep interiors than comparable shade leaves. But how much smaller? It is desirable to supplement this qualitative argument with some quantitative theoretical estimates.

The physiological significance of the variation of C through the thickness of the leaf lies in the relation of C to J_m , the flux of gaseous CO₂ into a mesophyll cell per unit area of mesophyll cell wall. Variations in J_m from cell to cell within the leaf may influence the local rate of photosynthesis [9].

This paper presents a model which provides an estimate of the extent of the variation of C and J_m within the leaf interior. The model is one-dimensional, steady-state, constant temperature [8], and includes two geometrically distinct regions of the leaf interior, corresponding to palisade and spongy mesophyll tissue, respectively.

The Model

The geometry of the intercellular air spaces within the leaf consists of torturous pathways winding around the mesophyll cells. The spongy mesophyll cells are irregularly shaped and the

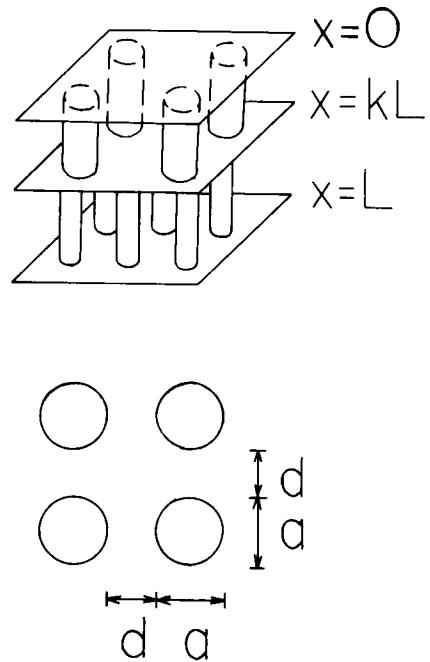


Fig. 3 Geometry of model. (a) Three-dimensional view. Palisade region has thickness kL while spongy region has thickness $(1-k)L$. (b) Typical cross section, $x = \text{const}$.

palisade mesophyll cells are approximately cylindrical. (See Figs. 1, 2.)

A realistic model of this geometry would be mathematically difficult to describe and the resulting boundary value problem would be intractable. Realism is therefore sacrificed in the one dimensional model presented here. Both the spongy and palisade mesophyll tissues are modeled by a regular arrangement of circular cylindrical cells (Fig. 3). The diameter of the cells, a , and the spacing between adjacent cells, d , are assumed constant within either tissue, but the values of a_s , d_s in the spongy tissue are allowed to be distinct from a_p , d_p in the palisade tissue.

The values of the parameters a_s , d_s , a_p , d_p , as well as the thickness of the spongy and palisade layers are chosen so that the model agrees with measurements of A^{mes}/A and V^{ias}/V (volume of intercellular air space per unit leaf volume) obtained from real leaves.

Although the model greatly simplifies the geometry of the leaf interior, it is nevertheless believed that the predictions drawn from this model are approximately applicable to the real leaf.

Let x represent the distance into the leaf from the upper leaf surface ($x = 0$). The interior of the leaf has total thickness L , with the palisade layer occupying the region $0 < x < kL$ and

Nomenclature

a = cell diameter (Fig. 3)
 A = area of leaf surface (one side of leaf only)
 A^{mes} = surface area of mesophyll cells under leaf area A
 B = area of intercellular air spaces under leaf area A
 C = concentration of CO₂ in intercellular air space away from walls
 C^* = concentration of CO₂ in intercellular air space at the walls
 \hat{C} = concentration of CO₂ in substomatal cavity

C_{liq} = concentration of CO₂ in cell wall liquid
 d = distance between cells (Fig. 3)
 D = diffusion coefficient of CO₂ in air
 $H = D/R$
 J_m = CO₂ flux into mesophyll cell walls
 k = fraction of leaf thickness composed of palisade tissue (Fig. 3)
 L = total leaf thickness (Fig. 3)
 N = number of mesophyll cells under leaf area A
 R = average distance from mesophyll cell walls to middle of intercellular air space

S = mesophyll cell wall circumference under leaf area A
 V = total leaf volume under leaf area A
 V^{ias} = volume of intercellular air space under leaf area A
 x = distance into leaf measured from upper leaf surface (Fig. 3)
 Ω = resistance associated with flux of dissolved CO₂ from mesophyll cell walls to chloroplasts

Subscripts

p = palisade tissue
 s = spongy tissue

the spongy layer $kL < x < L$. The lower leaf surface corresponds to $x = L$. (Here k is a parameter representing the fraction of the total internal leaf thickness composed of palisade tissue, $0 \leq k \leq 1$.)

Let $C(x)$ represent the concentration [g/cm^3] of gaseous CO_2 in the intercellular air space at cross section x . Although C actually varies from point to point in each cross section, the value of $C(x)$ will be identified with an average value of C away from the walls of the mesophyll cells which enclose the intercellular air space, at cross section x .

The following boundary conditions on $C(x)$ are assumed:

At the upper leaf surface, $x = 0$, there is no CO_2 flux,

$$-D \frac{dC}{dx} = 0, \quad x = 0 \quad (1)$$

where D = diffusion coefficient of CO_2 in air (cm^2/s). This boundary condition neglects the small flux of CO_2 through the cutinized upper leaf surface as well as the presence of stomata there. In those species in which there are significant numbers of stomata on the upper leaf surface this boundary condition would have to be changed to one which specifies the concentration C at $x = 0$, as is done in the present model at $x = L$.

At the lower leaf surface, $x = L$, the concentration is prescribed,

$$C = \hat{C}, \quad x = L \quad (2)$$

Here \hat{C} represents the concentration of CO_2 just inside the stomatal pore in the substomatal cavity. Since the model considers $C(x)$ to be a representative average value over a cross section, the value of \hat{C} represents an average over the lower leaf surface, portions of which are covered by cutin. (Actually \hat{C} depends upon the concentration of CO_2 in the ambient atmosphere as well as upon other parameters, e.g., resistances. By assuming that \hat{C} is prescribed, the flow of CO_2 inside the leaf becomes uncoupled from the flow in the stomatal pore and in those regions outside the leaf.)

As in [8] it is assumed that the absorption of CO_2 into the walls of the mesophyll cells is governed by the following expression for flux J_m ($\text{g}/\text{cm}^2\text{s}$).

$$J_m = H(C - C^*) \quad (3)$$

where

$C = C(x)$ = concentration of gaseous CO_2 in the intercellular air space away from the walls, at cross section x

$C^* = C^*(x)$ = concentration of gaseous CO_2 in the intercellular air space at the walls, at cross section x

and

$$H = D/R \quad (4)$$

where

R = average distance from walls to middle of intercellular air space, at cross section x .

The constant H represents the reciprocal of the resistance associated with the diffusion of gaseous CO_2 from the middle of the air spaces to the mesophyll walls. Since resistance is the ratio of distance diffused to diffusion coefficient ([7, pp. 303-304]), R represents the distance diffused. (The computation of R for an assumed cross section (Fig. 3) is unnecessary since, as will be shown in the forthcoming, R does not appear in the governing equation.)

Now consider an intercellular air space volume element Σ of thickness dx and lying under an area of leaf surface A (one side of leaf only) much larger than the cross-sectional area of a single mesophyll cell ($= \pi a^2/4$). The rate (g/s) at which CO_2 is lost from Σ due to the flux J_m is $J_m S dx$ where S is the mesophyll

cell wall circumference under area A . Here $S = N\pi a$ where N is the number of cells under area A (Fig. 3), $N = A/(a + d)^2$.

For mass to be conserved this flow rate must be balanced by the rate at which CO_2 is added to Σ due to diffusion in the x direction,

$$- \frac{d}{dx} \left(-D \frac{dC}{dx} B \right) dx$$

where B is the area of intercellular air spaces under area A . Here $B = A - N\pi a^2/4$.

Equating these rates and using equations (3), (4), obtain

$$\frac{d^2 C}{dx^2} + \frac{S}{BR} (C^* - C) = 0 \quad (5)$$

Note that S , B , R have different values in the palisade and spongy tissues, respectively.

At the interface between these two types of mesophyll tissue, $x = kL$, it is required that concentration C and rate of flow in the x direction, $-DB dC/dx$, be continuous:

$$C(x = kL^-) = C(x = kL^+) \quad (6)$$

$$B_p \frac{dC}{dx} \Big|_{x=kL^-} = B_s \frac{dC}{dx} \Big|_{x=kL^+} \quad (7)$$

where the subscript p again refers to palisade tissue ($0 < x < kL$) and the subscript s refers to spongy tissue ($kL < x < L$).

As in [8], the CO_2 concentration at the mesophyll cell wall, C^* , is assumed to result from equilibrium of gaseous CO_2 with the dissolved CO_2 in the cell wall liquid (a dilute aqueous solution.) Henry's law governs this situation ([7, p. 459]),

$$C^* = KM \quad (8)$$

where

K = a proportionality constant (temperature dependent)

M = mole fraction of CO_2 in cell wall liquid.

At typical leaf temperatures, evaluation of Henry's law shows that ([7, p. 330])

$$C^* \approx C_{liq} \quad (9)$$

where $C_{liq} = C_{liq}(x)$ = concentration of CO_2 in cell wall liquid.

Finally, conservation of mass is applied to the CO_2 absorption process: The flux of gaseous CO_2 from the intercellular air space into the mesophyll cell walls, J_m , equals the flux of dissolved CO_2 from the cell walls into the chloroplasts. This latter flux is proportional to the difference in CO_2 concentration between cell wall and chloroplast ([7, pp. 325-340]). Assuming that the CO_2 concentration in the chloroplasts is zero ([6, p. 98]; [3, p. 219]), the flux of dissolved CO_2 becomes C_{liq}/Ω , where Ω is the resistance associated with this flux.

Using equations (3), (4) conservation of mass requires that

$$J_m = \frac{D(C - C^*)}{R} = \frac{C_{liq}}{\Omega} \quad (10)$$

Eliminating C_{liq} from equations (9), (10), find

$$C^* = \left(1 + \frac{R}{D\Omega} \right)^{-1} C \quad (11)$$

For typical values of R , Ω , D , the parameter $R/D\Omega \ll 1$. E.g. with $R = 5\mu\text{m}$, $\Omega = 100 \text{ s}/\text{cm}$ ([2, 3]), $D = 0.16 \text{ cm}^2/\text{s}$, obtain $R/D\Omega = 3.1 \times 10^{-5}$. Expanding equation (11) in a Taylor series,

$$C^* = \left(1 - \frac{R}{D\Omega} \right) C, \quad \frac{R}{D\Omega} \ll 1 \quad (12)$$

Substituting equation (12) into equation (5), obtain

$$\frac{d^2C}{dx^2} - \omega_i^2 C = 0, \quad i = s, p \quad (13)$$

where

$$\omega_i^2 = S_i / (B_i D \Omega)$$

$$i = \begin{cases} p & \text{palisade for } 0 < x < kL \\ s & \text{spongy for } kL < x < L. \end{cases}$$

Note that the governing equation (13) does not contain R , as stated in the foregoing.

The solution to equation (13) with the four boundary conditions (1), (2), (6), (7) is

$$\frac{C(x)}{\bar{C}} = \begin{cases} \alpha_p \cosh \omega_p x, & 0 < x < kL \\ \alpha_s \cosh \omega_s x + \beta_s \sinh \omega_s x, & kL < x < L \end{cases} \quad (14)$$

where

$$\alpha_p = [\cosh \omega_p kL \cosh \omega_s(1 - k)L + \lambda \sinh \omega_p kL \sinh \omega_s(1 - k)L]^{-1}$$

$$\alpha_s = \alpha_p (\cosh \omega_p kL \cosh \omega_s kL - \lambda \sinh \omega_p kL \sinh \omega_s kL)$$

$$\beta_s = \alpha_p (\lambda \sinh \omega_p kL \cosh \omega_s kL - \cosh \omega_p kL \sinh \omega_s kL)$$

$$\lambda = \omega_p B_p / (\omega_s B_s) = \sqrt{S_p B_p / (S_s B_s)}$$

Geometric Properties of the Model

Before discussing the solution (14), selection of the geometric parameters a_s , d_s , a_p , d_p , k , L will be made by considering certain geometric properties of the model.

A number of investigators (see e.g., [5], [2], [3]) have experimentally obtained values of A^{mes}/A and V^{ias}/V (volume of intercellular air space per unit leaf volume) by dissecting real leaves. Their results are shown in Table 1.

In order to compare these experimentally obtained values with the comparable quantities associated with the model, the following expressions are needed:

$$A^{mes}/A = \frac{S_p kL + S_s(1 - k)L}{A} = \frac{\pi a_p kL}{(a_p + d_p)^2} + \frac{\pi a_s(1 - k)L}{(a_s + d_s)^2} \quad (15)$$

$$V^{ias}/V = \frac{B_p kL + B_s(1 - k)L}{AL} = k \left[1 - \frac{\pi}{4} \left(\frac{a_p}{a_p + d_p} \right)^2 \right] + (1 - k) \left[1 - \frac{\pi}{4} \left(\frac{a_s}{a_s + d_s} \right)^2 \right] \quad (16)$$

Numerical evaluation of equations (15), (16), shows that the model exhibits general agreement with Table 1 for a wide range of parameters. The following values are chosen as typical, although not referring to any particular species:

$$\begin{aligned} a_s &= a_p = 20 \mu\text{m} \\ d_s &= 0.15 a_s = 3 \mu\text{m} \\ d_p &= 0.03 a_p = 0.6 \mu\text{m} \end{aligned} \quad (17)$$

Three types of leaves are considered, each of which corresponds to these same values of a_s , a_p , d_s , d_p but which differ in k and L :

$$\begin{aligned} \text{Shade leaf} & \quad k = 0 & \quad L = 150 \mu\text{m} \\ \text{Intermediate light leaf} & \quad k = 1/2 & \quad L = 225 \mu\text{m} \\ \text{Sun leaf} & \quad k = 1 & \quad L = 300 \mu\text{m} \end{aligned} \quad (18)$$

Here the shade leaf is idealized as consisting of only spongy mesophyll cells while the sun leaf has only palisade mesophyll cells. The intermediate light leaf is half spongy, half palisade.

Substituting equations (17), (18) into (15), (16), find:

$$\begin{aligned} \text{Shade leaf} & \quad A^{mes}/A = 18 & \quad V^{ias}/V = 41 \text{ percent} \\ \text{Intermediate light leaf} & \quad A^{mes}/A = 30 & \quad V^{ias}/V = 33 \text{ percent} \\ \text{Sun leaf} & \quad A^{mes}/A = 44 & \quad V^{ias}/V = 26 \text{ percent} \end{aligned} \quad (19)$$

These values compare favorably with the general trends exhibited by Table 1, namely that sun leaves have higher values of A^{mes}/A and lower values of V^{ias}/V than corresponding shade leaves. Moreover the actual values of A^{mes}/A and V^{ias}/V exhibited by the model for these parameters are typical.

Predictions of the Model

In addition to the parameters selected in the previous section, values of D , Ω must be specified before the solution (14) can be evaluated:

$$\begin{aligned} D &= 0.16 \text{ cm}^2/\text{s} \\ \Omega &= 100 \text{ s/cm} \end{aligned} \quad (20)$$

It is to be noted that the resistance Ω of CO_2 in the cell wall liquid refers to flux per unit cell wall area rather than per unit leaf area [2, 3]. It is assumed that Ω is the same for shade, intermediate light and sun leaves [2, 3].

Using all the foregoing parameter values, the dimensionless concentration $C(x)/\bar{C}$ predicted by equation (14) is displayed in Fig. 4 as a function of x/L for the three types of leaves considered.

The flux of CO_2 into the cell walls, J_m , can be written (equations (10), (9), (12))

$$J_m = \frac{C_{liq}}{\Omega} \approx \frac{C^*}{\Omega} \approx \frac{C}{\Omega} \quad (21)$$

Table 1

Investigators	Species	Type of leaf	A^{mes}/A	$V^{ias}/V(\%)$	Comments
Turrell [5]	<i>Syringa vulgaris</i>	Shade	13.6	23.7	All Turrell's [5] values of A^{mes}/A must be multiplied by 2 to make his definition conform to that used in this paper.
		Sun	26.4	20.6	
Takenouchi (as quoted in [5])	<i>Tovara filiformis</i>	Shade	—	38.6	
		Sun	—	33.0	
Nius (as quoted in [5])	<i>Fagus sylvatica</i>	Shade	—	40	
		Sun	—	20	
Nobel, Zaragoza, Smith [2]	<i>Plectranthus parviflorus</i>	Shade	11.3	62	V^{ias}/V for spongy tissue only; for palisade, $V^{ias}/V = 29$ percent for both shade and sun leaves.
		Sun	49.9	36	
Nobel [3]	<i>Hyptis emoryi</i>	Shade	14.1	46	
		Sun	39.0	43	

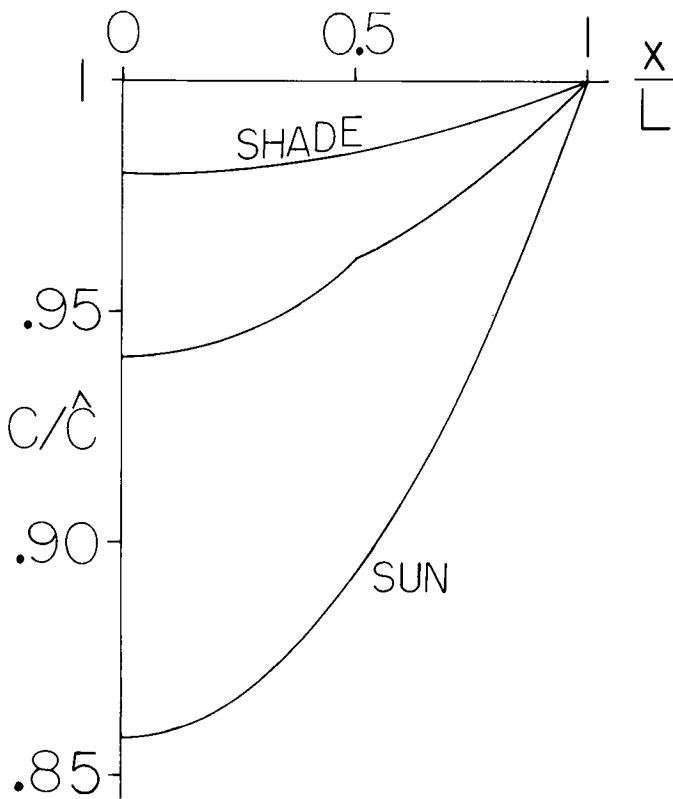


Fig. 4 Equation (14), $C(x)/\hat{C}$ versus x/L for shade, intermediate light and sun leaves. See text for parameter values.

Thus the ordinate of Fig. 4 is proportional to J_m .

Fig. 4 confirms what was suggested in the introduction: that C and J_m vary through the thickness of the leaf. Quantitatively this effect is more pronounced for sun leaves than for shade leaves. For the parameters used here, J_m in the leaf interior ($x = 0$) drops to 86 percent of its value at the stomatal pore ($x = L$) in sun leaves, while the comparable figure is 94 percent for intermediate light leaves and 98 percent for shade leaves.

The quantity which characterizes this effect is $J_m(0)/J_m(L)$ and from equation (14) it follows that

$$\frac{J_m(0)}{J_m(L)} = \frac{C(0)}{C(L)} = \alpha_p$$

$$= [\cosh \omega_p k L \cosh \omega_s (1 - k)L + \lambda \sinh \omega_p k L \sinh \omega_s (1 - k)L]^{-1} \quad (22)$$

Equation (22) is plotted in Fig. 5 for varying L and for fixed values of the other parameters (in particular for $k = 1/2$.) Note that for small L , $J_m(0)/J_m(L) \approx 1$, while for $L = 1000\mu\text{m}$, $J_m(0)$ has dropped to 40 percent of its value at $x = L$.

Thus in thick leaves with stomata on the lower leaf surface only, photosynthesis may be substantially reduced at cell sites near the upper leaf surface due to low values of C and J_m there. However, these cells will also generally have larger values of light intensity I than cells near the lower leaf surface (Beer's law, [9, Chapter 3]). Larger values of I tend to increase the rate of photosynthesis ([9, Chap. 4]) and thus tend to compensate for the reduction in photosynthesis due to smaller values of C .

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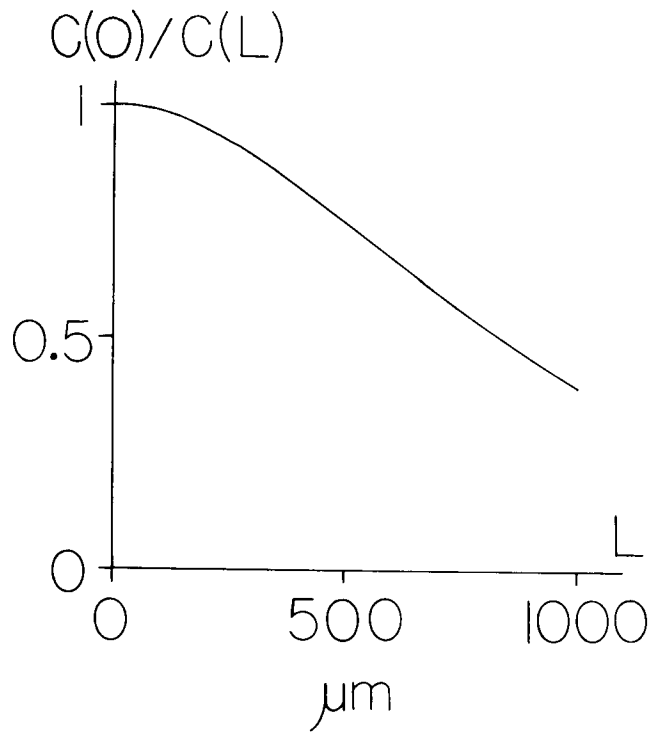


Fig. 5 Equation (22), $J_m(0)/J_m(L) = C(0)/C(L)$ versus L for $k = 1/2$ (other parameters as in text)

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