

Gaseous Diffusion in the Leaf Interior

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ABSTRACT

A one dimensional, steady state, constant temperature model of gaseous diffusion in the leaf interior is presented. The model is shown to predict that CO_2 is absorbed into mesophyll cell walls generally throughout the deep interior of the leaf, while water vapor essentially evaporates only from those cell walls near the substomatal cavity.

INTRODUCTION

When the stomata of a leaf are open, there is a diffusive flow of gases between the leaf interior and the air outside the leaf. Water vapor, during the process of transpiration, evaporates from the mesophyll cell walls and diffuses through the intercellular air pathway to the substomatal cavity, and then through the stomatal pore to the leaf exterior. On the other hand, CO_2 , used by the mesophyll cells in photosynthesis, diffuses in the opposite direction: from the leaf exterior, through the stomatal pore and into the intercellular air pathway. Gaseous CO_2 is finally absorbed into the mesophyll cell walls and CO_2 proceeds as a diffusing solute to the chloroplasts in the cell interior. The diffusive path for gaseous CO_2 is thought to be considerably longer than the comparable path for water vapor (Meidner, 1975; Aston and Jones, 1976).

This work presents a mathematical model of gaseous diffusion in the intercellular air pathway. The model includes diffusion from the mesophyll cell walls which line the air pathway (corresponding to evaporation or absorption), as well as diffusion along the length of the pathway. This provides a more realistic description of the movement of gases within the leaf than the usual resistance model which omits diffusion from the pathway walls (Meidner and Mansfield, 1968; Nobel 1974).

The model is shown to predict that CO_2 is absorbed into mesophyll cell walls generally throughout the deep interior of the leaf, while water vapor essentially evaporates only from those cell walls near the substomatal cavity. As Meidner (1975) has noted, "This fits the primary function of these walls, namely to offer a moist surface for the absorption of carbon dioxide rather than for evaporation."

THE MODEL

The intercellular air pathway is modeled as a cylindrical

Article was submitted for publication in November 1976; reviewed and approved for publication by the Soil and Water Division of ASAE in March 1977. Presented as ASAE Paper No. 76-5528.

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Acknowledgment: The author wishes to thank Professors J. R. Cooke, D. N. Seidman and T. R. Sinclair for valuable discussions.

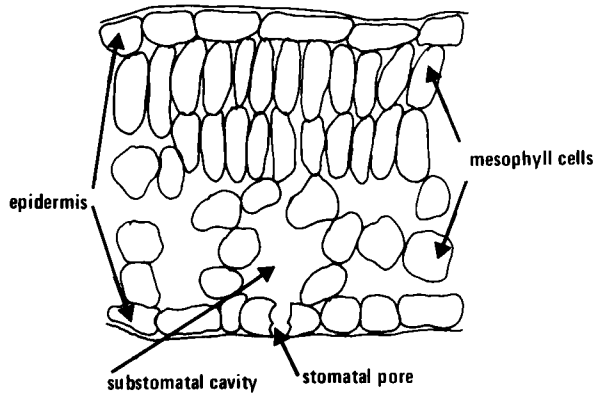


FIG. 1 Transverse section of a leaf [after Nobel, 1974, p. 3].

cal tube of circular cross-section. (It should be noted, however, that the analysis is easily generalized to apply to a cylinder of arbitrary cross-section, without changing the nature of the conclusions.) The model is one dimensional, steady state and of constant temperature. The actual situation in the leaf interior is, of course, of much greater complexity than that of such a simplified model (Fig. 1); nevertheless, it is believed that the conclusions drawn from this model are qualitatively applicable to the real leaf.

Let x represent the distance along the pathway of total length L , i.e., $0 \leq x \leq L$. The boundary $x = 0$ represents the leaf interior while the boundary $x = L$ represents the substomatal cavity (Fig. 2).

Let $C_1(x)$ and $C_2(x)$ represent the concentrations [g/cm^3] of water vapor and gaseous CO_2 , respectively, at the centerline of the air pathway, at cross-section x . Although C_i actually varies across the cross-section, the value of C_i at cross-section x will be identified with $C_i(x)$, the value at the centerline.

The following boundary conditions on $C_1(x)$ and $C_2(x)$ are assumed:

At $x = 0$ there is no flux,

$$J_i = -D_i \frac{dC_i}{dx} = 0, x = 0 \dots \dots \dots [1]$$

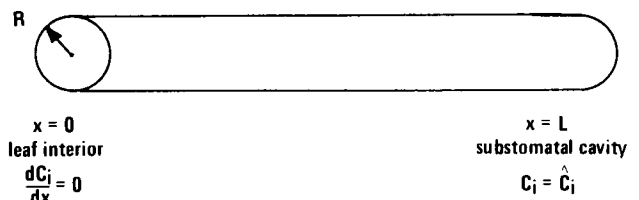


FIG. 2 One dimensional model of an intercellular air pathway.

where

J_i = diffusive flux, g/cm²s

D_i = diffusion coefficient in air, cm²/s

and where subscripts 1 and 2 again refer to water vapor and gaseous CO₂, respectively. Here $x = 0$ represents either a physical boundary (e.g. a "dead end"), or a plane of symmetry such that at cross-sections located at $x = 0^+$ and $x = 0^-$ the flow proceeds in opposite directions along the length of the pathway.

At $x = L$ the concentration is assumed constant,

$$C_i = \hat{C}_i, x = L \dots \dots \dots [2]$$

Here \hat{C}_i , the concentration of gas i in the substomatal cavity, is viewed as being given. (Actually \hat{C}_i depends upon the concentration of gas i in the atmosphere outside the leaf as well as upon other parameters, e.g. resistances. By assuming that C_i is given, the air pathway problem becomes uncoupled from that of the flow in the stomatal pore in the leaf exterior.)

It is assumed that the evaporation of water vapor from, and the absorption of CO₂ into the walls of the pathway are governed by the following expression for flux E_i (g/cm²s)

$$E_i = H_i(C_i^* - C_i) \dots \dots \dots [3]$$

where

$C_i = C_i(x)$ = concentration of gas i at the centerline of the air pathway, at cross-section x

$C_i^* = C_i^*(x)$ = concentration of gas i at the wall of the air pathway, at cross-section x ,

and where

$$H_i = D_i/R \dots \dots \dots [4]$$

where

R = radius of pathway cross-section.

Here $E_1 > 0$ for water to evaporate from the walls into the pathway, while $E_2 < 0$ for CO₂ to be absorbed into the walls. Equation [3], which models evaporation and absorption as diffusion processes, has been found to be applicable to the case of evaporation from open bodies of water in still air (Marciano and Harbeck, 1954, p. 61). (In the literature of heat transfer (also a diffusive process), equation [3] represents a "radiation" condition (Carslaw and Jaeger, 1959, p. 134).

The expression [4] for the proportionality constant H_i ("surface conductance" in heat transfer) results from consideration of the resistance associated with the diffusive flux of gas i between the centerline of the pathway and the pathway wall. By definition, (Nobel, 1974, p. 304)

resistance = concentration difference/flux
= distance diffused/diffusion coefficient.

Using equation [3] and taking R as the distance diffused, find that

resistance = $1/H_i = R/D_i$.

Now consider a volume element Σ of length dx and having the circular cross-section of the pathway. The rate [g/s] at which mass is added to Σ due to the flux E_i is $(2\pi R dx)E_i$. For mass to be conserved this must be balanced by the rate at which mass is lost from Σ due to diffusion, $(\pi R^2)(dJ_i/dx)dx$. Equating these rates and using equation [3] gives

$$\frac{d^2 C_i}{dx^2} + \frac{2}{R^2}(C_i^* - C_i) = 0 \dots \dots \dots [5]$$

Equation [5] with the boundary conditions (1) and (2) must be satisfied by both water vapor and CO₂; thus far the derivation is the same for both. When considering the quantity C_i^* , however, the two gases receive separate treatment.

The gas concentration C_i^* at the pathway wall is assumed to result from equilibrium of the gas i with the liquid in the mesophyll cell walls. (The mesophyll cells are assumed to be distributed uniformly around the walls of the pathway.) Assuming the cell wall liquid is a dilute aqueous solution, water will play the role of the solvent and CO₂, the solute.

The gas concentration C_1^* of the solvent (water) is governed by Raoult's law (Merva, 1975, p. 248; Nobel 1974, p. 459),

$$C_1^* = C_{1sat} N_1 \dots \dots \dots [6]$$

where

C_{1sat} = saturation value of C_1 in air at assumed (constant) temperature.

N_1 = mole fraction of water in cell wall liquid.

For a dilute solution, $N_1 \approx 1$. This leads to the assumption that (Slatyer, 1967, p. 258)

$$C_1^* = C_{1sat} = \text{constant} \dots \dots \dots [7]$$

The gas concentration C_2^* of the solute (CO₂) is governed by Henry's law (Nobel, 1974, p. 459),

$$C_2^* = KN_2 \dots \dots \dots [8]$$

where

K = a proportionality constant (temperature dependent)

N_2 = mole fraction of CO₂ in cell wall liquid.

At typical leaf temperatures, evaluation of Henry's Law shows that (Nobel, 1974, p. 330)

$$C_2^* \approx C_{2liq} \dots \dots \dots [9]$$

where

$C_{2liq} = C_{2liq}(x)$ = concentration of CO₂ in cell wall liquid.

In order to establish a more convenient expression for C_2^* , the conservation of mass is applied to the CO_2 absorption process: The flux of gaseous CO_2 from the pathway into the pathway wall equals the flux of dissolved CO_2 from the mesophyll cell walls into the chloroplasts. This latter flux is proportional to the difference in CO_2 concentration between cell wall and chloroplast (Nobel, 1974, pp. 325-340.) Assuming that the CO_2 concentration in the chloroplasts is zero (Monteith 1963, p. 98), the flux of dissolved CO_2 becomes $C_{2\text{liq}}/\Omega$, where Ω is the resistance associated with this flux.

Using equations [3], [4] conservation of mass requires

$$\frac{D_2(C_2 - C_2^*)}{R} = \frac{C_{2\text{liq}}}{\Omega} \dots \dots \dots [10]$$

Eliminating $C_{2\text{liq}}$ from equations [9], [10], find

$$C_2^* = (1 + \alpha^2)^{-1} C_2 \dots \dots \dots [11]$$

where

$$\alpha^2 = \frac{R}{D_2 \Omega} \dots \dots \dots [12]$$

As noted above, R/D_2 is the resistance associated with the CO_2 vapor flux from the centerline of the pathway to the wall. Thus the parameter α^2 is the ratio of two resistances encountered by diffusing CO_2 . For typical values of R , Ω , D_2 , the parameter $\alpha^2 \ll 1$. E.g. with $R = 5 \mu\text{m}$, $\Omega = 6 \text{ sec/cm}$ (Nobel, 1974, p. 340), and $D_2 = 0.16 \text{ cm}^2/\text{sec}$, obtain $\alpha = 0.023$. Application of the binomial expansion to equation [11] gives

$$C_2^* = (1 - \alpha^2) C_2, \alpha^2 \ll 1 \dots \dots \dots [13]$$

Now the expressions for C_1^* and C_2^* (equations [7] and [13]) are substituted into the governing equation [5], giving

$$\text{water vapor: } \frac{d^2 C_1}{dx^2} + \frac{2}{R^2} (C_{1\text{sat}} - C_1) = 0 \dots \dots \dots [14]$$

$$\text{CO}_2: \frac{d^2 C_2}{dx^2} - \frac{2\alpha^2}{R^2} C_2 = 0 \dots \dots \dots [15]$$

Equations [14], [15] together with the boundary conditions (1), (2) possess the following solutions

$$\text{water vapor: } C_1(x) = C_{1\text{sat}} + (\hat{C}_1 - C_{1\text{sat}}) \frac{\cosh \lambda \frac{x}{L}}{\cosh \lambda} \dots \dots [16]$$

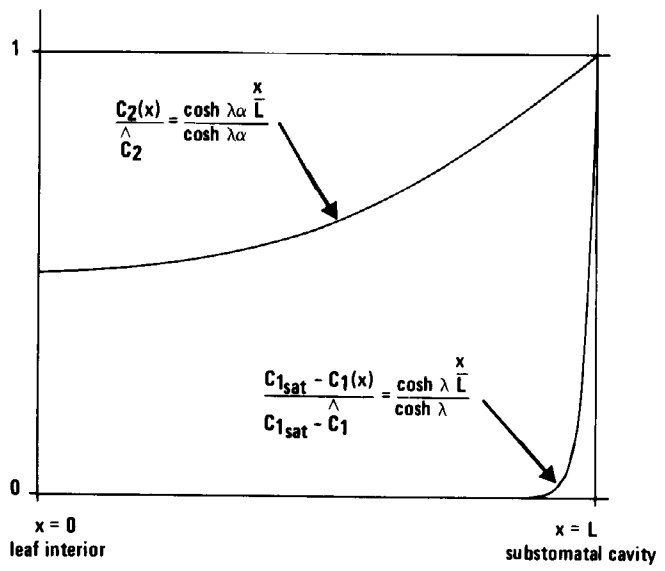


FIG. 3 Equations [16], [17] displayed in dimensionless form for parameter values $\lambda = 57$, $\alpha = 0.023$.

$$\text{CO}_2: C_2(x) = \hat{C}_2 \frac{\cosh \lambda \frac{x}{L}}{\cosh \lambda} \dots \dots \dots [17]$$

where

$$\lambda = \sqrt{2} \frac{L}{R} \dots \dots \dots [18]$$

and where \hat{C}_1 , \hat{C}_2 are the gas concentrations in the substomatal cavity, $x = L$ (equation [2]).

Jarvis and Slatyer (1970), p. 310, state that anatomical examination of cotton plants (*Gossypium hirsutum*) revealed that R varied from 0 to $7.2 \mu\text{m}$ while L was about $200 \mu\text{m}$. Taking $R = 5 \mu\text{m}$ and $L = 200 \mu\text{m}$, the parameter $\lambda = 57$. Equations [16] and [17] are displayed in dimensionless form in Fig. 3 for $\lambda = 57$ and $\alpha = 0.023$.

Discussion

Note from Fig. 3 that the solution for $C_1(x)$ shows that the evaporative flux of water vapor from the pathway walls, E_1 , occurs chiefly near the substomatal cavity end of the pathway, $x = L$. (From equations [3] and [7] it follows that E_1 is proportional to $C_{1\text{sat}} - C_1(x) / (C_{1\text{sat}} - \hat{C}_1)$ of Fig. 3). Comparison with $C_2(x)$ shows that the absorptive CO_2 flux, E_2 , occurs significantly all along the length of the pathway. (Equations [3] and [13] reveal that E_2 is proportional to $C_2(x) / \hat{C}_2$ of Fig. 3).

In order to quantify this observation, define a position along the pathway P_i such that the length of pathway $P_i \leq x \leq L$ is responsible for, say 90 percent of the total flux E_i through the pathway wall. Then P_i satisfies the following condition:

$$0.9 = \frac{\int_{P_i}^L E_i(x) dx}{\int_0^L E_i(x) dx} \dots \dots \dots [19]$$

For water vapor ($i = 1$), equations [3], [7], [16] yield after substitution into equation [19].

$$\sinh \lambda \frac{P_1}{L} = 0.1 \sinh \lambda \dots\dots\dots [20]$$

Again using $\lambda = 57$, equation [20] gives

$$P_1 = 0.96L \dots\dots\dots [21]$$

For CO_2 ($i = 2$), equations [3], [13], [17] yield after substitution into equation [19],

$$\sinh \lambda a \frac{P_2}{L} = 0.1 \sinh \lambda a \dots\dots\dots [22]$$

With $\lambda = 57$, $a = 0.023$, equation [22] gives

$$P_2 = 0.13L \dots\dots\dots [23]$$

Equations [21], [23] reveal that while 90 percent of all water vapor evaporation occurs within the first 4 percent of the pathway near the substomatal cavity, 87 percent of the pathway is required for 90 percent of all CO_2 absorption.

It is important to note that the qualitative nature of these results remains unchanged for a wide range of geometrical parameters R and L . Specifically, if $\lambda = \sqrt{2} L/R \gg 1$ (i.e. if the pathway length is much larger than the pathway radius) and if $a = (R/D_2\Omega)^{1/2} \ll 1$ (i.e. if the resistance of CO_2 diffusing as a solute from cell wall to chloroplast is much larger than the resistance encountered by gaseous CO_2 diffusing from

the centerline of the pathway to the pathway wall), while $\lambda a \approx 1$, then P_1 and P_2 attain values comparable to those presented above.

CONCLUSION

A mathematical model of the gaseous diffusion of CO_2 and of water vapor in an intercellular air pathway of a leaf has been presented. The mathematical treatment of these gases differs because CO_2 (considered as a solute in the cell wall liquid) obeys Henry's law, while water vapor (associated with the solvent) follows Raoult's law.

The model predicts that CO_2 is absorbed into mesophyll cell walls generally throughout the deep interior of the leaf, while water vapor essentially evaporates only from those cell walls near the substomatal cavity. This conclusion agrees with the recent experimental work of Meidner (1975) and Aston and Jones (1976).

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