Stomatal Dimensions and Resistance to Diffusion[1]

JEAN-YVES PARLANGE[2] AND PAUL E. WAGGONER
The Connecticut Agricultural Experiment Station, New Haven, Connecticut 06504

ABSTRACT

In the past, relations of diffusive resistance to stomatal geometry have concerned circular pores or pores that are replaced by equivalent circles of the same area. We calculated the resistance for general shapes that include the realistic slit. The resistance comprises two terms. The first is an outer resistance that depends only on ventilation and leaf geometry and is independent of stomata. The second is an inner resistance and is a function of stomatal interference and of stomatal geometry only. If interstomatal spacing is at least three times stomatal length, interstomatal interference is negligible. The inner resistance can then be calculated by adding the resistance of the two ends and the throat of each stoma. In the case of an elongated stoma, the part of the diffusive resistance per square centimeter determined by stomatal geometry is

$$\left(\frac{d}{\pi ab} + \frac{\ln (4a/b)}{\pi a} \right) \Big/ (Dn)$$

where a, b, d, and n are the semilength, semiwidth, depth, and density of the stomata, and D is the diffusivity. This is the familiar Brown and Escombe result applied to slits.

The evaporation from a stand of well watered vegetation is nearly as great as from open water (12). Evaporation is evidently affected by the stomata because a chemical that shrinks the aperture of stomata (20) can significantly decrease evaporation from a field (18) or forest (17). In the present article, therefore, the relation between stomata and the resistance to the evaporation of water is examined.

At the turn of the century, Brown and Escombe (2) calculated the resistance to diffusion through stomata as $1/n$ of the resistance to diffusion through a single stoma. The resistance through a single stoma was the sum of resistance to diffusion through a tube plus twice the resistance to diffusion away from a disk of the same area as the cross section of the tube. Later authors argued that interference between nearby stomata would increase the resistance. Recently Cooke (4) has pointed out that the addition of the resistance of tube and disks is illogical because it introduces a discontinuity at the juncture of the three parts. Another difficulty, but one usually overlooked, is replacing the actual stomatal shape by a simpler shape, such as a circle. Kelman (8) has shown exactly for a *circular*, isolated stoma, that the Brown-Escombe formula predicts the stomatal resistance with a 7% precision or better (as the stomatal depth gets larger). The interstomatal interference of

circular stomata has been studied in some detail by Keller and Stein (7) and more recently by Cooke (5). In the present paper, we extend the work of Kelman (8) and Cooke (5) for realistic stomatal shapes.

THE DIFFUSION RESISTANCE

The mass flux of water, ϕ, through a stoma is proportional to C_o, the difference between the water concentrations at the bottom of the substomatal cavity and in the air far from the leaf. This result is an immediate consequence of the linearity of the equations governing diffusion. Hence it is always possible to define a "resistance" to diffusion, R, which is independent of C_o, by

$$\phi = C_o/R \qquad (\text{I})$$

The study of diffusion consists of two parts, the determination of C_o and R. Usually it is accepted that the vapor in contact with the cells of the substomatal cavity is saturated with water. Hence C_o is easily computed from the temperature of the leaf and the humidity outside the leaf. Only under extreme water stress, *i.e.*, when incipient drying is about to kill the leaf, is this assumption invalid (14). Consequently this study is primarily concerned with the determination of R.

Since the total path of diffusion includes air at a considerable distance from the leaf, the resistance will be influenced by ventilation as well as stomatal geometry (16). When convection occurs outside the leaf, the diffusion equation must include convective terms. In the case of forced convection, the average boundary layer thickness for normal size leaves and usual wind velocities is of order 10^{-1} cm or less for small leaves or strong winds. Such a thickness is always much larger than the length of a stoma and is often much larger than the interstomatal distance as well. Consequently convective effects can usually be neglected up to distances from the leaf of the order of the interstomatal spacing. Close enough to the leaf then, convective terms are negligible (this is true *a fortiori* for natural convection and for diffusion in quiescent air). Consequently, two basic regions can be distinguished outside the leaf:

Region 1. Region 1 extends from the leaf to a plane parallel to it. The parallelism occurs at a distance comparable to the interstomatal spacing, where, owing to stomatal interaction the equiconcentration surfaces are roughly parallel to the leaf (see Fig. 1). Convective terms are negligible in this region.

Region 2. In region 2 equiconcentration lines are parallel to the leaf at first. Then convective effects or, in quiescent air, the three-dimensionality of the leaf affects the concentration field. In this region interaction effects with other leaves may have to be taken into account.

Resistances R_1 and R_2 can be associated with regions 1 and 2, respectively. The outer one, R_2, depends on the atmospheric conditions, the shape of the leaf, and the presence of other leaves, but obviously not on stomatal shape and distribution on the leaf. On the other hand, R_2 does depend upon the size of the array of stomata—*i.e.*, the leaf—and is a result of the multiplicity of stomata. Region 2 was called by Bange (1) the adhering air layer

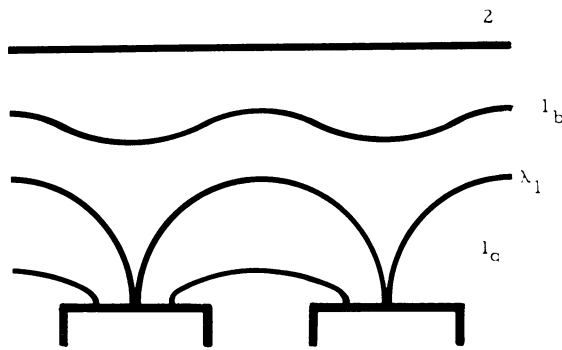[2] Permanent address: Engineering and Applied Science, Yale University, New Haven, Connecticut.

FIG. 1. Equiconcentration surfaces above the stomatal apertures and the location of region 2 and subregions $1a$ and $1b$.

FIG. 2. Schematic stoma of width $2b$ and depth d. The dotted line represents the limit of the substomatal cavity.

in his Figure 5. In general the air in region 2 is not still, and natural or forced convection takes place. Usually R_2 must be estimated by considering forced convection in a turbulent wind (11). In this paper we are interested in the influence of stomata on diffusion from the leaf. Hence we restrict ourselves to a study of region 1. Nevertheless, in an actual case the resistance R_1 computed here is only part of the total resistance, and an appropriate R_2 must be added to R_1.

First we shall obtain the resistance of a single elliptical stoma by adding three resistances as Brown and Escombe did. Then, we shall try to justify replacing an ideal cross section for a real one. The last step in analyzing a single stoma will be comparing the Brown-Escombe result for an elliptic slit with an exact result, as done by Kelman (8) for a circular opening. In the final section of the paper we shall evaluate all R_1, which includes interstomatal interference and compare its value with the resistance, R_s, of a single slit, as Cooke (5) did for circular stomata.

BROWN-ESCOMBE FORMULATION FOR A SINGLE STOMA

If water is diffusing from a single stoma, region 1 extends to infinity; and R_1 is R_s, stomatal resistance. Call C the water concentration at a given point minus the concentration in the air far from the leaf. Figure 2 shows a sketch of a stoma.

$C = C_o$ on the wetted cells of the substomatal cavity (dotted line on Fig. 2), and $C = 0$ far from the leaf since by definition C is the excess concentration over its value far from the leaf. The normal derivative of C is zero on the rest of the leaf (solid line on Fig. 2) as long as evaporation through the cuticle is negligible. Finally in the region of space occupied by humid air,

$$\nabla^2 C = 0 \qquad (II)$$

According to Brown and Escombe (2), C is a function of z alone in the duct joining the substomatal cavity to the outside $(0 \leq z \leq d)$. In that case R_s can be decomposed into three parts. One is the resistance, R_o, from the wetted cells to the bottom of the duct $(z = 0)$, another is the resistance, R_{od}, of the duct $(0 \leq z \leq d)$ and the third, R_d, is from the top of the duct $(z = d)$ to the outside. Obviously

$$R_{od} = D^{-1} \int_o^d dz/O(z) \qquad (III)$$

where D is the diffusion coefficient and $O(z)$ is the area of the cross-section of the duct (which is a function of z).

R_o and R_d depend on the shape of the duct opening (at $z = 0$ and d). For instance, when a dicotyledonous stoma is widely opened, the shape is ellipsoidal. Sometimes, particularly when the dicotyledonous stoma is partially closed, the shape is more akin to an irregular slit, and the stomata of monocotyledons are
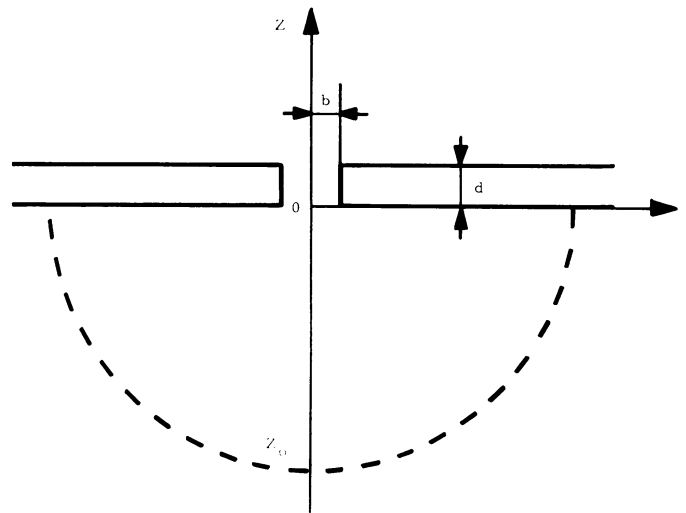
almost always slitlike. It is assumed that the exact shape of the openings is not crucial to the mass flux through them. This assumption makes it possible to replace the actual shapes by similar shapes that are geometrically simpler. For instance, it is plausible that a thin irregular slit can be replaced by an "ideal" slit having the same length and the same area, with minimal effect on the mass flux. The ideal slit could be, for instance, rectangular or elliptic in shape (both choices will be made later).

To calculate explicit values for R_o and R_d, we take elliptic openings (with semiaxes a_o, b_o and a_d, b_d). We assume further that the distance from the stoma to the wetted cells (z_o on Fig. 2) is much larger than a characteristic dimension of the stoma. Then (4)

$$R_o = K(\epsilon_o)/2\pi a_o D \qquad (IV)$$

with an equivalent expression for R_d. K is the usual elliptic integral (6) and

$$\epsilon_o^2 = (a_o^2 - b_o^2)\, a_o^2 \qquad (V)$$

Collecting R_o, R_{od}, and R_d together according to the Brown-Escombe approach, we obtain

$$DR_s = \int_o^d dz/O(z) + K(\epsilon_o)/2\pi a_o + K(\epsilon_d)/2\pi a_d \qquad (VI)$$

If the duct is a cylinder, equation VI is simplified and becomes

$$DR_s = d/\pi ab + K(\epsilon)/\pi a \qquad (VII)$$

where $a = a_o = a_d$, $b = b_o$, $\epsilon = \epsilon_0 = \epsilon_d$. Equation VI represents a slight generalization of the classical Brown-Escombe (2, 19) result, which applies to a circular cylinder $(a = b)$ for which

$$DR_o = DR_d = \tfrac{1}{4} a \qquad (VIII)$$

and

$$DR_s = d/\pi a^2 + \tfrac{1}{2} a \qquad (IX)$$

For simplicity, equation VI as well as its simplified versions, equations VI through IX, will be referred to as the Brown-Escombe result.

Another simplification is obtained in the case of an elongated slit when ϵ is close to one, then (6)

$$K(\epsilon) \simeq \ln (4a/b) \qquad (X)$$

and

$$DR_s = d/\pi ab + \ln (4a/b)/\pi a \qquad \text{(XI)}$$

REAL AND IDEAL CROSS SECTIONS

Equation XI can help us to justify the rules for replacing an actual slit by an equivalent shape. The first term in equation XI depends on the depth and the area of the stoma (not on the exact shape). Hence it is clear that an equivalent stoma must have the same *depth* and *area* as the original stoma. The second term depends linearly on the reciprocal of the length of the stoma and only logarithmically on the ratio a/b. Hence the *length* of the ideal stoma should be that of the actual stoma. In particular, notice that the replacement, often used (1, 10), of a slit by a circle having the same area may introduce considerable error in the second term since $\frac{1}{2} \sqrt{ab}$ is then used instead of $\ln (4a/b)/\pi a$ in equation XI. The error introduced by idealizing the shape of the stomatal opening can be evaluated. Suppose, for instance, that a rectangular stoma (length $2a$, width $2b$) is replaced by an equivalent elliptic stoma. By the previously defined rules, the ellipse must have the same length $2a$ and area; hence it must have a width $2b = 8b/\pi$. The error involved in using $\ln (4a/b)/\pi a$ for the resistance R_o and R_d of the rectangular stoma is of the order $\ln (b/\bar{b}) \simeq 0.2$. The relative error is then, $\ln (b/\bar{b})/\ln (4a/b)$, which is less than 10% for the stomata encountered in nature. This error is always negligible, particularly when compared to the total resistance. It is important to emphasize that the replacement of an actual stoma by an equivalent shape is possible because the replacement affects mostly the *width*. The resistance in turn is quite insensitive to the value of the width because it depends on it only logarithmically.

THE EXACT RESISTANCE OF A SINGLE SLIT

The function of this section is establishing a standard so that the error of treating R_o, R_{od}, and R_d as separate entities can be calculated for a slit. The duct is taken to be a cylinder, the openings being elongated slits which can be represented either by ellipses (semiaxes a, b) or by rectangles (length $2a$, width $2b$, with $4\bar{b} = \pi b$ for the slits to have the same area). If an exact solution of this problem can be found, it will be possible to compare the result with equation XI and check the *numerical* precision of the Brown-Escombe approach over the whole range of d/b and b/a.

By symmetry the concentration is equal to $C_o/2$ in the middle of the duct (BB' on Fig. 3); hence, the problem has to be solved only in a half-space. Figure 3 shows the cross section of a rectangular slit of width $2b$. By applying the Schwarz transform

$$dz/d\zeta = (\zeta^2 - \delta^2)^{1/2}/(\zeta^2 - \bar{\beta}^2)^{1/2} \qquad \text{(XII)}$$

the stoma in the Z-space is transformed in the ζ-space into another rectangular slit which has zero thickness and hence is much simpler to treat (see Fig. 3). Equation XII shows at once

FIG. 3. Correspondence between the Z-space and the ζ-space.

that

$$\bar{b} = \int_0^\beta (\delta^2 - \zeta^2)^{1/2}/(\bar{\beta}^2 - \zeta^2)^{1/2} \, d\zeta \qquad \text{(XIII)}$$

$$d/2 = \int_{\bar{\beta}}^\delta (\delta^2 - \zeta^2)^{1/2}/(\zeta^2 - \bar{\beta}^2)^{1/2} \, d\zeta \qquad \text{(XIV)}$$

which gives $\bar{\beta}$ and δ in terms of $\bar{b}$ and d. Or with standard notations (6) for the complete elliptic integrals E and D

$$\bar{b} = E(\bar{\beta}/\delta) \qquad \text{(XV)}$$

$$\delta d/2 = (\delta^2 - \bar{\beta}^2)D[(1 - \bar{\beta}^2/\delta^2)^{1/2}] \qquad \text{(XVI)}$$

Once the solution in the transformed ζ-space is known (for the transformed slit) the application of equation XII leads back to the solution in the Z-space. The Schwarz transform is applicable to two-dimensional problems. Since $a \gg b$, this is true near the stoma (except for end effects, which are negligible). Far from the stoma the transform degenerates to $Z = \zeta$ and does not affect the solution. Notice also that boundary conditions in the Z-space are automatically satisfied since they are satisfied by the solution in the ζ-space.

The mass flux through the slit can be obtained and because at large distances from the slit $dZ/d\zeta = 1$, the flux is the same in both spaces. To compute the mass flux in the ζ-space easily, the rectangular slit of width $2\bar{\beta}$ is replaced by the equivalent elliptic slit of width 2β (the two slits having the same length $2a$ and the same area, then $\pi\beta = 4\bar{\beta}$). The mass flux through the transformed and the original slit is (apply equation XI in the case of zero thickness, when that equation is exact)

$$\phi = DC_o\pi a/\ln (4a/\beta) \qquad \text{(XVII)}$$

where β is known in terms of $\bar{b}$ (or b) from equations XV and XVI. By analogy with equation XI, we can rewrite equation XVII as,

$$DR_s = [\ln b/\beta]/\pi a + [\ln 4a/\beta]/\pi a. \qquad \text{(XVIII)}$$

The d/b term in the Brown-Escombe result of equation XI is replaced by $\ln b/\beta$ in equation XVIII. When d/b is of order 2.5 and larger (this will often be the case in practice), well known expansions of elliptic functions (6) can be applied to equations XV and XVI, leading to

$$\frac{d}{b} \simeq \ln \left(\frac{8}{e\pi} \frac{b}{\beta} \right) \qquad \text{(XIX)}$$

and since $\ln 8/e\pi \simeq -0.07$, the Brown-Escombe result is basically correct if $d/b > 2.5$. For any d/b, equations XV and XVI can be solved using numerical tables (6). It is found that the difference $[\ln (b/\beta) - d/b]$ remains smaller than 0.1 for all values of d/b. This is even less than the earlier estimate of the error introduced by the replacement of a real stoma by an equivalent shape. In conclusion, the use of the Brown-Escombe formula is always justified and is relatively more precise for larger d/b, *i.e.*, for thin and deep slits.

STOMATAL INTERACTION

In the previous section we estimated the resistance to diffusion of a single stoma in quiescent air, R_s, and showed that the Brown-Escombe result is usually applicable. In this section we are going to estimate the resistance of region 1 previously defined and then compare its value to R_s. Since stomatal interference does not affect R_o and R_{od}, it is sufficient to compare R_d with the resistance of the region outside the leaf, which we still call R_1 for simplicity.

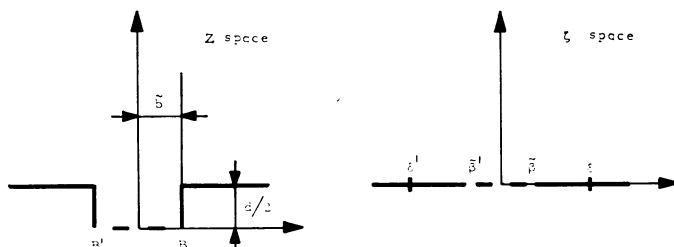We call $\bar{C}$ the average concentration in the surface of the top

stomatal aperture, which is assumed to have an elliptic shape. At the border of regions 1 and 2 the concentration can always be taken as zero without affecting the value of R_1. Interaction effects are clearly more important for smaller distances between the centers of adjacent stomata. Usually the interstomatal spacing is at least three times larger than the length $2a$ of a stoma. For instance, in bean leaves, the 30,000 stomata per cm² are on the average at a distance of 60 μ from their neighbors. Since they are 10 to 15 μ long, the interstomatal spacing is four to six times the stomatal length. For such spacings it is convenient to divide region 1 into two subregions $1a$ and $1b$. Subregion $1a$ is close enough to the stoma so that stomatal interactions do not affect the *shape* of the equiconcentration surfaces. On the contrary, in subregion $1b$ distortion due to stomatal interaction is important. The border between subregions $1a$ and $1b$ is, of course, not exactly defined, but it is at a distance from the center of each stoma roughly half the interstomatal spacing (see Fig. 1). Two resistances R_{1a} and R_{1b} are associated with the two subregions, and

$$R_1 = R_{1a} + R_{1b} \qquad (XX)$$

In Bange's (1) words region $1a$ is the "micro vapour cups over the individual pores," where "diffusion lines radiate out from the pores." Then in a transition region (our region $1b$) the "mutual interference of pores" distorts the diffusion lines until they finally become "perpendicular to the surface" of the leaf when they reach the "adhering air layer" (our region 2). Bange did not analyze region $1b$ because the "conception of interference hardly lends itself to quantitative considerations," and Lee and Gates (10) agreed. In the following paragraphs we try to make this quantitative analysis for elongated stomata with the aid of Cooke's (5) numerical analysis for circular pores. The flux, ϕ, through each stoma satisfies

$$\phi = (\bar{C} - C_1)/R_{1a} = C_1/R_{1b} = \bar{C}/R_1 \qquad (XXI)$$

We must now evaluate the value of C_1, concentration at the border of the two subregions. The concentration C in subregion $1a$ is given by (9)

$$2\pi DCa = \phi F(\epsilon, \psi) + A \qquad (XXII)$$

F is the usual elliptic integral (6) and ϵ is defined by

$$a^2\epsilon^2 = (a^2 - b^2) \qquad (XXIII)$$

Furthermore, ψ is given by

$$\psi = \cot^{-1} \lambda \qquad (XXIV)$$

where λ is a characteristic of the ellipsoidal surface of equiconcentration,

$$\frac{x^2}{a^2(1 + \lambda^2)} + \frac{y^2}{b^2 + a^2\lambda^2} + \frac{z^2}{a^2\lambda^2} = 1 \qquad (XXV)$$

The same solution of equation XXII also applies for an isolated stoma, except that in such a case the solution is valid in the whole space instead of being restricted to subregion $1a$. Consequently, for an isolated stoma $C = 0$ when $\lambda \rightarrow \infty$ or $\psi = 0$. Since $F(\epsilon, 0) = 0$ (6), equation XXII shows at once that $A = 0$ for an isolated stoma. In general A is not zero and characterizes interaction effects but without affecting the shape of the equiconcentration surfaces in subregion $1a$. If $\lambda = \lambda_1$ defines the surface separating the two subregions, we must have

$$2\pi D\bar{C}_1a = \phi F(\epsilon, \psi_1) + A \qquad (XXVI)$$

with

$$\lambda_1 = \cot^{-1} \psi_1 \qquad (XXVII)$$

By definition $\lambda = 0$ in the aperture where $C = \bar{C}$, hence

$$2\pi D\bar{C}a = \phi K(\epsilon) + A \qquad (XXVIII)$$

where $K(\epsilon) = F(\epsilon, \pi/2)$ was used previously in equation IV. Subtracting equation XXVI from equation XXVIII and substituting $(\bar{C} - C_1)$ from equation XXI, we obtain

$$2\pi DaR_{1a} = K(\epsilon) - F(\epsilon, \psi_1) \qquad (XXIX)$$

Equation XXIX can be combined with equation IV to yield

$$2\pi Da[R_d - R_{1a}] = F(\epsilon, \psi_1) \qquad (XXX)$$

In Figure 1 the surface λ_1 touches the leaf (*i.e.*, y and z equal zero) at half the interstomatal spacing, which is at least three times half the stomatal length, a. Equation XXV indicates for y and z equal zero, that $a^2(1 + \lambda_1^2)$ must be at least $9a^2$ or essentially

$$\lambda_1 \geq 3 \qquad (XXXI)$$

It is then possible to use an expansion of $F(\epsilon, \lambda_1)$ for large λ_1 (6), which is valid for all the leaves encountered in nature, or

$$2\pi D[R_d - R_{1a}] \simeq 1/a\lambda_1 \qquad (XXXII)$$

The parameter ϵ which characterizes the shape of the stomata has disappeared from equation XXXII. The difference $(R_d - R_{1a})$ is now a function of (λ_1a) alone; it is only a function of the interstomatal spacing. Similarly, when inequality (XXXI) applies, the surface $\lambda = \lambda_1$ is essentially a sphere, as shown by equation XXV. Hence it is clear that the surface $\lambda = \lambda_1$, and consequently the resistance R_{1b} as well, are functions of the interstomatal spacing but are independent of the shape of the stomata. Altogether this shows that $(R_1 - R_d)$ is also a function of the interstomatal spacing alone.

Cooke (5) has shown that

$$(R_1 - R_d) \simeq 0 \qquad (XXXIII)$$

for *circular* stomata and for the interstomatal spacings considered here. But we just proved that $(R_1 - R_d)$ was independent of the *shape* of the stomata. Consequently, equation XXXIII applies also for elliptic openings as long as equation XXXI holds. That is, quantitative analysis shows that resistance R_1 for *elongated* pores is the same as the resistance of an isolated stoma when the interstomatal distance is at least three times the longer dimension of a stoma. It is interesting to notice that R_{1a} is only slightly less than R_d, equation XXXII, since λ_1 is relatively large, hence Bange (1) made an excellent guess when he attributed the value R_d to the resistance of the "micro vapour cups." Equations XXXII and XXXIII show also that $2\pi DR_{1b} \simeq 1/a\lambda_1$ is small and compensates exactly for the difference between R_d and R_{1a}.

CONCLUSION

The conclusion is now clear. The resistance of a leaf to diffusion is composed of two terms R_1 and R_2. The stomata affect only the value of R_1, and interference effects are negligible for usual interstomatal spacings. Consequently, R_1 can be computed by considering each stoma independently. This stomatal resistance can in turn be evaluated following the Brown-Escombe scheme by adding three resistances R_o, R_{od}, R_d. We have also provided an equation for elongated slits that differs from the one used for equivalent circles. The resistance thus obtained agrees remarkably well, first, with the results of a more accurate mathematical analysis in the preceding pages of this report and, second, with the observed diffusions of water through plates with well defined pores (16).

In the three appendices, the present approach is applied to analyze some recent studies of stomatal diffusion.

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APPENDIX 1

In an experimental simulation of two-dimensional stomata, Cooke (4) observed strong interaction among them. This apparent contradiction with the results of the last section is due to basic difficulties associated with two-dimensional stomata as shown below.

From an elongated stoma the concentration field is indeed two-dimensional near the stoma. This is most easily seen from the analysis of the last section. Since the stoma is very long, a^2 is much larger than b^2. We then consider points close enough to the stoma so that λ^2 is much smaller than one. To avoid end effects, we also assume that x^2 is much less than a^2. Consequently, λ is independent of x, as shown by equation XXV. Hence, the concentration C given by equation XXII is also independent of x; i.e., the field is two-dimensional.

Let us now impose an additional restriction on λ, namely $\lambda^2 \gg b^2/a^2$, (we still have $\lambda^2 \ll 1$ and $x^2 \ll a^2$). The equiconcentration surfaces for such λ's are cylinders of equation

$$\lambda^2 = (y^2 + z^2)/a^2 \qquad \text{(XXXIV)}$$

Equation XXII reduces to

$$C/\bar{C} = 1 - \ln\,(2\lambda a/b)/\ln\,(4a/b) \qquad \text{(XXXV)}$$

As expected, the concentration has the characteristic behavior of a two-dimensional source. Equation XXXV shows also that in a two-dimensional simulation of a three-dimensional stoma, the condition $C = 0$ must be imposed for $\lambda \simeq 2$, in order to obtain

the correct concentration near the stoma (for $\lambda^2 \ll 1$). Hence the position of the surface $C = 0$ in Cooke's experiments gives effectively the length of the three-dimensional stomata which he considers implicitly. His Figures 8, 9, and 10 show clearly that the stomata are extremely long compared with the interstomatal spacing. Hence, his experimental results cannot represent the interference of realistic stomata. If Cooke had imposed the condition $C = 0$ at a proper distance from the simulated leaf, he would have found minimal interference effects, in agreement with the last section.

APPENDIX 2

Keller and Stein (7) considered a pore of radius a diffusing into a cylinder of radius b and length l, at the top of which the concentration is imposed. For simplicity we use Keller and Stein's notations even if they differ from those that we used previously. The reason for examining their work is 2-fold. First, the Brown-Escombe result is obtained below very simply, showing the simplicity of the method. Second, the agreement with Keller and Stein's numerical analysis is excellent, illustrating the remarkable precision of the Brown-Escombe approach.

The walls of the cylinder simulate the interaction with neighboring stomata, so that $2b$ is comparable to an interstomatal spacing. We define then a region 1 which extends to a distance αb from the leaf of order b, α being a number of order one. Region 2 extends to the top of the cylinder. From the Brown-Escombe approach we expect that

$$DR = D[R_1 + R_2] = \tfrac{1}{4}\,a + (l - \alpha b)/\pi b^2 \qquad \text{(XXXVI)}$$

Notice that for $b = a$, DR is exactly equal to $1/\pi b^2$, which is in agreement with equation XXXVI when $\alpha = \pi/4$. Hence

$$DR = \tfrac{1}{4}\,a + (l - \pi b/4)\pi b^2 \qquad \text{(XXXVII)}$$

It is implicitly assumed in equation XXXVII that l is sufficiently larger than a, for R to be effectively the sum of the two independent resistances R_1 and R_2. When l is comparable to a, the field near the stoma is affected by the top of the cylinder and R should be smaller than indicated by equation XXXVII. Indeed, Keller and Stein's numerical results (their Table I) are indistinguishable from those which are predicted by equation XXXVII as long as $l > 2a$.

APPENDIX 3

Membranes and plates with calibrated pores are geometrically well defined and are of great interest in simulating diffusion through stomata (10, 15, 16). Ting and Loomis (15) in particular have reported results for a variety of plates. They measured the total resistance R, which in our notations includes the stomatal resistance R_s, and two outer resistances on both sides of the plate. One, R_2, is the resistance above the plate in region 2 as before. The other, which we can call R_2' by analogy to R_2, did not appear in the stomatal study. It corresponds to the resistance between the water surface situated below the plate at a distance l and the stomatal region. Since the water surface can be far from the membrane (l = 1.2 cm for Ting and Loomis), such a resistance can be considerable. The quantity $(R_2' + R_2)/R$ was called the "percentage of interference" by Ting and Loomis, a legitimate name since this quantity is zero for one stoma alone. Following Bange, we prefer to call R_2 and R_2' outer resistances or resistances of "adhering air layers." In this paper interference effects refer specifically to the difference $(R_1 - R_s)$, which we found to be negligible in general.

For instance, let us consider the results reported by Ting and Loomis in their Figure 6 and let us assume that convection effects are negligible. In that case R_2 is the usual resistance of

the "macro-vapour cup" (1) and $R_2' \simeq (1 - \pi b/4)/\pi b^2$ with the notations of equation XXXVII, and R_s is given by equation X. For the membrane used by Ting and Loomis in the case reported in their Figure 6, R_2' is always the largest resistance. Altogether, using the dimensions of their membrane, we find easily $(R_2 + R_2')/R \simeq 1/[1 + a/96]$, where a is the pore radius expressed in microns. This formula agrees rather well with their experimental results of Figure 6. Notice that $a \leq 40 \mu$, hence $1/[1 + a/96]$ can be approximated roughly by $[1 - a/96]$, consequently the "percentage of interference" appears to be a "linear function of pore diameter" (15).

Another experiment by Cook and Viskanta (3) yields "interference effects" similar to those of Ting and Loomis but for actual leaves. This is a surprising result since we should expect $R_2' \simeq 0$ for their experiment and consequently little "interference." Cook and Viskanta replaced the elongated stomata by an "equivalent" circle using a "perimeter law"; i.e., they replaced the actual stoma by a circle of equal perimeter. If they had used our equation XI, they would have realized that the "perimeter law" leads to an equivalent radius which is much too large. For instance, for a/b as low as four, their r^2 is too large by a factor of two, and as a/b gets larger the error becomes rapidly worse. To compensate for this error, their "interference factor," F, must be artificially close to one (see their equation V). Their choice of a "perimeter law" to define an equivalent radius is all the more surprising since the standard rule (1, 10) of replacing the stoma by a circle of equal area is well known. Although less accurate than our equation XI, this rule would have given them a much better result than the "perimeter law." Another difficulty, experimental this time, is that their result depends crucially on the value of the excess water concentration between regions 1a and 1b, over the concentration away from the leaf. This difference is small and obviously quite difficult to measure. They tried to obtain it with an infrared beam of finite thickness, which is apparently comparable to their boundary layer thickness! This yields a difference in concentration which is too *low* and tends to make F even closer to one (see their equation V). Thus, their conclusion of large interference follows from their use of a perimeter law and their measurement of a low concentration, not from actual interference.