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Further Studies Concerning Stomatal Diffusion^{1, 2}

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In a previous paper (21), we presented data obtained when water was allowed to evaporate through commercial screens, and interpreted the results in terms of stomatal diffusion. The rule proposed by Brown and Escombe (3) and others (11, 23), that diffusion through single, isolated pores is proportional to the diameter rather than the area was shown to be valid down to 20 μ pores and to extrapolate to the origin at zero pore diameter.

The 5 commercial screens used in this work contained pores from about 20 to 130 μ in diameter, all spaced at approximately 10 diameters, or 200 to 1300 μ on center. The open area was near 1% in all screens but, because of the expected diameter relationship, the total diffusion through the screens with the smallest pores should have been 7 times that through the screens with the largest pores if Brown and Escombe's (3) conclusion of no interference between pores spaced at 10 diameters was valid. Instead of increased diffusion with smaller pores, we obtained uniform diffusion through all of the screens. This result indicates that the 10-diameter rule is not valid, and that interference increases rapidly when

smaller pores are spaced 10 diameters apart. These experiments did not include results with pores more nearly the 5 to 10 μ of average stomates, and yielded no data on the effect of wider spacings.

New screens made to our order, with pores 2.5 to 80 μ in diameter and, for some sizes, 10 to 160 diameters apart, have enabled us to survey the problem of multiperforate diffusion in considerably greater detail than has previously been possible.

Materials and Methods

Electroplated, nickel screens were made by the Buckbee Mears Company of St. Paul. Coated, glass plates were first engraved in squares, then etched, leaving coated squares of the sizes and spacings desired for the pores. These plates were then electroplated to a thickness of 10 μ , forming the primary screens. Some of the primary screens were replated, reducing the size of the pores and increasing the thickness of the screens to a maximum of 80, and an average of 30 to 40 μ . The replating tapered toward the pores (fig 1), and we were unable to measure any effect of the varying thickness. The characteristics of the 23 screens used are shown in table I.

Squares of screen 32 \times 32 mm were sealed with a heavy stopcock grease to the tops of special vessels made from 30-mm glass tubing. The vessels contained water at a distance of 10 to 12 mm below the screens. The evaporation and diffusion of water vapor

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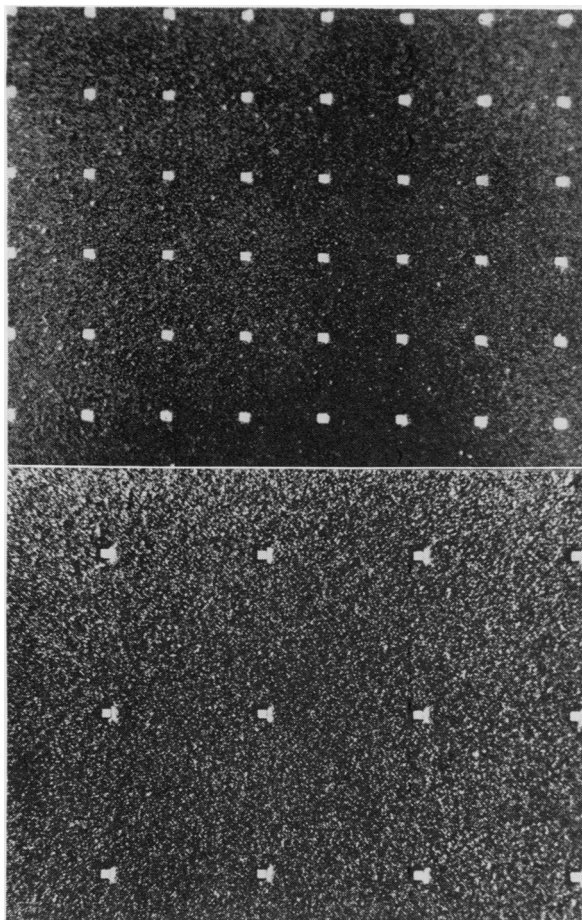


FIG. 1. Photomicrographs of 2 of the screens used as multipore membranes; (top) pores $10\ \mu \times 10$ diameters; (bottom) screen originally $20\ \mu \times 10$ diameters replated to $10\ \mu \times 20$ diameters. About $160\times$.

through the membranes was measured as weight loss per vessel over periods of several hours. Three replications were used, and controls of open vessels and vessels with single-pore membranes with $200\ \mu$ pores were included in all tests.

Single-pore membranes for studies of the diffusion of water vapor and $C^{14}O_2$ were prepared by drilling holes $100, 200, 400,$ or $800\ \mu$ in diameter through

Table I. Characteristics of Screens Used for Multipore Membranes

Tabular figures are the pore spacings in relative diameters.

Diameter μ	Pores per cm^2					
	39	156	625	2,500	10,000	40,000
2.5	160	80	40	20
5.0	...	160	80	40	20	10
10.0	160	80	40	20	10	...
20.0	80	40	20	10
40.0	40	20	10
80.0	20	10

brass stock $50, 250,$ or $750\ \mu$ thick. $C^{14}O_2$ diffusion experiments were conducted in a special gas chamber. The diffusion cups contained $4\ ml$ of $1\ M$ NaOH to act as a CO_2 trap. Samples were prepared for counting by precipitation to form disks of "infinite" thickness (1).

Results and Discussion

Diffusion Through Isolated Pores. The diffusion through small, isolated pores of any size will vary directly with the diameter of the pores (21), providing the pore-tube length is small. This is readily understandable by a consideration of the complete equation describing small pore diffusion. Brown and Escombe's (3) equation is

$$Q = (Dp)/[(L/\pi r^2) + (1/2r)], \quad I$$

where Q is the diffusion, D is the diffusion coefficient for the gas, p is the gas concentration difference, L is the length of the pore tube, and r is the radius of the pore. An identical equation was recently derived from a dimensional argument by Patlak (9). The 2 resistances to diffusion are the pore resistance, $L/\pi r^2$, and an end correction, $1/2r$. The latter is necessary to account for the increase in diffusion path length due to the diffusion shells formed above and below the pores. Diameter proportionality will be obtained only when the ratio of L to r is small so that the term $L/\pi r^2$ will be small relative to $1/2r$. The diffusion will then be approximated by

$$Q = Dp2r = Dpa, \quad II$$

where a is the diameter. When the ratio of the pore-tube length to the radius is large so that the term $1/2r$ will be small relative to $L/\pi r^2$, the diffusion will be approximated by

$$Q = (Dp\pi r^2)/(L) \quad III$$

or area proportionality.

The data in figure 2 show the diffusion of water vapor through isolated pores $100, 200, 400,$ and $800\ \mu$ in diameter, with pore-tube lengths of $50, 250,$ and $750\ \mu$. Good diameter proportionality was obtained with the $L = 50\ \mu$ series, while the 250 and $750\ \mu$ series deviated significantly. The diffusion through the latter 2 series was proportional to $r^{1.5}$ and $r^{1.7}$ respectively. The validity of equation I can be determined by replotting the data in figure 2 against the term

$$(r)/[(L)/(\pi r) + (1)/(2)],$$

obtained by multiplying equation I by r/r . The points (fig 3) fall on a straight line which extrapolates to the origin at zero r . These data emphasize that diffusion will vary directly with the diameter of the pore only if the ratio of the pore-tube length to the radius is small. The 1 additional qualification necessary for diameter proportionality is that the diffusion shells remain nearly spherical. This would not be expected with large pores (20), or under certain conditions of air turbulence (6, 13, 20, 22).

Diffusion of $C^{14}O_2$ through the $L = 50\ \mu$ single-

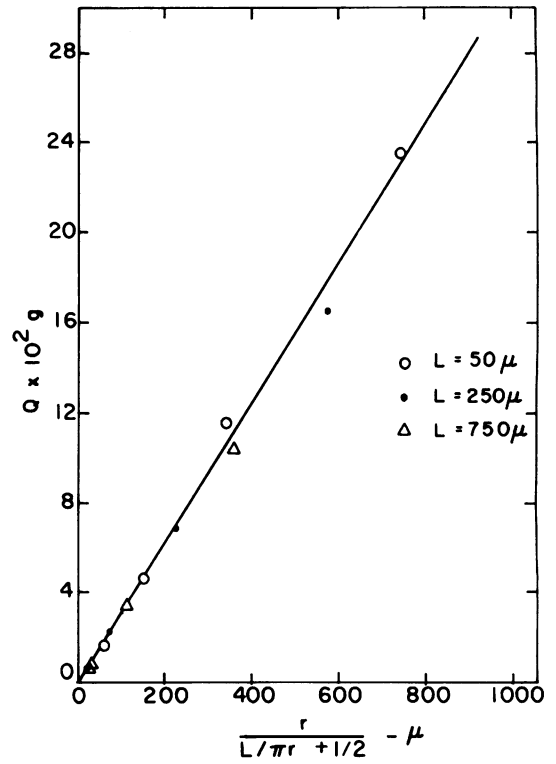
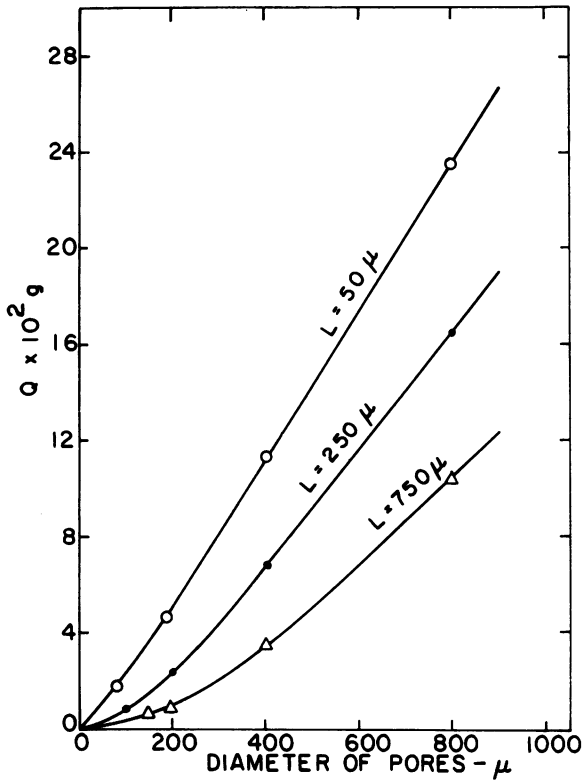


FIG. 2. (left) Diffusion of water vapor through single-pore membranes of 3 thicknesses (L), as a function of pore diameter. Good diameter proportionality was shown with the $L = 50 \mu$ series, while the others approached area proportionality.

FIG. 3. (right) A replot of the data in figure 2, using equation I to correct for thickness (L).

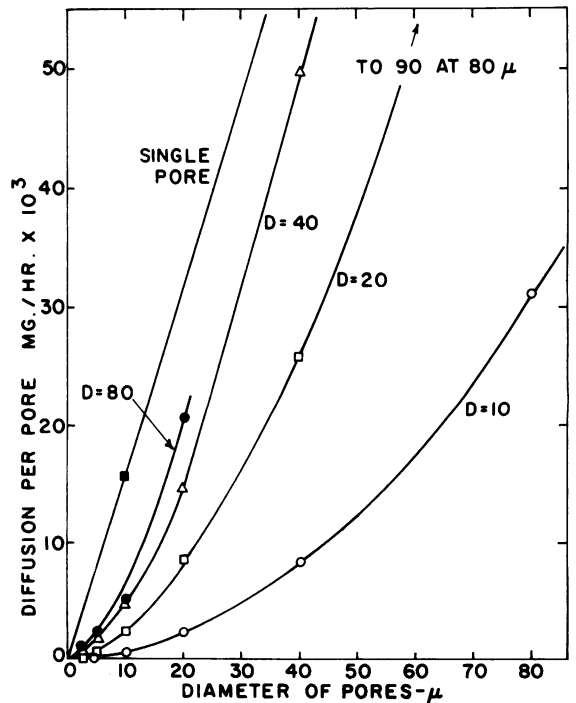
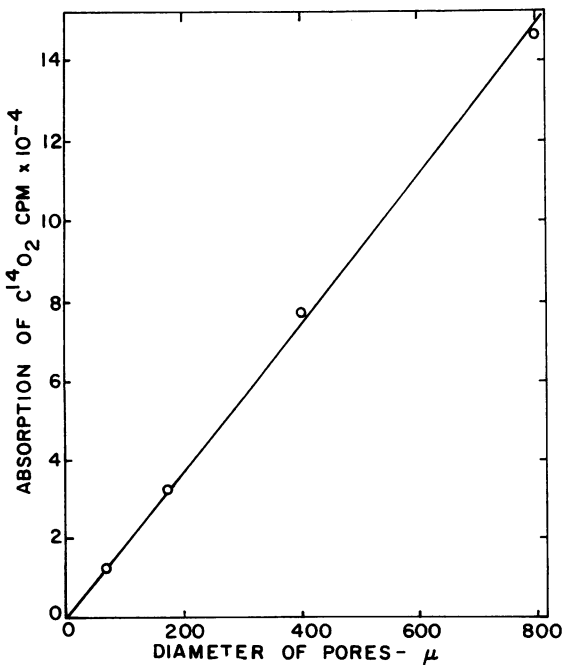


FIG. 4. (left) Diffusion of $C^{14}O_2$ through the $L = 50 \mu$ single-pore membranes as a function of pore diameter. Diameter proportionality is shown.

FIG. 5. (right) Diffusion of water vapor per pore through a single-pore membrane and through multipore membranes with pores at 4 spacings (D).

pore membranes showed good diameter proportionality over the range of pore sizes, with a smooth extrapolation to zero diffusion at zero pore diameter (fig 4). The same curve was obtained for the diffusion of water vapor (21).

It is thus seen that diffusion through small, isolated pores will be adequately described by a linear equation based on diameter if the pore-tube length is relatively small. Large ratios of pore-tube length to diameter will tend to shift the relationship toward area proportionality. A large, isolated, open stomate associated with guard cells $10\ \mu$ thick would be expected to show the diameter relationship. Increased diffusion path lengths, as with sunken stomates or thick guard cells, would shift the diffusion toward area proportionality. Gas flow, relating the movement to r^4 (4), might occur in long narrow tubes, in which case the diffusion-diameter relationship would change from $a^1 \rightarrow a^2 \rightarrow a^4$ as pores of stomatal dimensions close. All of our single-pore data, however, are described adequately by diffusion theory rather than gas flow, even with L to r ratios of 10 to 1.

Diffusion Through Multiperforate Septa. A consideration of multipore diffusion must take into account that the diffusion through any given pore is not independent of adjacent pores (21). The single-pore equation, equation I, can be adapted for multipore diffusion by adding an additional term to account for all remaining resistances to diffusion (10). The additional term was first suggested by Maskell (8) to account for the merging of diffusion stream lines (interference) which tends to saturate the region above the surface, thus reducing the overall gradient. By dividing the pore resistances of equation I by the number of pores per unit area, n , and adding I for the remaining resistances, equation IV is obtained. This equation has recently been used successfully to correlate transpiration and CO_2 assimilation with stomatal aperture (12, 25).

$$Q = (Dp)/[(L)/(n\pi r^2) + (1)/(n2r) + (I)] \text{ IV}$$

In an earlier communication (21), we presented data showing that the interference between pores $20\ \mu$ in diameter spaced at 10 diameters was as high as 95% when calculated as the percentage difference between the loss per pore of a multipore membrane and an isolated pore of equal diameter. Extrapolation of interference curves over the range of stomatal sizes indicated that the diffusion through pores 5 and $10\ \mu$ in diameter would be only 2 to 3% of the expected rate. Data obtained with pores 2.5 to $80\ \mu$ in diameter, spaced at 10 to 80 diameters are shown in figure 5. A curve describing isolated pore diffusion, obtained by extrapolation from a $200\ \mu$ single-pore, is included for reference. These data show that interference not only increased with decreased relative spacing, but also increased with decreased pore sizes. Interference reached a maximum of 98%, representing only 2% of the calculated rate, with the $5\ \mu$ pores spaced at 10 diameters; it decreased to 68% with a pore size of $80\ \mu$ at this same diameter spacing. The percentage interference values for the $5\ \mu$ pores at spacings of 20, 40, 80, and 160 (not shown) diameters

were 92, 79, 74, and 72% respectively. It was only with the larger pores and wider spacings that interference was low. Interference with the 40 and $80\ \mu$ pores at 40 and 20 diameters was 27 and 29%.

The percentage of interference with pores spaced at 10 diameters was a linear function of pore diameter (fig 6). An identical curve obtained with larger

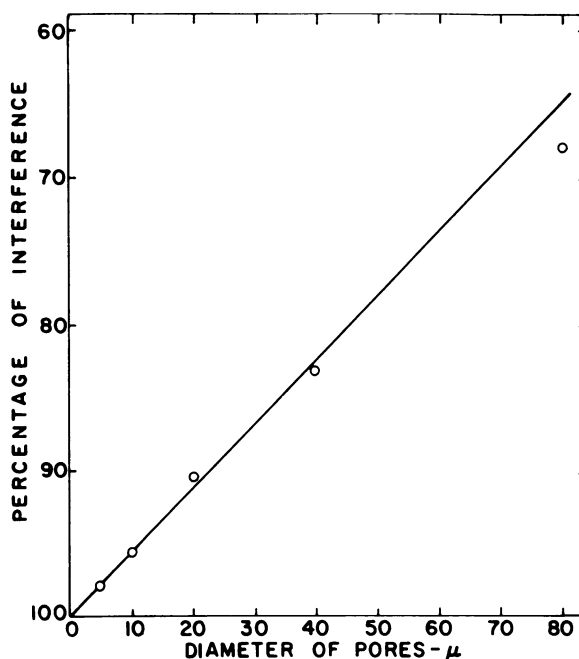


FIG. 6. Percentage of interference between pores spaced at 10 diameters. With these pore sizes, the interference is a linear function of pore diameter.

pores ($20\text{--}130\ \mu$) was previously reported (21). At greater spacings the relationship tended to be logarithmic, indicating that the interference approached a minimum at a slower rate as the pore size and absolute spacing increased.

Pores 5 and $10\ \mu$ in diameter showed a rapid increase in the diffusion per pore as the spacing was increased from 10 to 40 diameters; there was then little more diffusion through pores at 160 diameters than through those spaced at 40 diameters (fig 7). Pores $20\ \mu$ in diameter showed a significant increase between the 40 and 80 diameter spacings, indicating an apparent interference up to 80 diameters. This effect is visible with the $10\ \mu$ pores in figure 7. Verduin (23) and Weishaupt (24) found little interference above a spacing of 20 diameters, but their minimum pore sizes were 200 to $300\ \mu$. Even though our experiments (fig 7) showed no increase in diffusion between 80 and 160 diameter spacings, the calculated rate based on diffusion through a $200\ \mu$ single-pore was considerably higher than the observed. We have shown diffusion through single-pores to be directly proportional to the diameter between 20 and $800\ \mu$, and no explanation for the discrepancy found here is available.

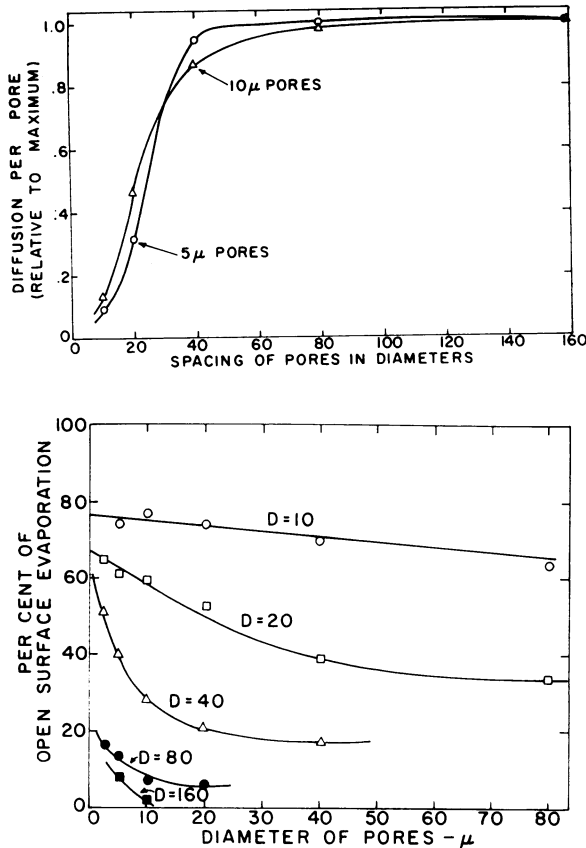


FIG. 7. (upper) Diffusion of water vapor through 5 and 10 μ pores as a function of pore spacing. Interference is shown up to a spacing of 40+ diameters.

FIG. 8. (lower) Diffusion per cm^2 through multipore membranes at 5 relative spacings (D), expressed as a percentage of open surface evaporation.

Diffusion of C^{14}O_2 through the multipore membranes described in an earlier communication (21) indicated no significant differences between the diffusion of this gas and of water vapor. Interference values obtained by extrapolation over the range of stomatal sizes were, as with the water vapor experiments, greater than 95%.

Since the spacing curves (fig 5) are power functions, the diffusion through each pore as a function of diameter can be easily determined. The relationship can be described by $Q = Ka^n$, where n will equal 1 with diameter proportionality and 2 with area proportionality. By taking the logarithm of both sides of the equation and plotting $\log Q$ against $\log a$, n can be evaluated from the slope. For the spacing curves of 10, 20, 40, and 80 diameters, the diffusion per pore varied with $a^{1.95}$, $a^{1.80}$, $a^{1.60}$, and $a^{1.55}$. The regressions of $\log Q$ on $\log a$ were all significant at the 99% level. It is thus seen that the effect of closer pore spacing and increased interference was to shift the relationship toward area proportionality (a^2). The degree to which thickness has influenced these analyses (cf. fig 2) is uncertain, although the thickness effect would be similar within all membrane series.

Effect of Pore Size and Distribution on Total Diffusion. Previous data have indicated that the diffusion per unit area through membranes with pores spaced at 10 diameters is nearly uniform and independent of pore size (14, 16, 21). At a constant relative spacing the number and the size of the pores are not independent variables. The number of pores increases by a factor of 4 with a 50% reduction in pore diameter. Assuming no interference, the diffusion should increase logarithmically as the pore size decreases (21, table II). The diffusion per unit area of membrane as a function of pore diameter for spacings (D) of 10, 20, 40, 80, and 160 diameters is shown in figure 8. The 10-diameter spacing curve is a nearly horizontal line, showing a small but not significant change in the diffusion with a change in pore diameter, yet the potential for diffusion through the membrane with 5 μ pores was 16 times that of the membrane with 80 μ pores. The ratio of diffusion through the membrane with 5 μ pores to that of the 80 μ pores was 1.13 rather than the expected 16. The 20-diameter spacing curve shows the effect of decreased interference with the wider pore spacing in terms of actual distances. The expected logarithmic increase with a decrease in pore size was nearly obtained at the 40 and 80 diameter spacings, although a doubling of the rate with a 50% reduction in pore size was not realized. At the closer pore spacings the diffusing vapor saturates the space above the membrane so that the entire surface tends to act as a unit. With wider relative spacings interference was decreased and the effect of increased pore number accompanying the decrease in pore size resulted in an increase in the diffusion rate in the expected manner, i.e., the pores were acting more nearly independently and showed less interference.

The above data are predictable, in part, from equation IV. Since $n = (1)/[D^2(2r)^2]$, where D is the relative spacing between pores (Dp represents the diffusion coefficient and the gas concentration difference), equation IV can be rewritten as

$$Q = (Dp)/[(4D^2L)/(\pi) + (2D^2r) + (I)]. \quad V$$

From equation V, it can be seen that when the diameter or radius (r) of the pores is large, the interference (I) will be less important, and the diffusion will vary inversely with r . The second way in which I may become small, is when D is large, i.e., when the pores are widely spaced. When D and r are both large, interference will be negligible, and when D and r are both small, interference will be large.

We conclude that the diffusion through small pores spaced at 10 diameters or less will so saturate the diffusion paths as to be nearly independent of pore size and number. With wider relative spacings, resulting in less than saturation, pore size and number become variables affecting the total diffusion. Among many plant species the stomatal dimensions and densities are highly variable, yet their relative spacing when fully open is about 10 diameters (23). Insofar as this generalization remains valid, gaseous movement through open stomates will be high and nearly independent of stomatal density and size.

The low resistance to evaporation attributable to a multipore membrane placed over a water surface is shown in figure 8. The diffusion through the 10 μ pores of the membrane with 10,000 pores per cm^2 and a thickness of 10 μ approached 80 % of free surface evaporation, even though the open area was only 1 %. Sierp and Seybold (15) have discussed the relationship between multipore diffusion and open surface evaporation. It is sufficient to state that evaporation and diffusion through a multiperforate septum will not exceed that from an open surface.

Effect of Stomatal Opening or Closing. The diffusion through model systems allows the estimation of the shape of the diffusion curve associated with stomatal closing, when the epidermis is considered solely as a multipore membrane. The results of an experiment with membranes intended to simulate stomatal opening or closing are shown in figure 9. All of the membranes had 2,500 pores per cm^2 with absolute spacings of 200 μ . The largest pores were 20 μ in diameter spaced at 10 diameters. These membranes would approximate an epidermis with large, open stomates. A 50 % pore closure to a diameter of 10 μ resulted in a relative spacing of 20 diameters. Subsequent 50 % closures to 5 and 2.5 μ gave spacings of 40 and 80 diameters. The latter spacings were in the range of little or no interference (cf. fig 7). The first 50 % closure to 10 μ was associated with a 11 % reduction in the diffusion rate. Closures to 5 and 2.5 μ resulted in reductions of 41 and 65 % of the rate at 20 μ . It is noteworthy that the magnitude of the evaporation through these membranes is comparable to measurements with living plants under controlled conditions (25). The curve shows that the pores were sufficiently far apart at small openings to act nearly independently. As the pore openings increased, with a consequent decrease in relative spacing, the diffusion paths became saturated so that additional pore aperture did not significantly increase the diffusion rate. The shape of this curve is in agreement with those published by Stålfelt (17) using

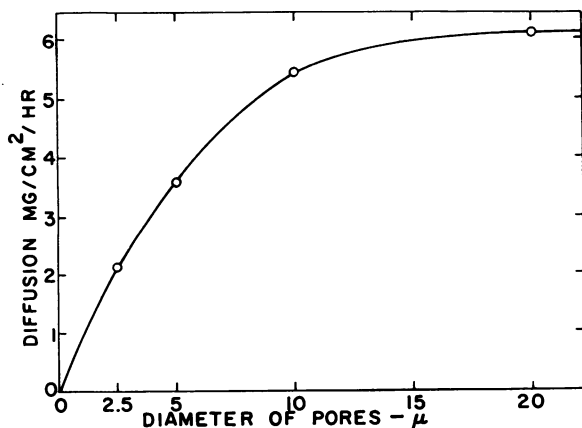


FIG. 9. Stomatal closing curve. All membranes had 2,500 pores per cm^2 with a center-to-center spacing of 200 μ .

Betula leaves and by Bange (2) using *Zebrina* leaf disks.

These data (fig 9) may be fitted to equation IV with the use of a double reciprocal plot (25), and from this the regression of $1/Q$ on the pore resistances, $(L)/(\pi r^2) + (1)/(n2r)$, may be determined. The regression is linear with a slope equal to $1/Dp$ and an intercept equal to I/Dp . For our model systems with square pores, πr^2 is calculated by a^2 . Since the resistances to diffusion through an isolated pore can be accounted for by the terms of the pore resistances (cf. fig 3), the value of I , calculated from the ratio of the intercept to the slope, should be a measure of the interference. The linear regressions for data obtained under a variety of conditions of wind and relative humidity gave correlation coefficients of 0.99 and greater, all significant at the 99 % level (fig 10). Despite the high significance, in still air I does not appear to be a constant, but rather is composed of a variable and a constant component (see the upper 3 curves of fig 10). I is, therefore, not en-

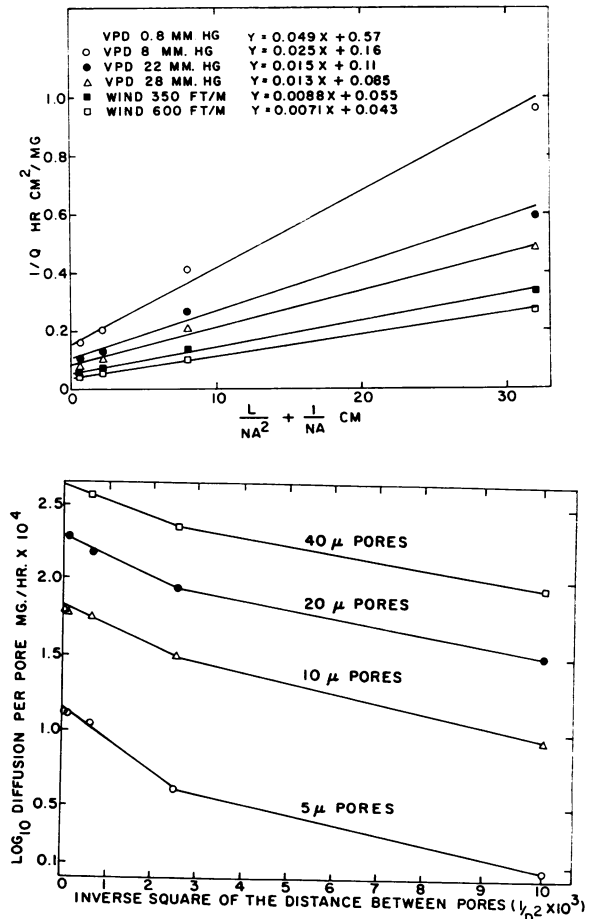


FIG. 10. (upper) Double reciprocal plots of data obtained with the membrane series simulating stomatal opening or closing. The data are fitted to equation IV. FIG. 11. (lower) A plot of our data with Verduin's interference equation (VI). A straight line was not obtained, indicating that the equation is not valid for these pore sizes.

tirely independent of the terms associated with the pores $[(1)/(na^2) + (1)/(na)]$. In wind, the variable component is apparently removed (see the lower 2 curves of fig 10). Nevertheless, these plots indicate that equation IV is adequate to describe diffusion through multipore systems, at least to a first approximation. More elaborate equations which depict the resistances to diffusion in greater detail are available (2).

The hyperbolic shape of the stomatal opening or closing curve is such that at small openings pore change is accompanied by a nearly linear response of diffusion. At wider openings, particularly at 50 % or more of maximum, saturation of the diffusion paths decreases the effectiveness of subsequent pore changes. Stomatal control is thus more effective at the smaller percentage openings. A 50 % stomatal closure from wide open should be accompanied by a 10 to 20 % decrease in the diffusion, except possibly at very low gradients, in which case the saturating vapor may not diffuse away from the surface at a rapid enough rate to result in even this decrease. The effect of increased diffusion gradients is simply an increase in the diffusion rate with little or no change in the shape of the curve or the relationships.

Verduin's Interference Equation. Verduin (23) developed an equation to evaluate interference,

$$\log Q = \log Q_1 - (k)/(D^2), \quad \text{VI}$$

where Q is the diffusion per pore of a multipore system, Q_1 is the diffusion of an isolated pore of equal diameter, k is a proportionality constant, and D is the

relative or absolute spacing between pores, depending on the value of k . A test of this equation can be made by plotting $\log Q$ against $1/D^2$. Since this is a linear equation, a straight line should be obtained with a slope equal to $-k$ and an intercept equal to $\log Q_1$. Data obtained with pores 5, 10, 20, and 40 μ in diameter spaced at 10 to 80 pore diameters do not fit as a straight line function (fig 11). Furthermore, the values of $\log Q_1$ obtained from the intercept of figure 11 considerably underestimated empirical diffusion rates from isolated pores. Verduin supported his equation with data obtained from pores 200 μ in diameter and larger. The data of Huber (5), obtained with pores 11.3 mm in diameter, will fit Verduin's equation; however, his data from smaller pores down to 50 μ will not, and give plots resembling those in figure 11. Verduin's equation seems, therefore, to be valid only for relatively large pores. This effect is noticeable in figure 11 in the trend toward a straight line with the larger pores. Calculations (21) based on Verduin's equation indicated that stomatal closure would be accompanied by an increase in the diffusion potential. Since the equation does not hold with pores as small as stomates, the extrapolation based on the calculations was not justified.

The Effect of Wind. The diameter proportionality relationship is relatively stable to air currents. Results of experiments with our single-pore membranes indicated that the diffusion would vary directly with the diameter (a^1) of pores 100 to 800 μ in diameter and wind velocities to 800 ft/m (fig 12). A wind velocity of 1,000 ft/m shifted the relationship to $a^{1.55}$,

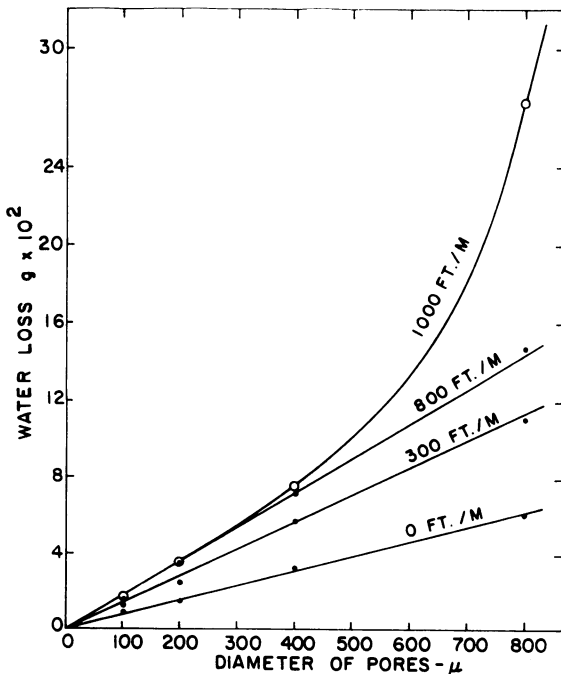


FIG. 12. (left) Effect of wind on the diffusion of water vapor through single-pore membranes. Only the 1,000 ft/m velocity had a significant effect in changing diameter proportionality.

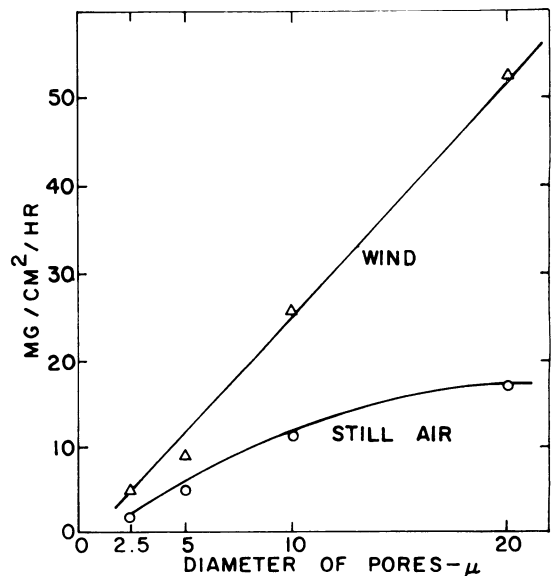


FIG. 13. (right) Effect of wind on the diffusion of water vapor through multipore membranes when the membranes were placed on moist filter paper. The lower curve (still air) shows a 35 % increase in the diffusion from 10 to 20 μ . Wind of 400 ft/m (upper curve) shifted the relationship to diameter proportionality.

which was attributable to the response of the largest (800 μ) pores. The stability to wind of diffusion through the smaller pores is shown in figure 12 by straight lines through 400 μ in all tests and through 800 μ at wind velocities of 800 ft/m and less. The 3 lower curves show diffusion functions of $a^{0.94}$, $a^{1.08}$, $a^{1.06}$. Regression analyses showed that these exponents are not significantly different from one.

Wind not only increases the diffusion gradient (fig 12) but may disrupt the diffusion shells which account for the diameter relationship. To reduce the resistance by diffusion shells below the membranes, where they are protected from wind, the membranes were placed directly on moist filter papers. With this arrangement a wind velocity of 700 ft/m gave a significant increase from the diameter relationship to $a^{1.25}$. We conclude from these results that a single set of intact diffusion shells was maintaining diameter proportionality in our previous experiments, and that the high value obtained in 1,000 ft/m wind was due to disruption of the inner, protected diffusion shells by air turbulence acting through the 800 μ pores. Clearly, this effect would be still more pronounced with larger pores. Pores of stomatal size, however, should be well within the range of stability, even with high wind velocities.

Analyses by Jeffreys (6) and comments by Stiles (19) concerning diffusion in a steady wind indicated that the diffusion through small pores should shift from a^1 to $a^{1.5}$ rather than a^2 as reported by Sierp and Noack (13). Our experiments with pores as large as 100 to 400 μ still gave values of approximately a^1 , and so do not agree with their conclusions. We consider it significant that none of our diffusion values have approached a^2 proportionality in wind.

Air currents over a multipore membrane should increase the diffusion per pore toward diameter proportionality by removing or reducing the outer vapor shells which account for part of the interference. With our membrane series simulating stomatal opening, an increase in pore size from 10 to 20 μ resulted in a 10 to 20% increase in diffusion (fig 9). In wind velocities of 350 to 600 ft/m the increase was about 35%. When the membranes were placed directly on moist filter papers in wind of 400 ft/m, evaporation through the 20 μ pores was double that through the 10 μ pores, or diameter proportionality (fig 13). These data indicate that the combination of filter paper and wind eliminated interference between pores, but left enough of a diffusion shell system to give diameter proportionality. Bange (2) and Stålfelt (18) have reported similar results with leaves.

If the lower curve of figure 13 (still air) is compared with figure 9, we find that the gain in diffusion between 10 and 20 μ pores was doubled by placing the evaporating surface in contact with the membrane instead of 10 mm below it, thus largely eliminating one set of diffusion shells. Wind of 400 ft/m reduced the upper shells to the point where they showed little or no interference, but still maintained diffusion at diameter proportionality. We might conclude that partial closing of the stomates in wind would have a

major effect on transpiration. The data of Manzoni and Puppo (7) and our own results (22), however, show much smaller effects of wind than would be predicted by these experiments. It seems probable that internal diffusion shells, or equivalent resistances to evaporation at the mesophyll walls, may restrict transpiration in wind.

Note added in proof: Since this manuscript was submitted, a paper by Lee and Gates (Am. J. Botany 51: 963) has misquoted our discussion of the diameter law of diffusion through small pores (Am. J. Botany 50: 866). We showed experimentally that diffusion through single pores as small as large stomates was proportional to the diameter of the pores. Lee and Gates have changed pores to tubes, which we noted specifically will show less than diameter proportionality. Figures 2, 3 and 4 in this paper are further evidence that single-pore diffusion is proportional to diameter when corrections are made for tube length or membrane thickness effects.

On page 972 the authors state that the constant diameter/length ratio of our earlier multiperforate membranes was, "a sufficient condition for diameter proportionality of diffusion." The point of our data is that we do not obtain diameter proportionality for diffusion through multiperforate membranes. We find, on the contrary, that interference is directly proportional to pore diameters when small pores are spaced 10 diameters apart (fig 6). More evidence on the effect of membrane thickness is contained in the D-10 curve of figure 8, this paper. These membranes, with pores 5 to 80 μ , were uniformly 10 μ thick and showed uniform diffusion. The multiperforate effect is in interference, which increases as smaller pores are closer together in actual distance.

Summary

Specially designed screens with pore diameters from 2.5 to 80 μ , spaced from 10 to 160 pore diameters, were used as multipore membranes to study diffusion of water vapor and $C^{14}O_2$. For supporting studies, single-pore membranes were prepared from 50 to 750 μ thick brass stock by drilling holes 100 to 800 μ in diameter. Experiments were conducted in still air under different vapor pressure deficits and in wind. The results are interpreted in terms of stomatal transpiration and CO_2 assimilation.

Diffusion through single-pore membranes followed the diameter law of Brown and Escombe, providing that the ratio of pore-tube length to diameter was not much greater than one. Larger ratios tended to shift the relationship toward area proportionality. No indication of gas flow or streaming was found; all data were adequately described with diffusion theory.

Multipore membranes with pores 5 to 80 μ spaced at 10 diameters tended to act as a unit; thus the diffusion through membranes with 40,000, 5 μ pores was nearly the same as that through membranes with 156, 80 μ pores, even though the calculated capacity of the former membrane was 16 times that of the latter.

Membranes with pores at wider spacings, up to 160 diameters, approached the expected logarithmic response to the increasing pore number which accompanies the decrease in pore size at a constant relative spacing.

The interference between pores was found to be a function of both pore size and spacing so that large pores at any relative spacing more closely approached calculated diffusion rates than small pores. Similarly, small pores at wide spacings more closely approached calculated rates than small, closely spaced pores. Interference between pores of the 5 and 10 μ average size of stomates reached a maximum of 96 to 98 %, representing a diffusion rate per pore of only 2 to 4 % of the expected rate. Decreased pore spacing shifted the diffusion relationship from diameter toward area proportionality.

A membrane series with pores varying from 2.5 to 20 μ , all spaced 200 μ apart, was intended to simulate a stomatous leaf epidermis with opening or closing stomates. Diffusion through this series increased rapidly as the pore size increased from zero, representing a linear response of diffusion to pore diameter; then slowed until there was only 11 % more diffusion through fully open pores (20 μ) than 50 % open (10 μ). The effect of wind was to increase the pore size range where diffusion was nearly linear with pore diameter. It is concluded that stomatal control of transpiration in still air would be significant only at smaller openings. Additional aperture, particularly that greater than 50 % of maximum, results in saturation of the diffusion paths so that little more diffusion results. In a steady wind, the range of stomatal control is extended to wider openings.

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