# Mutual Diffusional Interference Between Adjacent Stomata of a Leaf[1]

## G. D. Cook[2] and R. Viskanta

School of Mechanical Engineering, Purdue University, Lafayette, Indiana 47907

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*Abstract.* The mutual diffusional interference between adjacent stomata in laminar flow over a leaf is shown to play a decisive role in determining overall transpiration. The magnitude of this interference varies with the interaction of the vapor diffusional shells forming above each stoma and the air flow over the leaf. The interference decreases with increasing incident radiation and wind velocity. The effect of interference on the stomatal resistance to diffusion plays a major role in the overall variations in transpiration.

Many attempts have been made over the last three quarters of a century to relate analytically the rate of transpiration from a leaf to the geometry of stomata and the physical conditions in them. The diffusion from a single circular opening in a septum was first presented in 1881 (11) in an attempt to describe diffusion from a single stoma. Recently a more mathematically rigorous derivation of an expression for such diffusion was presented (8). Attempts to apply the earlier equation to the case of multiperforate septa were not very successful. It was discovered (1) that with such a multiperforate septum there is a mutual interference of diffusion from the individual pores, and this interference phenomenon has to be accounted for in any attempt to describe the overall diffusion. Although attempts (14) were made to determine such interference analytically, the results failed to describe accurately transpiration from a leaf.

Recently, Ting and Loomis (12, 13) undertook a comprehensive study of diffusion from the pores of a multiperforate septum. The interference which occurs in diffusion from adjacent openings in septa is due to the fact that the diffusional shells (or surfaces of constant vapor conc) which form above each opening overlap. This overlapping of the diffusional shells decreases the average concentration gradient at the surface of the septum and thus reduces the transpiration. Ting and Loomis have shown that interference can reduce the diffusion per pore to one-tenth of what it would have been if no interference had existed. These authors have also shown experimentally that interference increases with pore diameter, decreases with pore spacing, and is virtually constant with wind velocities up to 460 cm/sec.

Most of the attempts at obtaining an analytical model for stomatal diffusion have been based on a multiperforate septum as a physical or experimental model. Since the septa most commonly used have negligible thickness compared to the pore diameter, whereas in many cases the stomatal pores have a significant depth when compared with the stomatal diameter, the applicability of such results is limited (8). In fact Lee and Gates (8) have shown that in leaves the depth and geometry of stomatal pores may be the major source of diffusional resistance. Recently Cooke (5) has reported a rigorous analysis of stomatal diffusion by assuming that the gas outside of the pore is stagnant. He has presented both some limiting analytical solutions for a single stomata and some approximate electrical analog results for stoma having separation distances of 20 to 5 times the diameter. The coupling between the diffusion in the pore and the convective mass transfer outside of the leaf has been ignored. Unfortunately, the extremely complex boundary conditions make it impossible to couple the diffusion in the stoma and the convective mass transfer outside of them using Cooke's approach.

Virtually no experimental data are available on the interference between stomata of leaves. The purpose of the work presented here was to make such experimental determinations on leaves themselves and compare the results with those for multiperforate septa.

## Theory

Since the multiperforate septum of negligible thickness was not considered a suitable physical model for stomatal diffusion (8), a more appropriate model was needed. Brown and Escombe (1) have

[2] Present address: Yerkes Laboratory, Film Department, E. I. du Pont de Nemours, Buffalo, New York.

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presented such a model, characterizing diffusion through a stoma as diffusion through a cylindrical tube with mirror image diffusion shells at either end of the tube. The equation by which they described such diffusion is as follows

$$M_p = \frac{D_{12} \ (\rho_{1A} - \rho_{1B})}{(L/\pi \ r^2) + (1/2r)}$$

where $M_p$ is the diffusion rate for a single tube, $(\rho_{1A} - \rho_{1B})$ is the water vapor density difference between the 2 ends of the tube, $D_{12}$ is the diffusion coefficient, and $r$ and $L$ are the radius and length of the pore tube respectively. This equation accounts for both the resistance to diffusion through the stomatal pore and the resistance of the diffusional shells at the ends of the tube. If $L$, the length of the pore, is set equal to zero, the equation reduces to that for a perforate septum of negligible thickness.

In order to describe the total transpiration from a leaf, the interference between stomata must be taken into account. For this purpose let $F$ be the fractional loss in transpiration due to the presence of the interference phenomenon. Then, by multiplying Brown and Escombe's equation for single pore diffusion by $N$, (the no. of pores per unit area), and by the factor $(1-F)$, (the remaining fraction of diffusion after subtracting the loss due to interference), a formula is obtained for overall transpirational flux. Assuming that the water vapor at the base of the stomatal pore is saturated and that the water vapor at the other end of the pore is that at the surface of the leaf, the formula for transpiration can be written as

$$M = (1-F) \left( \frac{2N \ \pi \ r^2}{2L + \pi r} \right) D_{12} \ (\rho_{1sat} - \rho_{1s})$$

where $M$ is the transpirational flux and $\rho_{1sat}$ and $\rho_{1s}$ are the water vapor densities at saturated conditions and at the leaf surface, respectively. Rewriting this equation in terms of the mass fraction, one obtains

$$M = \frac{1}{\rho} (1-F) \left( \frac{2N \ \pi \ r^2}{2L + \pi r} \right) D_{12} \ (W_{1sat} - W_{1s})$$

(I)

where $W_1 = \rho_1/\rho$.

In order to investigate the diffusion from leaves more closely, the effect of air flow over the leaf must be examined. Brown and Escombe's equation for single pore diffusion was originally derived for stagnant air, and thus equation I, which is derived from their equation, is also valid for this case. It can be shown that these equations also apply for laminar and turbulent flow over a leaf. This is because for such flow conditions the velocity in the vicinity of the diffusional shells is close to zero due to the formation of a velocity boundary layer above the leaf surface. Although the components of the velocity which are parallel and perpendicular to the leaf surface are small enough so that equation I is still valid, they are not zero, and thus there may be some slight disturbances to the diffusional shells which will alter the interference factor, $F$. In contrast, Ting and Loomis (13) have stated that the diffusional shells are virtually unaffected by wind up to velocities of 460 cm/sec.

For laminar flow over a leaf an equation for the average transpirational flux through the boundary layer above the leaf surface can be written by defining an average mass transfer coefficient $h_m$, i.e.,

$$M = h_m \ (W_{1s} - W_{1x})$$

(II)

where $W_{1x}$ is the free stream mass fraction of water vapor. Through addition and transposition of equations I and II, the following formula for the transpirational flux is obtained

$$M = \frac{W_{1sat} - W_{1x}}{\dfrac{\rho \ L}{N \ \pi \ r^2 \ D_{12} \ (1-F)} + \dfrac{\rho}{2 \ N \ r \ D_{12} \ (1-F)} + \dfrac{1}{h_m}}$$

(III)

The above equation gives the average transpirational flux in terms of the concentration difference across the stomata and boundary layer and in terms of the 3 resistances to diffusion. These resistances to diffusion given by the 3 terms in the demoninator of equation III are the resistance to diffusion along the pore, the resistance to diffusion by the diffusional vapor shells at either end of the pore, and the convective resistance to diffusion. The first 2 resistances are wholly dependent on the pore geometry and the interference factor while the convective resistance is dependent on the flow conditions over the leaf.

It has been proven both analytically and experimentally (4), that for laminar flow over a leaf the mass transfer coefficient may be given by

$$Sh = \frac{h_m \ x_o}{\rho \ D_{12}} = 0.56 \left( \frac{V_x \ x_o}{\nu} \right)^{\frac{1}{2}} = 0.56 \ (Re)^{\frac{1}{2}}$$

(IVa)

where $Sh$ and $Re$ are the dimensionless Sherwood and Reynolds numbers based on a characteristic length $x_o$ equal to the length of the leaf, and where $\rho$ is the average total density of moist air, $V_x$ is the free stream velocity, and $\nu$ is the kinematic viscosity of air. For turbulent flow over a leaf the following equation has been obtained (7),

$$Sh = \frac{h_m \ x_o}{\rho \ D_{12}} = 0.030 \left( \frac{V_x \ x_o}{\nu} \right)^{0.8} = 0.030 \ (Re)^{0.8}$$

(IVb)

Equating formulas I and II and substituting into the resulting equation the value of the mass transfer coefficient from equation IVa (i.e., for laminar flow) or from equation IVb (i.e., for turbulent flow), an expression can be obtained for the interference factor. Since in many cases the air flow over a leaf can be characterized as laminar and such flow can be easily investigated experimentally, this investigation was limited to a study of laminar flow over a leaf. For

such flow the following formula for $(1-F)$ is obtained

$$(1-F) = 0.56 \ \rho^2 \left(\frac{2L + \pi r}{2N \ \pi \ r^2}\right)\left(\frac{V_\infty}{\nu x_0}\right)^{\frac{1}{2}} \left(\frac{W_{1s} - W_{1\infty}}{W_{1sat} - W_{1s}}\right) \quad (V)$$

This formula gives the interference factor for a leaf in terms of quantities which can be measured experimentally. By measuring these quantities under a variety of environmental conditions, the resulting values of $(1-F)$ could be calculated from equation V. In this way the variations in the interference factor with changes in the environment could be studied and the results compared with the published values which were obtained using multiperforate septa.

## Materials and Methods

A low speed atmospheric wind tunnel was built so that the flow over the leaf would approximate the conditions of the analytical model. It was necessary that the flow over the leaf be uniform and parallel in order that the experimental results would be reproducible. The final 5 centimeters of this wind tunnel was the test section, where it was possible to insert a leaf (still attached to a plant). Figure 1, which is an overall schematic diagram of the apparatus, depicts the test section location at the end of the wind tunnel. An elevating and traversing device was also located in the test section. This device enabled the leaf to be held in any horizontal flat position desired, within the test section, without disturbing the flow over the leaf.

In order to determine the mass fraction at the surface of the leaf, $W_{1s}$, needed in equation V, a short pathlength spectroscopic hygrometer was built. This hygrometer shown in figure 1, yielded an



FIG. 1. A schematic diagram of the spectroscopic hygrometer.

infrared beam $(1.5 \times 10 \text{ mm})$ containing radiation between the wavelengths of $6.32 \ \mu$ and $6.68 \ \mu$ which included the strong absorption band of water vapor at $6.3 \ \mu$. Thus, by passing such a beam horizontally over a leaf (i.e., parallel to the plane of the leaf) at different heights above the leaf surface, the absorptivity could be related to the water vapor concentration. The optical components for producing such a beam were completely enclosed in a tank (as shown in fig 1) which could be purged with nitrogen and dried with silica gel so that a negligible amount of water vapor remained in it. The measurement of radiation intensities was accomplished by using a high sensitivity, custom-made vacuum thermopile, the signal being amplified and then measured on a chart recorder. The change in water vapor concentration from the surface of the leaf to the free stream was determined by measuring the change in radiation intensity when the infrared beam was moved from a path just above the leaf surface to a path far enough removed from the leaf surface so as to be outside the boundary layer (4).

In addition to the water vapor concentration determinations, experimental data on net radiation exchange, leaf temperature, and pore geometry were taken. Experimental data were taken using both tomato (*Lycopersicon esculentum*, L.) and potato plants (*Solanum tuberosum*, L.). Tomato plants were used because their stomatal size and distribution are similar to those for the pores of a multiperforate septum of Ting and Loomis. Potato plants were used because the net radiation exchange to these leaves could easily be measured. Such a measurement was accomplished by determining the radiative characteristics of the potato leaves upon irradiation with a 1000 watt incandescent bulb [calculations given in (4)].

Free stream air temperatures were measured by using copper-constantan thermocouples. The temperatures of the leaves, which differed from that of the ambient air, were measured by inserting thermocouples under the leaf epidermis as described previously (2, 3). Free stream humidity was determined using wet and dry bulb thermometers. Pore geometry was determined by measuring the elliptical breadth and width of the pore opening under the microscope. Pore depth was measured in a similar manner using histological sections. Averages of the dimensions of 25 pores were used for a given leaf. In order to insure that the measurements of stomatal opening corresponded to those existing when the leaf was in the test section, epidermal strips were taken directly from the leaf and dipped in absolute alcohol [Lloyd's method (6)] in a manner described and successfully employed by Loftfield (9). The microscopic measurements were then made on these epidermal strips. Pore radii were calculated from the measured width and breadth using Verduin's method of perimeter equivalence (14). The free stream velocity of the flow over the leaf in the test section was measured using a hot wire anemometer.
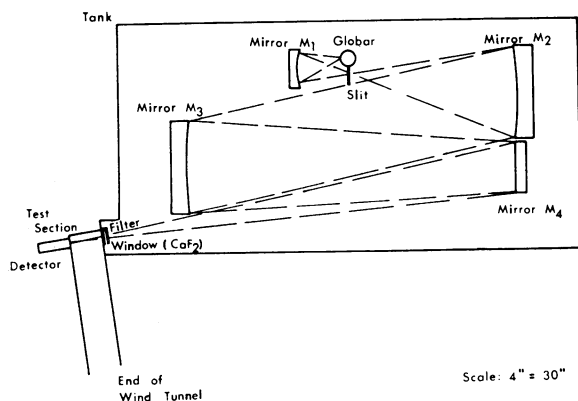
## Results

Using the experimental procedures described above and assuming all physical properties constant at 25° the necessary data for evaluating the interference factor from equation V could be obtained. These data appear in table I for a variety of environmental conditions. At the bottom of the table are listed the data for the depth of the stomatal pores and the number of stomata per unit area. Based on these data, values of the factor $(1-F)$ could be calculated from equation V. It should be noted that the results were tabulated as values of $(1-F)$ rather than values of $F$ because it is the term $(1-F)$ which is of greatest physical significance. Also the data are tabulated in this form because the term $(1-F)$ appears in all the equations and because such data are comparable to those presented by previous investigators (13). Actually 2 sets of values were calculated for $(1-F)$ for each test. The value $(1-F)_T$ was obtained from equation V by setting $L$ equal to zero, for comparison with the results of Ting and Loomis (13) for multiperformate septa of negligible thickness.

In table I no actual values appear for $q_r$ for tomatoes since the radiative characteristics of tomato leaflets were unknown. To indicate that the incident radiation for these tomato tests corresponded to that for the potato tests, $P$-1 through $P$-3, the net radiation exchange for the tomato plants was given as some function "$f$" of the radiation exchange for the corresponding potato test. Cook (2) gives temperature variation across the boundary layer on a tomato leaflet for a range of environmental conditions. Finally, it should be noted that in the case of potato leaves an approximate value of the incident radiation on the leaf can be obtained by multiplying the tabulated values of $q_r$, the net radiation exchange to the leaf, by 2.5. (Such an approximation is

obtained from the fact that the leaf was emitting very little energy compared to that which was absorbed, and from the leaf absorptivity which was approximately 0.4 for the radiation involved.) The values of incident radiation thus obtained can then be compared to the solar constant (i.e., approximately 2 cal/min cm²) in order to estimate the magnitude of the radiation term.

## Discussion

A comparison of the calculated values of $(1-F)_T$ and $(1-F)_c$ presented in table I is quite revealing. As one would expect these values are larger for tomato plants than for potato plants since the stomatal openings in tomato are smaller and fewer per unit area yielding a smaller interference factor, and hence a larger $(1-F)$ value.

The values of $(1-F)_T$ for the tomato leaves in Tests $T$-1 to $T$-3, being calculated for the case of $L=0$, can be compared with Ting and Loomis' values for multiperforate septa of similar geometry. Ting and Loomis (13) have presented a plot (for pores spaced 10 diam apart) of interference factor as a function of the pore diameter. Tomato stomata are spaced about 9.5 stomatal diameters apart, and thus an interference of approximately 0.04 can be read from their plot. From the measured values of $(1-F)_T$ in table I, it can be seen that the experimental results approximate the value obtained from Ting and Loomis' data although the average of our experimental results is $(1-F)_T$ AVERAGE = 0.0614 or about 50 % higher. Such a difference is not unreasonable when one considers that the published value of 0.04 was based on a stomatal spacing of 10.0 stomatal diameters rather than the observed spacing of 9.5.

From the data presented in table I it is evident that as irradiation of the leaves is increased (i.e.,

Table I. *Effects of Laminar Flow Velocity* $(V_\infty)$ *and Net Radiation Absorbed* $(q_r)$ *on the Difference in Relative Humidity Between Leaf and Ambient Air* $(\Delta\phi)$ *and on Interference Between Stomata Calculated According to Equation V,* $(1-F)_c$ *and by Setting* $L = 0$ *in Equation V,* $(1-F)_T$

$r$ = Stomatal aperture, and other stomatal characteristics were as noted. Tests with tomato (T) and potato (P) are reported.

| 1<br>No. of<br>test | 2<br>$V_\infty$ | 3<br>$\phi_\infty$ | 4<br>$T_\infty$ | 5<br>$q_r$ | 6<br>$r$ | 7<br>$\Delta\phi$ | 8<br>$(1-F)_c$ | 9<br>$(1-F)_T$ |
|---|---|---|---|---|---|---|---|---|
| | *cm/sec* | *%* | *deg* | *cal min⁻¹/cm⁻²* | *μ* | *%* | | |
| T-1 | 86.5 | 28 | ≅25 | f($3.12 \times 10^{-2}$) | 3.28 | 3 50 | 0.0982 | 0.0350 |
| T-2 | 86.5 | 32 | ≅25 | f($6.06 \times 10^{-2}$) | 3.46 | 5.40 | 0.152 | 0.0559 |
| T-3 | 86.5 | 35 | ≅25 | f($11.07 \times 10^{-2}$) | 4.03 | 5.35 | 0.230 | 0.0934 |
| P-1 | 86.5 | 25 | 24.6 | $3.12 \times 10^{-2}$ | 4.84 | 4.74 | 0.0503 | 0.0252 |
| P-2 | 86.5 | 25 | 23.6 | $6.06 \times 10^{-2}$ | 5.60 | 7.24 | 0 0611 | 0.0334 |
| P-3 | 86.5 | 25 | 25.7 | $11.07 \times 10^{-2}$ | 7.03 | 8.26 | 0.0537 | 0.0319 |
| P-4 | 230 | 33 | 24.4 | $11.07 \times 10^{-2}$ | 6.10 | 5 44 | 0.0720 | 0.0402 |
| P-5 | 350 | 37 | 23.7 | $11.07 \times 10^{-2}$ | 6.10 | 6.27 | 0.110 | 0.0617 |

| | | Tomato | Potato |
|---|---|---|---|
| | Pore depth | 9 29μ | 7.56μ |
| | Pore density | 13,000/cm² | 16,100/cm² |

from Tests $T$-1 to $T$-3, and from Tests $P$-1 to $P$-3), the interference factor $F$ decreased (*i.e.*, the value of $(1-F)_T$ or $(1-F)_c$ increased). Such a phenomenon is readily explainable on a physical basis. Since for all 6 of these tests the free stream velocity was constant, from equation IV it follows that the mass transfer coefficient was also constant. Thus, it is obvious from equation II that any change in the transpirational flux over these tests would have to be reflected in a change in the concentration difference across the boundary layer, $(W_{1w}-W_{1\infty})$. The change in the value of $\triangle\phi$ across the boundary layer is a way of determining the change in the concentration difference. From the values of $\triangle\phi$ in table I it is evident that as the net radiation exchange to the leaf was increased (column 5) the transpiration increased (column 7). An increase in transpiration means an increase in the size of the diffusional shells. As the diffusional shells increase in size they protrude farther into the boundary layer on the surface of the leaf and thus are subjected to greater distortions by the transverse velocities. Such increased disruption of diffusional shells due to increased transpiration (with increasing net radiation exchange) is the apparent explanation for the decrease in the interference factor. Some of the increase in diffusional shell disturbance may also be due to increases in the transpiration or diffusion velocity itself.

The decrease in the interference factor $F$ with increasing radiation exchange could also be caused by increases in the stomatal diameter and the resulting decrease in the distance between adjacent pores. But since in the tomato leaf tests the variation in pore radius was very slight (*i.e.*, 3.28–4.03 $\mu$) such an explanation would not account for the large variation in the interference factor.

An increase in the free stream velocity decreases the boundary layer thickness which in turn should increase the diffusional shell disturbance and thus, again, lessen the interference factor between pores. To examine this possibility in Tests $P$-4 and $P$-5 wind velocities were increased but the same radiation exchange to the leaf was maintained. The data in table I ($P$-3–$P$-5) show that the concentration difference across the boundary layer (column 7) first decreased as the free stream velocity was increased from 86.5 to 230 cm/sec and then increased slightly as the free stream velocity was increased from 230 to 350 cm/sec. Using equations II and IV along with the data in table I for Tests $P$-3, $P$-4, and $P$-5, it can be shown that the transpirational flux increases with increasing free stream velocity. In fact the transpirational flux at 230 cm/sec is approximately 1.02 times what it was at 86.5 cm/sec, while that at 350 cm/sec is 1.41 times that at 230 cm/sec.

The trends observed in the variation of transpiration appear to differ from the results reported by Mellor (10) who concluded from his experimental data that transpiration decreases logarithmically with increasing wind velocity. The difference between the results presented here and those of Mellor appears to be due to differences in the magnitude of the incident radiation and the type of flow over the leaf. In the tests presented here, the irradiation was much smaller than that used by Mellor so that even at low wind velocities the leaves were never more than fractions of a degree above the air temperature. With small temperature differences such as this, the increase in convective cooling with wind velocity was minor when compared to the effect caused by the increased disturbance to the diffusional shells. It should also be mentioned, that in Mellor's experiment the flow over individual leaves was turbulent and non-uniform and this might account for some of the differences in the experimental results.

It is interesting to observe in the tests $P$-3, $P$-4, and $P$-5, that the condition of the diffusional shells is again greatly affected by the transpiration as evidenced by an increase in the factor (1-$F$) with increasing wind velocity (table I). With increasing free stream velocity the boundary layer becomes thinner, the velocity gradient at the leaf surface increases, and there is an increased disturbance of the diffusional shells above the pores. This results in a decrease in the interference factor or an increase in the value of (1-$F$). These results disagree with the findings of Ting and Loomis for multiperforate septa. Ting and Loomis contend that for such septa the interference factor is virtually constant over the velocity range from 0 to 460 cm/sec.

Another interesting aspect of the leaf transpiration problem can also be noted from table I. Recognizing the analogy between diffusion of mass and conduction of electricity and making use of Ohm's law, the following formula can be written

$$M = \left(\frac{\triangle\phi}{R}\right)_{Boundary\ layer} = \left(\frac{\triangle\phi}{R}\right)_{Pores} = \left(\frac{\triangle\phi}{R}\right)_{Pores+Boundary\ layer} \quad (VI)$$

where $R$ represents diffusion resistance. From this the ratio of the convective resistance (to diffusion) to the pore resistance (to diffusion) is directly proportional to the change in relative humidity across the 2, *i.e.*,

$$\frac{R_{Boundary\ layer}}{R_{Pores}} = \frac{\triangle\phi_{Boundary\ layer}}{\triangle\phi_{Pores}} \quad (VII)$$

Using the data from table I, the relative magnitudes of these resistances can be estimated. From these data the convective resistance was usually one-sixth that of the pores or less. It is also obvious that although the convective resistance is smaller than that of the pores, it does significantly affect the overall diffusion. This is in disagreement with the commonly accepted practice of neglecting the external resistance when dealing with diffusion from a leaf. Even Lee and Gates (8), who recognize the

importance of the convective resistance in free convection and give values for such resistance, contend that this resistance is zero when the wind velocity exceeds 50 cm/sec. Of course, Lee and Gates were working with leaves which probably had higher pore resistance than those used in this work (*i.e.*, their leaves had a much smaller number of pores per unit area).

From the data in table I, the change in the relative magnitude of these 2 resistances with the change in environmental conditions can also be analyzed. It is evident from the data presented in table I and equation VI, that as the wind velocity increases, the sum of the convective and pore resistances decreases. It is also seen from table I that the concentration difference across the boundary layer decreased as the free stream velocity was increased from 86.5 to 230 cm/sec but then increased over the velocity range of 230 to 350 cm/sec. As has already been shown, the transpiration increased slightly as the free stream velocity was increased from 86.5 cm/sec to 230 cm/sec and increased more rapidly as the velocity was increased from 230 cm/sec to 350 cm/sec. Thus, from equation VI, it can be shown that as the velocity increased from 86.5 to 230 cm/sec the convective resistance had to decrease.

Similarly it can be demonstrated that the convective resistance also decreased in the velocity range from 230 to 350 cm/sec. In an analogous manner it can be shown that the resistance of the pores also had to decrease with increasing free stream velocity, and this decrease in resistance over the velocity range of 86.5 to 350 cm/sec was at a more rapid rate than the decrease in the convective resistance. This is probably attributable to the fact that the increase in wind velocity caused a decrease in the interference factor, thus decreasing the pore resistance. It is interesting to note that the major effect of the wind was on the pore resistance and not the convective resistance.

An analogous analysis to the above can be made for the variations in the convective and pore resistance under conditions of increasing incident radiation to the leaf. From such an analysis it can be shown that as the incident radiation increased, the convective resistance decreased while the pore resistance decreased more rapidly. Again, this can be attributed to the decrease of the interference factor. Thus, it would appear that the major effect of these environmental changes is in altering the pore rather than altering the convective resistance.

From the foregoing discussion and data, 2 important conclusions can be reached concerning the role which the mutual interference between pores plays in determining the overall transpirational flux. First, the interaction of the boundary layer and the vapor diffusional shells is critical to the determination of the interference factor (and the resulting transpiration), and because of such interaction the interference to transpiration is not constant with wind velocity. These variations in the interference

factor must be taken into account if one is to predict accurately transpiration rates. Secondly, the changes in transpiration brought about by changes in light and wind are basically due to changes in the pore resistance rather than in convective resistance. Although changes in the convective resistance are not the prime cause of changes in transpiration, still such a resistance must be taken into account when considering the total mass transfer. The latter point is important because it implies that an instrument such as porometer, although suitable for investigating stomatal resistance, will not be effective in studies of the overall resistance to transpiration.

## Acknowledgments

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