

ON THE QUANTITATIVE EXPLANATION OF STOMATAL TRANSPIRATION

BY

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I. INTRODUCTION

A. *The question of stomatal regulation*

The study of leaf anatomy and of the mechanism of the opening and closing of stomatal guard cells leads one to suppose that the stomata constitute the main or even the sole regulating system in leaf transpiration. Nevertheless this supposition has been questioned on other grounds by many authors.

One might say that the classical work of BROWN and ESCOMBE (1900) on evaporation and gaseous exchange through porous films contained one of the main sources of doubt. As is well known these investigators stated that the transpiration in leaves of *Helianthus annuus* L. was 6 times smaller than they had expected from their theoretical considerations, so that, apart from the stomata, it would seem that other factors have a profound influence on the transpiration rate.

Subsequently this idea was corroborated by several other investigators. LIVINGSTON (1906), expressing his results in terms of relative transpiration to eliminate the influence of environmental factors, found the daily maximum of transpiration occurred before that of evaporation. He did not consider the stomata responsible for the fact that both maxima do not coincide, because the phenomenon appeared before any stomatal closure was to be expected. LLOYD (1908), finding very little correlation between transpiration rate and stomatal aperture, concluded that the stomata influence the transpiration only at their smallest apertures. LIVINGSTON and BROWN (1912), obtaining results similar to those of LIVINGSTON (1906), put forward the theory that, as a consequence of the water loss from the leaf, an incipient drying of the cell walls lining the intercellular spaces should cause an additional resistance to transpiration. The same conclusion was drawn by SHREVE (1914) from similar experiments. TRELEASE and LIVINGSTON (1916), using the porometer method, found that in the course of the day the maximum of stomatal aperture was reached some hours after the maximum of transpiration, so that another mechanism seemed to play a role in regulating transpiration. KNIGHT (1917, 1922) also accepted a dual influence on the transpiration rate: — the incipient drying of the cell walls would control it in case of bright weather and wide open stomata, while at low light intensities and small apertures the stomata themselves would be the main controlling factor.

However, not all the English and American authors were of the same opinion. DARWIN (1916) stated a reasonable parallelism between transpiration rate and stomatal aperture. LOFTFIELD (1921) concluded from his experiments that the stomata regulate the transpiration to a great extent, although in his opinion at more than 50 % of the maximal aperture evaporation factors become more important than the stomata.

Evidently the scepticism among the authors cited as to the controlling power of stomata mainly concerned the greater apertures. The question arises as to whether this scepticism was justified.

B. *The diffusion resistance*

BROWN and ESCOMBE based their theoretical considerations on Fick's diffusion law, one expression of which is as follows: —

$$m/t = k \cdot (c - c') \cdot O/l$$

(m = quantity of matter diffusing through a tube in time t ,
 l = length of tube,

O = sectional area of tube,
 c, c' = concentration of matter at beginning and end of tube,
 k = diffusion constant, the value of which depends on the quality of the diffusing substance and of the diffusion medium and on the temperature).

It is easily seen that this diffusion law represents an analogue of Ohm's law for the conduction of electricity through a homogeneous conductor, the expression of which is

$$\frac{e}{t} = f \cdot (v-v') \cdot \frac{O}{l} = \frac{v-v'}{1/f \cdot l/O} = \frac{v-v'}{r}$$

e = quantity of electricity flowing through a conductor in time t ,
 l = length of conductor,
 O = sectional area of conductor,
 v, v' = electrical potential at beginning and end of conductor,
 f = conductivity constant, the value of which depends on the quality of the conducting material and on the temperature,
 r = electrical resistance of conductor).

As a consequence we may define the diffusion resistance as an analogue of the electrical resistance and represent it by

$$r = 1/k \cdot l/O.$$

For a number of conductors in series Ohm's law reads

$$\frac{e}{t} = i = \frac{v-v'}{r+r'+r''+r'''+\dots} = \frac{v-v'}{R}$$

i = strength of current,
 $v-v'$ = total potential difference,
 R = total resistance of the series equalling the algebraic sum of the separate resistances r, r', r'', r''' etc.).

As Ohm's law for electrical currents and Fick's law for diffusion are completely analogous in the case of single conductors, there is no reason why this analogy should not be extended to the case of a series of conductors. Thus, with the assumption of a steady state, the formula for the diffusion rate through a series of tubes becomes

$$\frac{m}{t} = i = \frac{c-c'}{r+r'+r''+r'''+\dots} = \frac{c-c'}{R}$$

i = diffusion rate,
 $c-c'$ = total concentration difference,
 R = total diffusion resistance of the series equalling the algebraic sum of the separate resistances r, r', r'', r''' etc.).

Our problem therefore is greatly simplified by the facts that

1. only concentrations c and c' at the beginning and end of the diffusion path are needed for the calculation of the diffusion rate and the intermediate ones are not required;

2. the total diffusion resistance in a heterogeneous system may be obtained by simple addition of the respective resistances of the component parts. One may call this the "principle of successive resistances". This principle has already been applied by several authors in different cases, e.g. by BROWN and ESCOMBE (1900) and RENNER (1910) to transpiration and by PENMAN and SCHOFIELD (1951) also to carbon dioxide assimilation.

This formulation of Fick's law, however, is only applicable if, in the system used, the surfaces of equal vapour concentration are flat and therefore the diffusion lines perpendicular to these surfaces are parallel lines. These conditions are not satisfied in the case of a circular evaporating surface lying in a flat non-evaporating plane (fig. 1). Theoretical deductions (STEFAN 1881) have shown that in

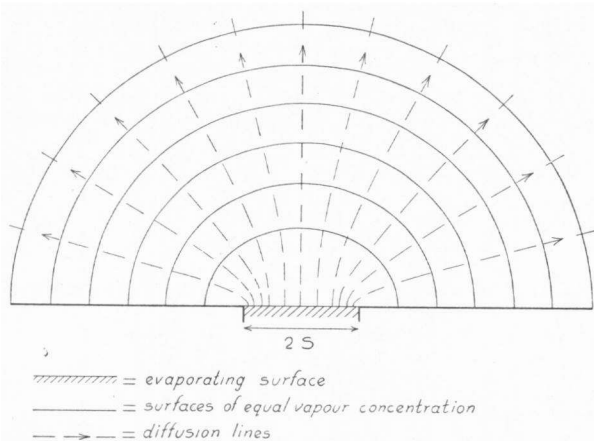


Fig. 1. Diffusion lines and surfaces of equal vapour concentration over a circular evaporating surface lying in a flat non-evaporating plane.

this case the surfaces of equal vapour concentration are halved oblate spheroids (formed by rotating the upper half of an ellipse about its short axis) and that the diffusion lines are hyperbolas, the focal circles, respectively the foci coinciding with the margin of the evaporating surface.

In this system STEFAN and later BROWN and ESCOMBE calculated the diffusion resistance to be

$$r = 1/k \cdot 1/4s$$

(s = radius of evaporating surface). According to this formula, which only holds for absolutely still air, the evaporation rate is proportional to the radius of the surface (Stefan's diameter law).

Additional resistances are introduced if a septum perforated by circular pores is placed over such an evaporating surface (fig. 2). In this case the total diffusion resistance will consist of three different parts, viz: —

1. The resistance in the pores

$$r_p = 1/k \cdot l/\pi s_1^2 \cdot 1/N$$

(s_1 = radius, l = depth and N = number of pores).

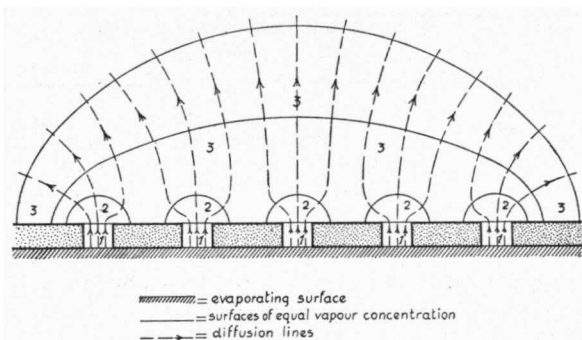


Fig. 2. Diffusion lines and surfaces of equal vapour concentration over an evaporating surface over which a perforated septum has been placed.

2. The resistance in the micro vapour cups over the individual pores, amounting to

$$r_{d1} = 1/k \cdot 1/4s_1 \cdot 1/N.$$

3. The resistance in the macro vapour cup over the entire septum. Its value is

$$r_{d2} = 1/k \cdot 1/4s_2$$

(s_2 = radius of septum).

Therefore the total diffusion resistance of this system will be

$$R = r_p + r_{d1} + r_{d2} = \frac{1}{k} \cdot \left\{ \frac{1}{N} \cdot \left(\frac{l}{\pi s_1^2} + \frac{1}{4s_1} \right) + \frac{1}{4s_2} \right\}.$$

If in a transpiring leaf one assumes a saturated water vapour concentration in the substomatal spaces and pays due consideration to the elliptical shape of the pores, it may be considered as comparable to the above system.

BROWN and ESCOMBE developing their formulae in this way made calculations which proved to agree fairly well with the results of their experiments with models. They also tried to compute the rate of water loss from a leaf of *Helianthus annuus*, but due to an oversight they omitted the evaluation of the macro vapour cup over the leaf. Consequently the remaining resistance calculated was too low and the theoretical transpiration rate derived from it became several times greater than the one observed. Much confusion would have been avoided, if they had not made this small omission, which apparently caused several authors to accept an additional transpiration resistance inside the leaf.

As RENNER pointed out clearly as early as 1910, neglect of the macro vapour cup leads to the preposterous conclusion that, if a perforated septum be placed over a free water surface, the evaporation rate should be increased.

The formula derived by STEFAN and BROWN and ESCOMBE for the diffusion resistance over a circular evaporating surface theoretically applies only if the vapour cup is of unlimited size. Obviously this will never be the case as "still air" is never quite still and the vapour cup is always more or less disturbed by convection currents. It is impossible, however, to evaluate theoretically the degree of this disturbance.

Nevertheless if the total diffusion resistance is to be calculated for leaf transpiration, it is necessary to obtain the real value of the resistance in the macro vapour cup. VAN DEN HONERT (1948) pointed out that this resistance may be represented by that of a hypothetical, completely still air layer of a certain thickness over the transpiring surface. On the outside this hypothetical air layer is thought to be bordered by air which is continuously renewed and which has the same water vapour concentration as the rest of the surrounding air. Its diffusion resistance may be determined empirically, in any particular case, by measuring the evaporation rate from a free water surface of exactly the same shape and under the same conditions as the object. The thickness of this air layer depends on the degree of air convection and may be calculated using the diffusion constant of water vapour in air and applying Fick's law. In still air this may amount to anything from several mm to one cm depending on the diameter of the evaporating surface.

We are well aware that a rather simplified conception of the conditions is involved in the assumption of a rigid air layer of a certain thickness. Meanwhile, WELTEN (1933) using cobalt paper showed that there are actually vapour cups of the same order of thickness over evaporating surfaces, so there is no doubt that, at least in still air, a considerable diffusion resistance outside the leaf actually occurs.

So the total diffusion resistance in a leaf may be calculated by addition of the three successive diffusion resistances which the water vapour has to pass, viz: —

1. The resistance in the stomata. If the latter are represented by cylindrical tubes with an elliptical section, this resistance per cm^2 leaf surface amounts to

$$r_s = 1/k \cdot l/\pi ab \cdot 1/N$$

(l = length of tube,

a = half the short axis of the ellipse,

b = half the long axis of the ellipse,

N = number of stomata per cm^2 leaf surface).

With variation of the stomatal aperture only the short axis is considered to be variable. This is not far from reality.

2. The resistance in the micro vapour cups over the individual

stomata. The total resistance per cm^2 leaf surface of these vapour cups may be calculated by BROWN and ESCOMBE's formula

$$r_d = 1/k \cdot 1/4\sqrt{ab} \cdot 1/N$$

(\sqrt{ab} = radius of the circle with an area equal to the elliptical section of the stoma).

3. The resistance in the macro vapour cup over the whole surface of the leaf (= the hypothetical still air layer). Its value may be derived from the evaporation rate in the way already described.

For the sake of simplicity we will for the moment leave out of account the resistance 2 as being of minor importance. In this case the total resistance consists of two, mutually independent, partial resistances. The stomatal resistance r_s is variable and inversely proportional to the stomatal aperture while that of the macro vapour cup or still air layer, which we call A , is constant.

The diffusion rate i may now be computed

$$i = (c - c') / (r_s + A)$$

(c = concentration of water vapour in the substomatal space,

c' = concentration of water vapour in the surrounding air).

As long as r_s is large compared to A , that is with small apertures, r_s will practically determine the transpiration rate and the transpiration will be approximately proportional to the stomatal aperture. However, the greater the aperture, the more important A becomes and eventually it may constitute the main limiting factor in transpiration. Consequently the curve representing the relation between the stomatal aperture and the transpiration rate in still air (fig. 3) will have an initial steep part, but will gradually flatten.

RENNER as early as 1910 had already shown a clear insight into

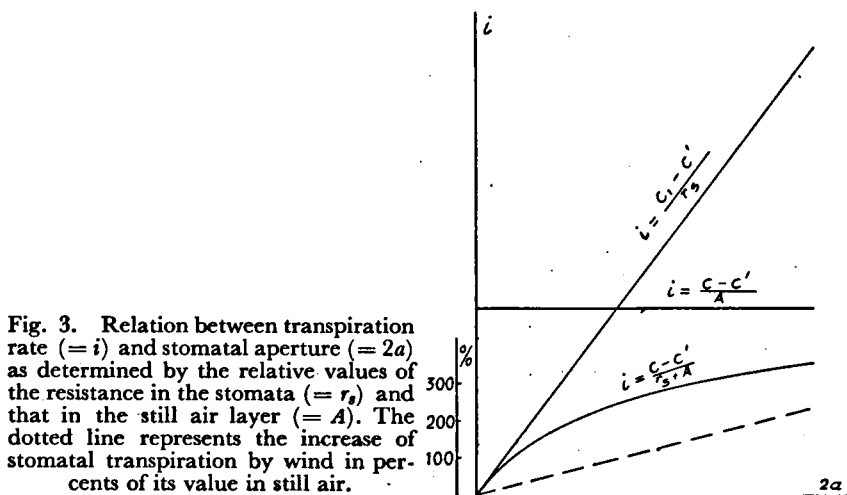


Fig. 3. Relation between transpiration rate ($= i$) and stomatal aperture ($= 2a$) as determined by the relative values of the resistance in the stomata ($= r_s$) and that in the still air layer ($= A$). The dotted line represents the increase of stomatal transpiration by wind in percents of its value in still air.

these principles; as mentioned earlier he was the one to detect the flaw in BROWN and ESCOMBE's calculation of stomatal transpiration. He also disputed LLOYD's conclusion that stomata have no regulating influence at greater apertures and found a fairly good agreement between the transpiration rates calculated theoretically and those actually determined.

LARMOR (1918) again brought forward a similar point of view. It is surprising that the later German and Swiss workers did not use and extend these principles. SEYBOLD's (1929*a* and *b*) theoretical considerations therefore remained rather unprofitable. SIERP and SEYBOLD (1927 and 1929) determined evaporation rates through perforated brass septa and in their opinion these did not agree with those calculated by means of BROWN and ESCOMBE's formula. From these results they concluded that in practice the principles developed by BROWN and ESCOMBE were not valid for pores of the order of magnitude of the stomata. That this conclusion was a little premature may appear from fig. 4 A and B. In this figure SIERP and SEYBOLD's data concerning the relation between pore diameter and relative evaporation rate are compared with the results of a theoretical analysis of their experiments according to the principle of successive resistances (see Appendix, part IV). The agreement is so close that these experiments might even be used as an empirical proof of how well the foregoing principle applies.

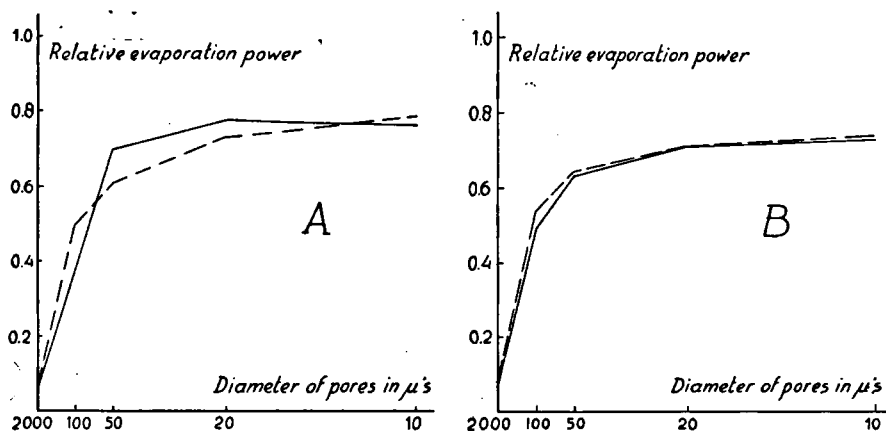


Fig. 4. SIERP and SEYBOLD's curves for the relation between pore size and relative evaporation power (drawn lines) compared with the results of our theoretical analysis (dotted lines). A. No filter paper used. B. Filter paper used.

In his later articles SEYBOLD (1930, 1931*a*, 1934) developed a conception of transpiration resistance (see also SEYBOLD and FÜSSER 1931, BACHMANN 1932, FÜSSER 1933) which BREWIG (1933) showed to be identical with

$$w = \frac{p_{\max} - p_0}{p_s - p_0}$$

(p_{max} = saturated water vapour pressure at leaf temperature,
 p_s = water vapour pressure at leaf surface,
 p_o = water vapour pressure of surrounding air).

Where in our terms $\text{Evaporation} = (p_{\text{max}} - p_o)/r_{\text{air layer}}$ and $\text{Transpiration} = (p_s - p_o)/r_{\text{air layer}}$ it is clear that, as MAXIMOV (1931) and WELTEN (1933) rightly remarked, such a conception of transpiration resistance is nothing but the reciprocal value of LIVINGSTON's (1906) relative transpiration T/E , provided evaporation and transpiration are measured under comparable conditions (same value of $r_{\text{air layer}}$).

WELTEN's (1933) formula of transpiration resistance

$$W_s = W_1/f + W_2$$

(W_s = total transpiration resistance,

W_1 = part of resistance that is inversely proportional to width of stomatal slit,

W_2 = part of resistance that is independent of width of stomatal slit,

f = transpiring area)

has the advantage, as MONSI (1944) observed, of consisting of one part varying with stomatal aperture and another independent of it. MONSI therefore could show it to be identical with RENNER's conception of transpiration resistance.

HUBER's (1930) experiments with perforated septa deserve special consideration. He gave a qualitative explanation of his results by means of the conception of "mutual interference of pores" and expressed his empirical "interference law" in a mathematical formula.

The conception of interference hardly lends itself to quantitative considerations, although VERDUIN (1947) made such an attempt.

The mutual interference of pores is brought about by the diffusion lines, which radiate out from the pores at first, becoming parallel

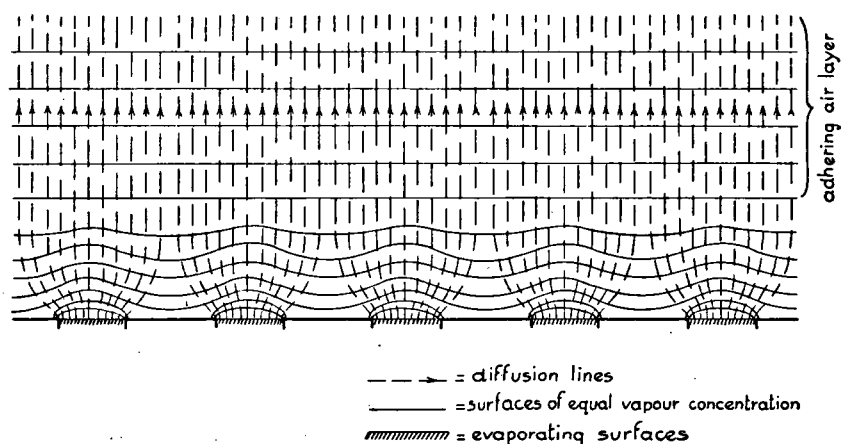


Fig. 5. Transition of micro vapour cups in adhering air layer (mutual interference of pores).

to each other and perpendicular to the surface. It should be stressed that there is essentially no difference between this conception and the view developed in this paper. That section where the lines become parallel is to be regarded as an adhering air layer forming an external resistance (fig. 5).

Again, HUBER's curves can be explained quantitatively in terms of successive resistances. In fig. 6 the relation between the total pore surface and the relative evaporation rate of septa with pores of 1 mm^2 and $2000 \mu^2$, as empirically determined by HUBER, is represented by a continuous line, whereas the corresponding theoretical values are given by a dotted line (for the calculation see Appendix, part V). The agreement between theory and experiment appears to be satisfactory.

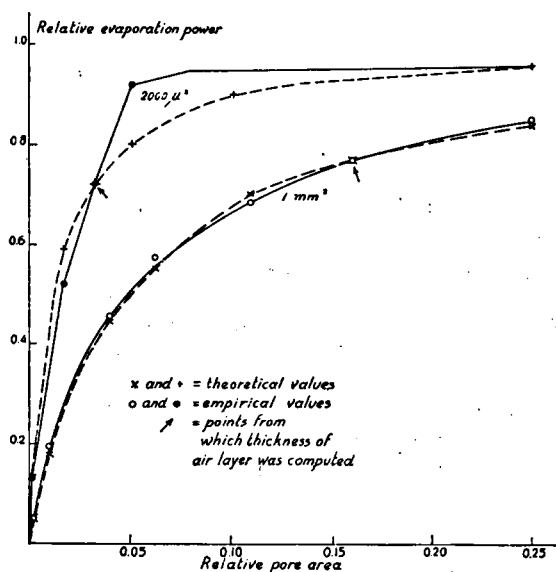


Fig. 6. HUBER's curves for the relation between relative pore area and relative evaporation power of septa with pores of 1 mm^2 and $2000 \mu^2$ (drawn lines) compared with the results of our theoretical analysis (dotted lines).

The relation between stomatal aperture and transpiration rate has been investigated by no one more carefully and thoroughly than by STÅLFELT (1932a, 1935). His curves (fig. 7) — the first of their kind in the literature on transpiration — are steep at first, but flatten off at greater stomatal apertures. In explaining his results STÅLFELT too based himself on the conception of mutual interference of pores. VAN DEN HONERT (1948) pointed out that, if the transpiration rate is mainly determined by a variable resistance in the stomata and a constant resistance in the adhering air layer, a similar shape of the curve is to be expected (cf fig. 3).

MONSI (1944) also found curves of this shape and tested them by

RENNER's formulae. There was some agreement between theory and experiment.

GÄUMANN and JAAG (1938) in their theoretical derivation of the transpiration rate thought in terms of water vapour effusion instead

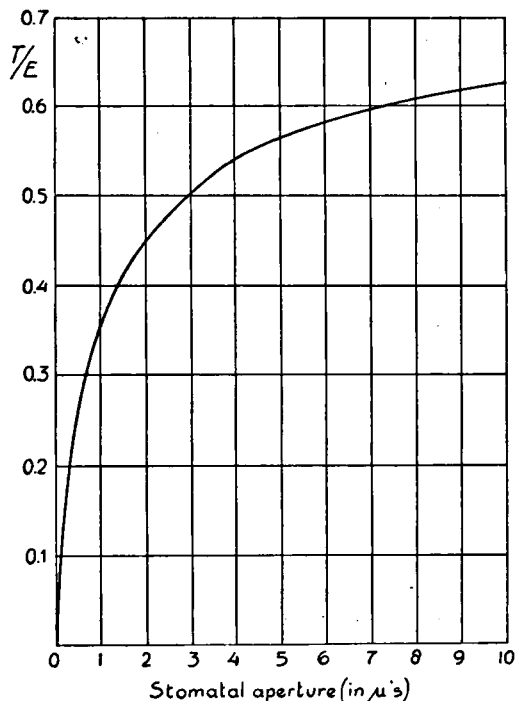


Fig. 7. STÄLFELT's curve for the relation between relative transpiration ($= T/E$) and stomatal aperture in still air (*Betula pubescens*).

of diffusion and applied Poiseuille's law. It is difficult to see how there can be a gas-stream through the stomata except in anomalous cases.

C. The influence of wind

The question arises as to which relation is to be expected between transpiration rate and stomatal aperture in wind.

The rate of evaporation from a free water surface is greatly increased by wind. This may safely be attributed to the partial elimination of the diffusion resistance in the macro vapour cup or, in other words, to the decrease in the thickness of the adhering air layer. In a leaf where the macro vapour cup and the micro ones have been blown away and so the external resistance has been reduced to a negligible value, the only remaining resistance is that inside the leaf. The greater part of it is that in the stomata which, as has been shown (page 260), equals

$$r_s = 1/k \cdot l/\pi ab \cdot 1/N.$$

Accordingly in wind the transpiration rate should be directly proportional to the stomatal aperture (fig. 3), at least if the wind is strong enough to blow away all external diffusion resistances. For small leaf areas this seems to be the case even at low wind velocities, as STÅLFELT (1932*b*) found that for a leaf area of 25 cm² wind of a velocity as low as 0.5 m/sec is sufficient to effect a maximum increase of transpiration (fig. 8). The experience that fairly low wind velocities suffice for blowing dust from a smooth surface accords with this statement.

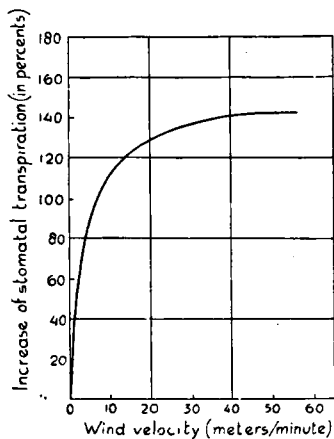


Fig. 8. STÅLFELT's curve for the relation between the increase of stomatal transpiration by wind and the wind velocity.

From the foregoing it will be clear that the measure of increase of transpiration by wind is largely independent of the stomatal aperture. The greater the aperture and so the smaller the stomatal resistance, the greater the relative value of the external resistance which is blown away and so the greater the effect to be expected (fig. 3). Failure to appreciate this is certainly one of the main causes of the controversies concerning the influence of wind on transpiration. A few opinions may be mentioned.

WIESNER (1887) stated that transpiration may be largely increased by wind.

RENNER (1910) had found some quantitative agreement between transpiration rates measured in wind and the respective values calculated according to the principles described.

SEYBOLD (1929*a* and *b*, 1931*b*), however, was of the opinion that in still air convection currents are sufficiently strong to eliminate the micro vapour cups over the stomata so that wind could not increase stomatal transpiration. He attributed any observed increase of transpiration by wind to an increase of cuticular transpiration.

FIRBAS (1931) found in most cases an increase of transpiration by wind.

The same was found by STÅLFELT (1932*b*, 1935). Again he was the first (1935) to publish a curve representing the relation between stomatal aperture and transpiration rate in wind (fig. 9). The relation

is nearly linear as STÅLFELT expected, as in this case no interference of pores would occur.

WRENGER (1935/36) concluded from her experiments that in xeromorphous plants wind has less influence on the transpiration rate

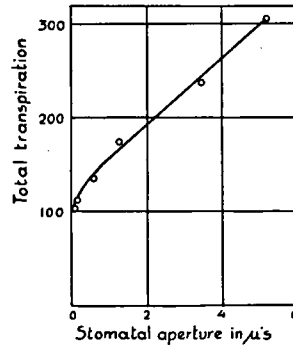


Fig. 9. One of STÅLFELT's curves for the relation between transpiration rate and stomatal aperture in wind (*Avena sativa*).

than in mesomorphous plants and that its influence is greater with larger stomatal apertures. These results are entirely in accordance with our theory.

The experiments of GÄUMANN and JAAG (1939*a* and *b*) have the drawback that the aperture of the stomata was considered to be a linear function of the light intensity which according to STÅLFELT's (1927, 1929) results is hardly justified.

SEYBOLD's opinion that evaporation through pores of stomatal size is not enhanced by wind was founded on the results of his own (1929*a*) experiments with porous septa and those of SIERP and SEYBOLD (1929). However, it is subject to serious doubt if this conclusion was justified. Similar experiments by HUBER (1930) showed that the closer the pores, the less evaporation through the septum differs from free evaporation in wind and that the total poral area is far more important in determining the effect of wind than the diameter of the pores at constant poral area. These results fit completely into our theory.

A review of the literature leads to the conclusion that the work of BROWN and ESCOMBE and of RENNER seemed to open the way to a quantitative explanation of stomatal transpiration as a diffusion process in a system of successive variable resistances. However, the further elaboration necessary and the completion of their principles failed to appear, so their practical applicability was questioned and explanations of an other kind were sought.

The purpose of the following experiments was to investigate whether stomatal transpiration can be explained quantitatively as a diffusion process of water vapour in air in a system of successive variable resistances. The experiments and the conclusions to which they led are described in the following chapters. The mathematical analysis of the diffusion resistances and other calculations will be given in the Appendix.

II. MATERIAL AND METHODS

A. Selection of the test plant

Zebrina pendula Schnizl. was chosen as a test plant. The reason was that this species has relatively large stomatal pores (mean long axis = 35μ) with deep substomatal spaces (fig. 10), consequently under the microscope the image of the underlying cells does not interfere with that of the pores and the apertures can be measured without using an immersion oil as recommended by STÅLFELT (1929a) for *Betula*, *Vicia* etc.. *Zebrina* has been used by other workers (PAETZ 1930) for the same reason.

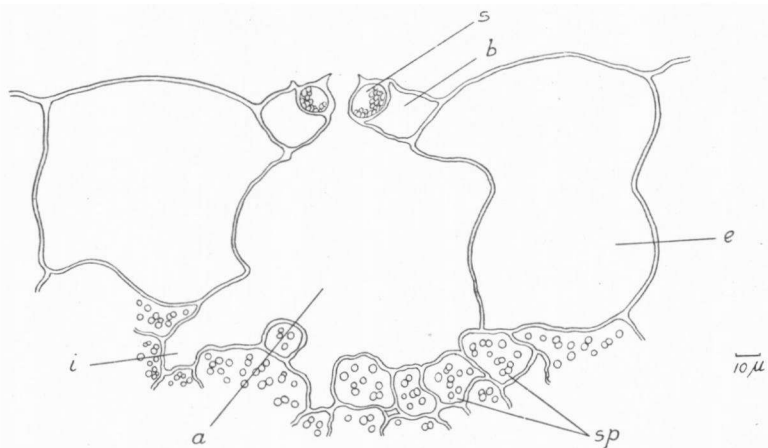


Fig. 10. Transverse section through a stoma of *Zebrina pendula* (*s* = guard cell, *b* = accessory cell, *a* = substomatal cavity, *i* = intercellular space, *sp* = spongy parenchyma, *e* = epidermal cell).

B. Determination of stomatal transpiration in still air and in wind

The transpiration rate is expressed in terms of grams of water vapour given off by 1 cm^2 leaf surface per second at a concentration difference corresponding to 1% saturation deficit. It was determined by measuring the loss of weight of a leaf disc during a given time on an air damped balance.

To obtain comparable results two factors should be constant, viz: —

1. The surface of the leaf disc, as the size of the macro vapour cup (thickness of the adhering air layer) depends on the size of the leaf disc.
2. The temperature of the leaf disc.

A constant leaf surface was obtained by punching out discs from *Zebrina* leaves with a diameter of $\pm 2.8\text{ cm}$. The punch (fig. 11A) consisted of a brass cylinder (*a*) with a rubber stopper (*b*) inside it which was used to hold two razor blades (*c*) in a circular position adjacent to the metal cylinder. The cut was made in such a way that the mid-rib passed approximately through the centre of the disc. Evaporation from the cut margin was eliminated by putting the leaf disc into a holder. Fig. 11B shows this leaf holder which consisted of

a short brass cylinder (d) closed at the top and with rounded edges. The leaf disc (e) is put on top of this cylinder and then a thin rubber ring (f) of the same external diameter is placed over it. This in turn is covered by a brass cap (g) which is almost completely open at the top but just covers the rubber ring. Paraffin wax (h) is used to seal the space between this cap and the cylinder round the side. The remaining free area of the leaf disc measured exactly 5 cm².

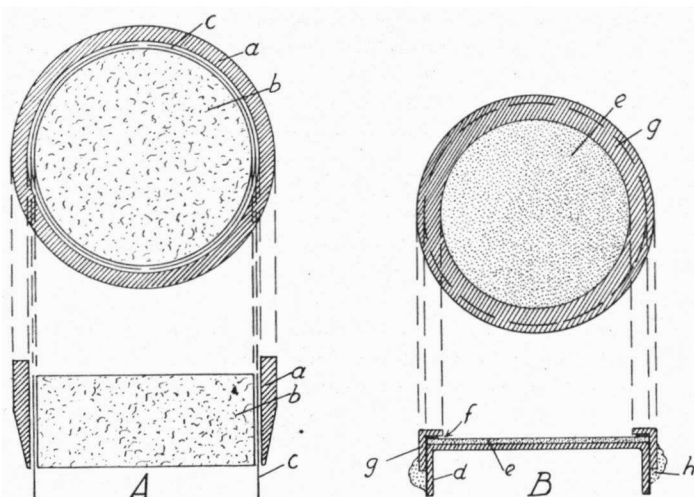


Fig. 11. A. Leaf punch. B. Leaf holder. Explanation in the text.

This method had the additional advantage that the transpiration of the upper and lower sides of the leaf disc could be estimated separately.

The cooling effect of transpiration is difficult to evaluate, therefore we tried to eliminate it, as far as possible, in the following way:—

1. Before the transpiration measurement the leaf disc in its holder was covered by a watch glass in order to bring it into temperature equilibrium with its environment. The weighing began about 10 seconds after removal of the watch glass which time can be computed to suffice amply in most cases for filling up the adhering air layer with water vapour and so reaching a steady state of evaporation or transpiration. In cases of very low transpiration rates the inaccuracy introduced was eliminated by taking the weighing times correspondently longer (on the average 5 minutes).

2. The time of transpiration was kept as short as possible taking into account the sensitivity of the balance. On the average it amounted to 1 minute, but was often shorter or longer depending on the transpiration rate.

3. The heat conduction towards the leaf disc was accelerated by making the leaf holder of a good conducting material (brass) and by putting on the balance scale a small brass pedestal fitting into the leaf holder from below.

The determinations in still air were made in the closed balance case. For those in wind a fan of the type used for hair drying (a so called Föhn), but with the air heating coil switched off, was placed in front of the open door of the balance case with its funnel directed towards the leaf disc at a distance of about 12 cm. The wind velocity over the leaf disc amounted certainly to several meters per second, amply sufficient to blow away all external resistances (cf page 266).

The determinations described above were made with leaf discs upside down and yielded the total (stomatal + cuticular) transpiration rate; the stomatal transpiration rate was obtained by subtracting the cuticular. The latter was determined after the measurement of the stomatal aperture (see below) by inverting the leaf disc in the holder and making a second transpiration measurement in the same way. In so doing one takes for granted that the cuticular transpiration rates of the upper and lower sides of the leaf are equal and that cuticular and stomatal transpiration are not interdependent. These suppositions may be questionable, but we will leave them out of the discussion because of the relatively small values of the cuticular transpiration rates (cf figs 13 and 14)*.

At the beginning of each transpiration measurement the air temperature was read on a thermometer (accurate to 0.5°C) and the air humidity on a Haenni hair hygrometer (accurate to 1 % relative humidity).

C. *Determination of stomatal aperture*

The measurement of stomatal aperture took place immediately after the transpiration measurement of the lower leaf side. The leaf disc was taken out of its holder and put dry on to a slide. It was inspected under the microscope in transmitted light with a magnification of 450 x. The measurements were made by means of a calibrated ocular micrometer, the scale divisions of which corresponded to 3.5μ . Apertures were estimated to 1/10 of a scale division, i.e. to 0.35μ .

As mentioned earlier the stomatal slit in this test plant gives a sharp image against the deep substomatal space below. The measurement was made at the middle of the slit with the microscope focussed at its narrowest part.

There was always considerable variation of stomatal apertures within a leaf, so about 25 measurements were taken at random over the area concerned and the mean calculated from them. These measurements took about 10 minutes. Subsequently, in the same leaf disc two measurements (one on each side of the mid-rib) were made of the number of stomata in the field of vision at a magnification of 55 x, this number varying considerably in different leaves. Again the mean of these two values was calculated and the number N of stomata per cm^2 computed.

An objection against this method might be that during the expe-

* The difference between the cuticular transpiration in still air and in wind is not at all significant.

riment the apertures may change. In that case it would mostly be a closure as the water content of the leaves used is generally suboptimal (STÅLFELT 1929). To check this point the values were grouped as first, second, third etc. measurements. If any general trend had occurred, it would appear from examination of these data. Fig. 12, however, shows no appreciable decline with time, so the conclusion may be drawn that the apertures did not change during the course of the experiment.

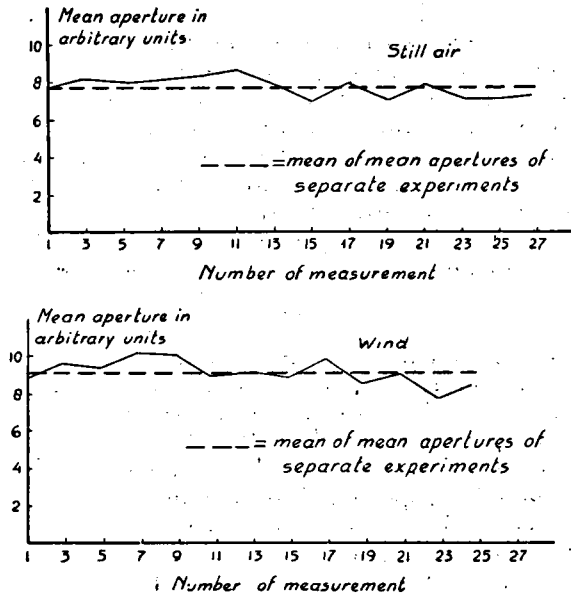


Fig. 12. Mean change of stomatal aperture during a series of 27, resp. 25 measurements.

D. Determination of evaporation in still air

This was done in exactly the same manner as the determination of transpiration, only instead of a leaf disc a disc of wet filter paper was put into the leaf holder. A mean was taken from 14 determinations.

E. Evaluation of the experimental data

As said earlier the water loss from leaf and filter paper discs was expressed in grams per second per cm^2 per % relative humidity deficit. Here the supposition holds that the concentration difference of water vapour $c - c'$ is directly proportional to the external humidity deficit. This means that c , the concentration of water vapour at the walls of the substomatal cavity, is supposed to correspond to the saturated water vapour concentration at the given temperature.

This is not entirely correct since the cells have a certain suction tension or D.P.D. (= diffusion pressure deficit). This D.P.D. tends to lower the water vapour concentration which is in equilibrium with

these cells. However, as GRADMANN (1928) rightly observed, this decrease is very small. Examination of SHULL's (1939) table, which gives the relation between D.P.D. and relative humidity, shows that a D.P.D. value of 13 atm., probably never reached by the leaf cells in our experiments, corresponds to a humidity deficit of only 1 %. Therefore the D.P.D. of the leaf cells could be considered as negligible in comparison with the average humidity deficit of 35 % in our experiments.

To make the data obtained mutually comparable two corrections were still necessary, viz: —

1. for the temperature variations in the experimental room;
2. for the number of stomata per cm^2 leaf surface.

In the experimental room the temperature varied between 21 and 25° C. All transpiration values were reduced to 23° C by multiplication by the ratio between the saturated water vapour pressure at 23° C and that at the prevailing temperature. This, of course, means a correction for the concentration difference $c-c'$. The diffusion constant k is hardly affected by these temperature differences as it increases proportionally to the square of the absolute temperature only

$$k_2 = k_1 (T_2/T_1)^2.$$

Therefore it was assumed to remain constant.

Also a correction for the number of stomata per cm^2 leaf area should be applied, but this is possible only if the validity of the principles, which has to be proved, is already taken for granted. Nevertheless these corrections have been applied. In wind the transpiration rate is taken to be directly proportional to the number of stomata per cm^2 . In still air the correction is more difficult to calculate as will be explained in the Appendix (part VI).

Reduction of the transpiration rates to the average number of stomata per cm^2 leaf surface has the effect of diminishing the spread in the scatter diagrams without essentially changing their position (cf figs 13 and 14). This is what we would expect if our theory is correct.

III. EXPERIMENTAL RESULTS

Figs 13 and 14 show the experimentally determined relation between stomatal aperture and transpiration rate. The spread of the points will be due partly to inaccuracies of the balance since in wind a few negative transpiration rates were found.

The general trend of the curves is in accordance with the theoretical expectations: — in still air a diminishing influence of the stomata with increasing aperture, in wind an approximately linear relation.

However, the curve in wind is certainly not quite linear, being much steeper near its origin (between apertures 0 and 2μ). In STÅLFELT's curves also we observe this steepness at small apertures (cf figs 7 and 9).

Several avenues were explored in a vain attempt to find an explanation of this phenomenon, until the solution was found to lie in

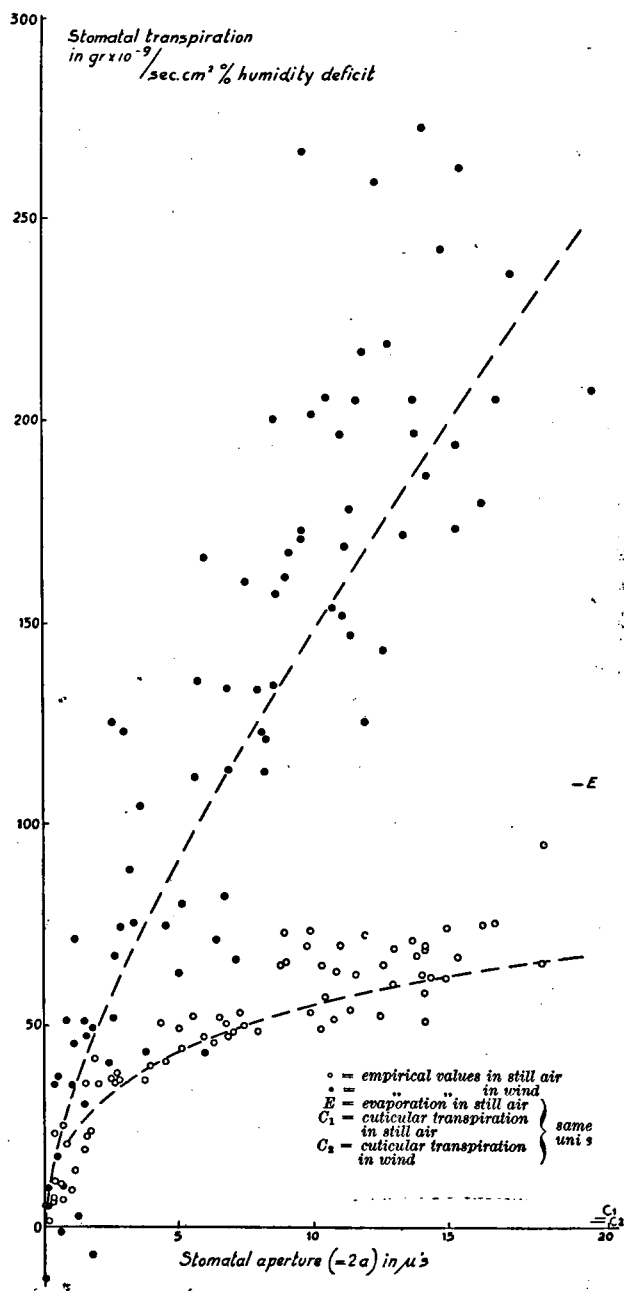


Fig. 13. Relation between stomatal transpiration and aperture in still air and in wind (non-reduced values). The dotted lines represent the corresponding theoretical values.

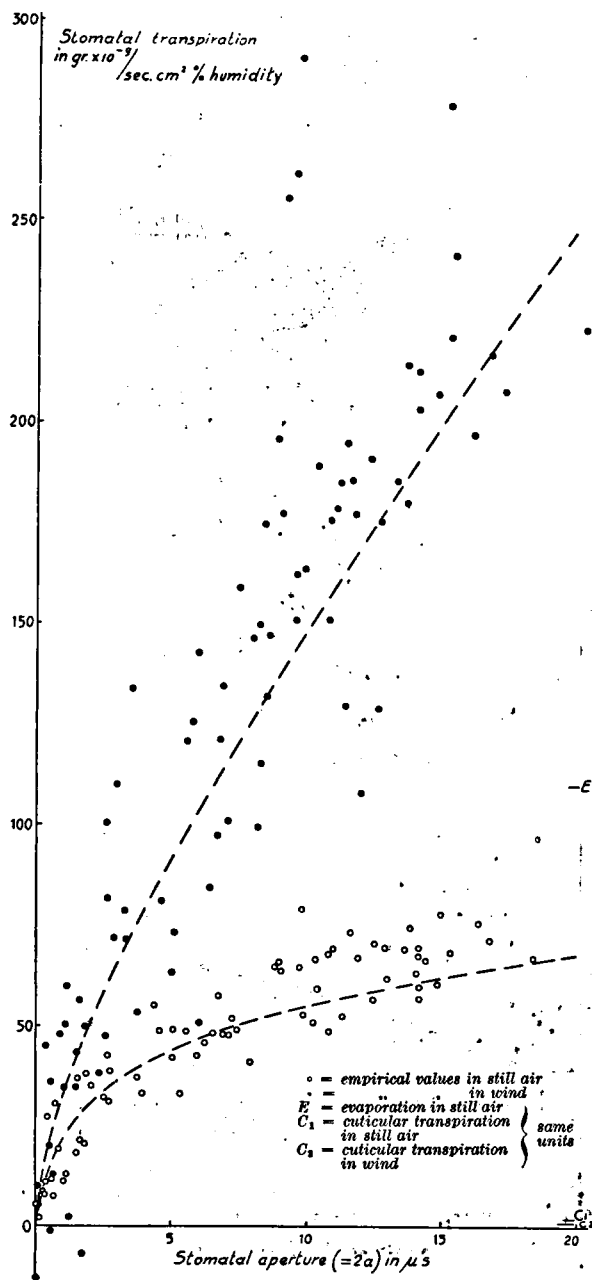


Fig. 14. Relation between stomatal transpiration and aperture in still air and in wind (reduced values). The dotted lines represent the corresponding theoretical values.

the shape of the stomatal pores. In transverse section these pores are hour-glass shaped, i.e. they have a short narrow central part which leads on each side into a long wider part as is shown in fig. 15. This configuration must be responsible for the phenomenon observed on the following grounds:—

Through a slit of small depth (fig. 16A) the diffusion rate will

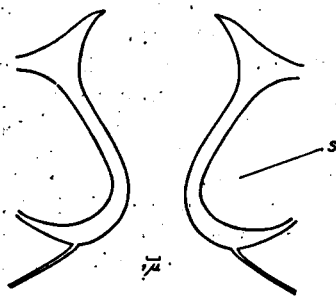


Fig. 15. Transverse section through stomatal pore of *Zebrina pendula* (s = guard cell). Averaged after several drawings with drawing prism.

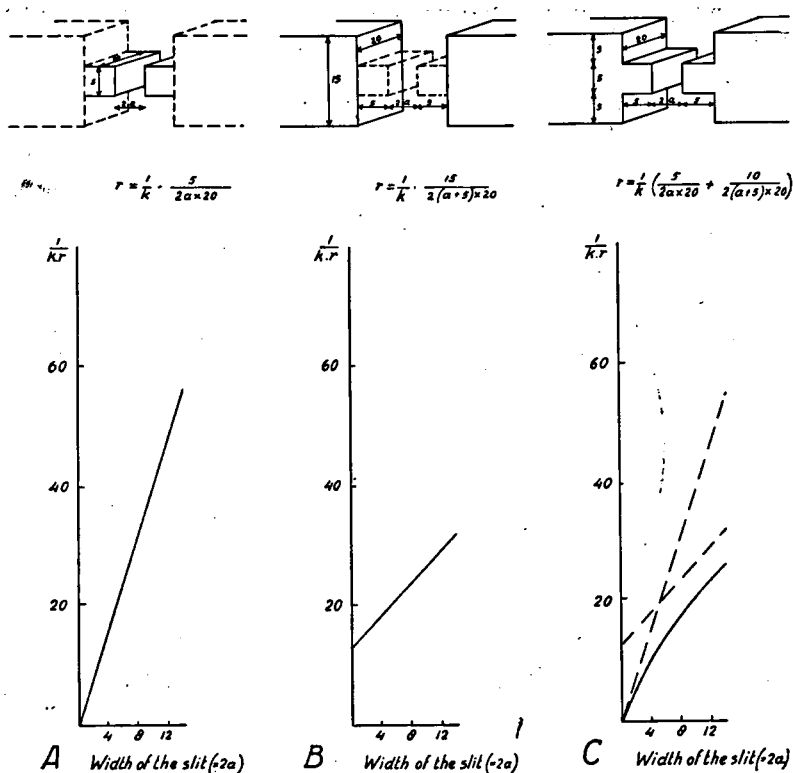


Fig. 16. Scheme of the influence of the configuration of the stomatal pore on the relation between stomatal transpiration and aperture in wind. A. Slit of small depth. B. Slit of great depth. C. Combination of A and B.

increase very rapidly with increasing width resulting in a steep diffusion curve. The corresponding diffusion curve for a deep slit (fig. 16B) will be much less steep. If we now take a combination of the two in such a way that the shallow part projects inward from the deeper part (fig. 16C) the following effect will be obtained. If the slit is nearly closed, it is the shallow part which has the greater resistance of the two and therefore determines the steepness of the diffusion curve. The wider the slit opens the more the curve tends to become parallel to that of the deeper part.

The same reasoning explains why even at microscopically "closed" stomata still a relatively large transpiration ("substomatal transpiration", cf STÅLFELT 1932) can occur.

The question still remained whether the experimental data could be explained quantitatively by means of the principles outlined in the introduction. To decide this point all diffusion resistances had to be calculated as exactly as possible in their relation to the stomatal aperture, viz: —

1. The resistance in the substomatal cavity* which was represented by a spherical space; for mathematical reasons the lower part of the stoma was included in this calculation (fig. 17).

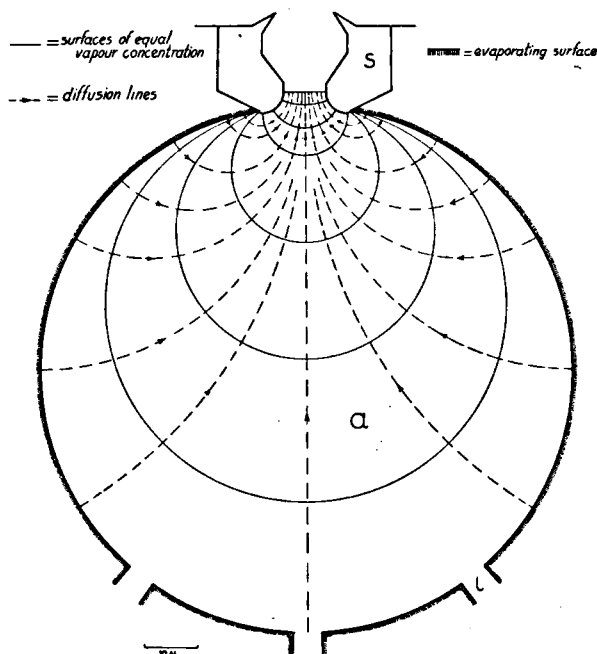


Fig. 17. Schematic representation of the substomatal cavity (a = substomatal cavity, s = stomatal guard cell, i = intercellular space)

* For the sake of simplicity we left out of account this resistance in the introduction and supposed the water vapour concentration in these cavities to be saturated.

2. The resistance in the remaining part of the stoma (fig. 18); as in calculation 1 the actual shape of the stomata was taken into account as much as possible.

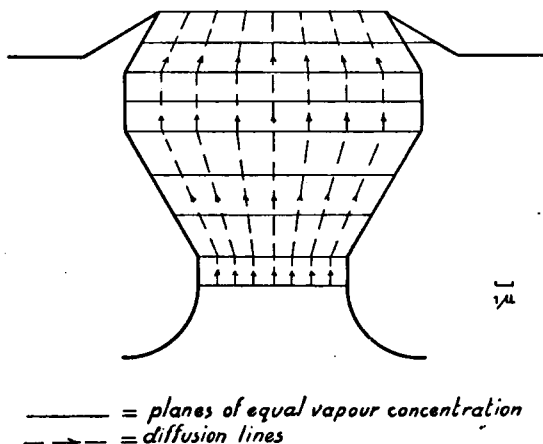


Fig. 18. Schematical representation of the stomatal pore.

3. The resistance in the micro vapour cups over the stomata making allowance for their limited size (fig. 19).

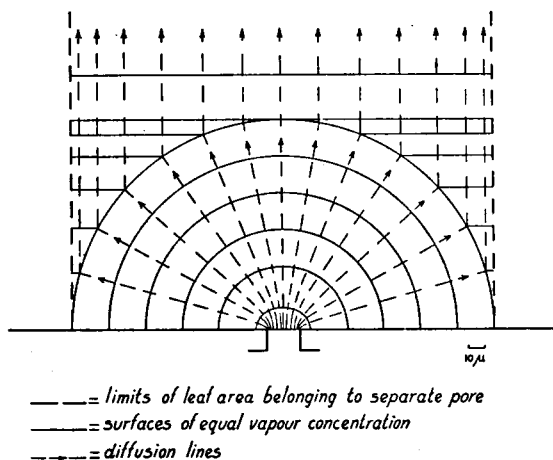


Fig. 19. Schematical representation of a micro vapour cup of limited size.

The corresponding calculations may be found in the Appendix (parts I, II and III).

As mentioned in the introduction the fourth resistance, that of the macro vapour cup, was determined empirically. It appeared to be equivalent to that of a still air layer of a thickness of 0.55 cm.

Fig. 20 shows the relation between these four resistances (calculated

for 1 cm² leaf area with a mean of 1625 stomata) and the stomatal aperture. It is clear that the resistances 1 and 2 which both include the narrowest part of the stoma approach infinity at complete stomatal closure. This is not the case for the third resistance (micro vapour cups) as this begins at the outer part of the stoma which is never completely closed.

In still air the total diffusion resistance was obtained by addition of all four, in wind we assumed (cf page 266) that the two external resistances had been eliminated (fig. 20).

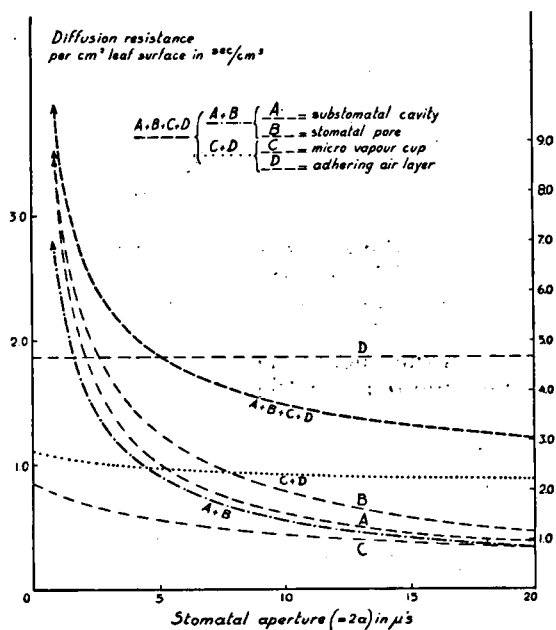


Fig. 20. Theoretical value of the separate and combined diffusion resistances in relation to the stomatal aperture. The ordinate to the left applies to the separate resistances, the ordinate to the right to the combined ones.

Knowledge of the total resistance enables us to calculate the corresponding transpiration rate. This is done by dividing this resistance into the concentration difference $c-c'$ for 1 % saturation deficit.

The curves in figs 13 and 14 are not free-hand curves drawn through the scatter diagrams, but the theoretical curves calculated in the manner described. The agreement between theory and experiment is very good, even though the theoretical curves are somewhat too low. The cause of this discrepancy may be found either in the inevitable errors in making approximations for the shape of the diffusion system or in the choice of the value of the diffusion constant of water vapour in air. According to STEFAN (cf BROWN and ESCOMBE 1900) the theoretical value of this constant at 0° C. is 0.229, yielding 0.269 for its value at 23° C (see formula page 272), but the values determined

experimentally deviate from it in both directions. We took SUMMER-HAYE's (LANDOLT-BÖRNSTEIN 1935) experimental value of 0.282 at 16.1° C from which a value of 0.296 at 23° C was derived. As STEFAN's theoretical value applies only to completely still air which will hardly ever exist the choice of a somewhat higher experimental value may be justified.

IV. DISCUSSION

The experimental results lead us to the conclusion that in our case stomatal transpiration could be explained quantitatively as an evaporation of water in air through a variable system of successive diffusion resistances. Consequently, under the experimental conditions described, for all apertures, up to the widest encountered, the stomata were the only physiological factor controlling transpiration.

From this it follows that no measurable resistance against water loss was found apart from that in the gaseous phase and that there was no evidence of any influence of incipient drying of cell walls.

This does not prove that incipient drying will never be of any importance. One might argue that in our experiments the time of transpiration was too short to bring about this phenomenon. It is a pity that the experiments of STÅLFELT (1932*a* and *b*) in which the time of transpiration was much longer do not allow an exact theoretical analysis because of lack of data about the temperature of the leaves and evaporimeters.

STÅLFELT himself (1932*a*), however, collected evidence against such an incipient drying by proving that the rate of transpiration was largely independent of the leaf water content. This result was confirmed by GREGORY and co-workers (1950).

Meanwhile, we do not set a great value upon this argument. The D.P.D. values of the leaf cells, even at a water loss of 39 % (STÅLFELT), are not very low in comparison with those of the air (SHULL 1939, cf page 272). It is quite imaginable that incipient drying phenomena, if at all present, only occur at high transpiration rates, when a sufficient D.P.D. gradient through the cell walls lining the intercellular spaces occurs. Therefore, in our view much stronger evidence against an incipient drying of mesophyl cell walls, not mentioned by STÅLFELT, is provided by his statement that the relative transpiration rate at given stomatal aperture is completely independent of the actual evaporation rate which varied in his experiments from 110 to 1000 mg per hour and per 25 cm².

Altogether relating our results to those of others we consider the evidence for an incipient drying regulation of stomatal transpiration rather scarce. Yet we do not deny its theoretical possibility, the more so as it has become probable that all mesophyl cell walls are clothed with a submicroscopic cuticle like layer (FREY-WYSSLING and ELSA HAUSERMANN 1941, cf LEWIS 1948). We are aware that this fact renders the theoretical arguments against incipient drying of RENNER (1915) and VAN DEN HONERT (1948) less conclusive because in them

the supposition prevails that the walls of intercellular spaces are structurally identical with the walls between cells.

Finally it may be stressed that both STÅLFELT and we used hygromorphous test plants, so our conclusion may hold for this ecological type only and not for the meso- or xeromorphous type. This problem must be solved experimentally.

To conclude we may say that there is not sufficient evidence to throw serious doubt on the theory of stomatal control of transpiration.

SUMMARY

The old question, whether the stomata are the only mechanism by which the plants can regulate their transpiration rate or whether other physiological factors beside the stomata play a regulating role, was subjected to an experimental study.

To this purpose experimental transpiration rates in still air as well as in wind were compared to those to be expected theoretically at the same stomatal aperture, if the stomata really are the only factor regulating transpiration. The former were determined by weighing leaf discs of the test plant — *Zebrina pendula* — before and after a short time of transpiration, the latter by calculating in simplified models the successive resistances to water vapour diffusion in the leaf in their relation to the stomatal aperture. The external resistance only, which exists in still air and which is hardly amenable to an exact theoretical analysis, was derived from comparable evaporation experiments. Stomatal apertures were determined by direct measurement under the microscope.

On comparison there appeared to be a close agreement between the experimental and theoretical values.

To test the applicability of the principles used in the calculation an analysis along the same lines of thought was made of the experiments on evaporation through multiperforate septa by SIERP and SEYBOLD (1929) and by HUBER (1930). The agreement with their experimental results was satisfactory.

The conclusion was drawn that under the conditions of the experiments the stomata, up to their maximal aperture, were the only physiological factor controlling transpiration.

APPENDIX

I. CALCULATION OF THE DIFFUSION RESISTANCE IN THE SUBSTOMATAL CAVITY

This calculation will be based on the evaluation of the diffusion resistance in a body which is formed by allowing the thick-lined part of fig. 21 to rotate on its axis of symmetry GF. Only the concave part of the inner wall of this body (indicated by shading) is supposed to

be evaporating. Between the convex bodies it is open at the upper side.

In this body the surfaces of equal vapour concentration are supposed to be parts of spherical surfaces the centres of which lie on the axis of rotation GF and which all pass through the circle drawn by the

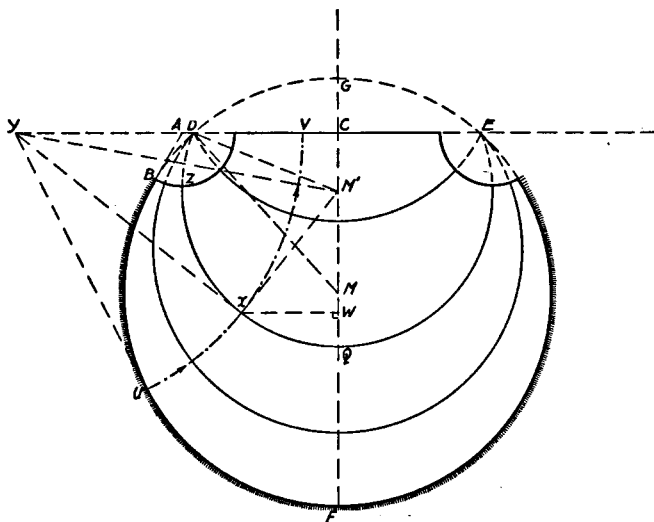


Fig. 21

rotation of point D (E). The corresponding diffusion lines may be constructed as shown in the figure. Their perpendicular relation to the surfaces of equal vapour concentration is apparent from the equality

$$YU^2 = YX^2 = YD \times YE.$$

We are aware that these surfaces do not satisfy the Laplace equation, but they are supposed to be a sufficiently close approximation to the actual conditions (see page 283).

For the sake of brevity we will use the following symbols:—

$AB = a$	$\text{arc } DF = b$	$M'X = s(v)$
$AC = p$	$XY = u$	$XW = w(u, v)$
$DC = q$	$YC = y(u)$	$\text{arc } XV = x(u, v)$
$MF = MD = r$	$M'C = v \text{ or } -v \text{ (according to the situation of } M' \text{ on this side or on the other side of } C)$	$\text{arc } XZ = z(u, v)$

As in this case the surfaces of equal vapour concentration are not flat we must use the following expression of Fick's law

$$i = k \cdot \partial c / \partial x,$$

wherein i = quantity of matter diffusing through unit of area of a surface of equal vapour concentration in unit of time.

This expression is applicable to any point in the body of rotation. We will apply it to point X of an arbitrary surface of equal vapour concentration.

Choosing u and v as independent variables in our calculation we get (on the above assumption)

$$(1) \quad i = k \cdot \frac{\partial c}{\partial x} = k \cdot \frac{dc}{dv} \cdot \frac{\partial v}{\partial x}.$$

Now we have

$$x = u \cdot \text{angle VYX (in radians)}$$

and

$$\sin \text{VYX} = \sin (\text{VYM}' + \text{M}'\text{YX}) = \frac{uv + ys}{u^2 + s^2} = S \text{ (say),}$$

whence

$$x = u \cdot \sin^{-1} S \quad (\text{if angle VYX} < \pi/2)$$

or

$$= u (\pi - \sin^{-1} S) \quad (\text{if angle VYX} > \pi/2).$$

We are now able to compute how x changes in relation to v , as

$$\frac{\partial x}{\partial v} = \frac{\partial x}{\partial S} \cdot \frac{\partial S}{\partial v} = \frac{u}{\sqrt{1-S^2}} \cdot \frac{\partial S}{\partial v} \quad (\text{if angle VYX} < \pi/2)$$

$$\text{or} = \frac{-u}{\sqrt{1-S^2}} \cdot \frac{\partial S}{\partial v} \quad (\text{if angle VYX} > \pi/2)$$

$$= \frac{u}{s} \cdot \frac{(u^2 - s^2)(us + yv) + 2usq^2}{(u^2 + s^2)(uy - vs)} \quad (\text{in either case})$$

$$= \frac{u}{s} \cdot T \quad (\text{say}).$$

Substitution in equation (1) yields

$$(1a) \quad i = k \cdot \frac{s}{u} \cdot \frac{1}{T} \cdot \frac{dc}{dv}.$$

If now we introduce the quantity J = quantity of matter diffusing through a surface of equal vapour concentration in unit of time, we have

$$(2) \quad J = \int i \cdot dO = k \cdot \int \frac{s}{u} \cdot \frac{1}{T} \cdot \frac{dc}{dv} \cdot dO.$$

In this expression dO represents the area described by the element of area in the point X when rotating on the axis of symmetry GF. In this rotation the point X describes a circle with radius w (u, v).

We can compute dO as a function of u and v in the following way. We have

$$dO = dz \cdot 2\pi w = dz \cdot 2\pi s \cdot \sin \text{VYX} = dz \cdot 2\pi s \cdot \frac{uv + ys}{u^2 + s^2}.$$

As the quantity O is considered to be defined on the surfaces on which v is constant, the changes of z in relation to u only are of interest. Since

$$z = \text{arc } ZQ - \text{arc } XQ = \text{arc } ZQ - s \cdot \text{angle } VYX,$$

z changes in relation to u according

$$\frac{\partial z}{\partial u} = \partial \left(-s \cdot \sin^{-1} \frac{uv+ys}{u^2+s^2} \right) / \partial u \quad (\text{if angle } VYX < \pi/2)$$

$$\text{or} = \partial \left(-\pi s + s \cdot \sin^{-1} \frac{uv+ys}{u^2+s^2} \right) / \partial u \quad (\text{if angle } VYX > \pi/2)$$

$$= \partial (\pm s \cdot \sin^{-1} S) / \partial u$$

$$= \frac{\partial z}{\partial S} \cdot \frac{\partial S}{\partial u} = \frac{\pm s}{\sqrt{1-S^2}} \cdot \frac{\partial S}{\partial u}$$

$$= \frac{s}{y} \cdot \frac{(u^2-s^2)(us+yv)+2usq^2}{(u^2+s^2)(uy-vs)} \quad (\text{in either case})$$

$$= \frac{s}{y} \cdot T.$$

Consequently

$$dO = T \cdot \frac{s}{y} \cdot 2\pi s \cdot \frac{uv+ys}{u^2+s^2} \cdot du.$$

Substitution in equation (2) yields

$$\begin{aligned} J &= k \cdot \int \frac{s}{u} \cdot \frac{1}{T} \cdot \frac{dc}{dv} \cdot T \cdot \frac{s}{y} \cdot 2\pi s \cdot \frac{uv+ys}{u^2+s^2} \cdot du \\ (2a) \quad &= 2\pi k \cdot \int \frac{s^3}{uy} \cdot \frac{uv+ys}{u^2+s^2} \cdot \frac{dc}{dv} \cdot du. \end{aligned}$$

Denoting

$$\frac{s^3}{uy} \cdot \frac{uv+ys}{u^2+s^2}$$

by $f(u,v)$ for convenience' sake this expression runs

$$(2b) \quad J = 2\pi k \cdot \int f(u,v) \cdot dc/dv \cdot du.$$

It can be demonstrated* that if the spherical surfaces considered should be such that one function c exists depending on v only and satisfying the Laplace equation, then $f(u,v)$ can be written as $m(u)/n(v)$ and c satisfies the equation

$$dc/dv = \kappa \cdot n(v).$$

In this case equation (2b) passes into

$$\begin{aligned} J &= 2\pi k \cdot \int \frac{m(u)}{n(v)} \cdot \kappa \cdot n(v) \cdot du \\ &= 2\pi k \cdot \kappa \cdot \int m(u) \cdot du, \end{aligned}$$

whereas

$$(c-c') = \kappa \cdot \int n(v) \cdot dv.$$

* The author owes the arguments printed in small type to Dr H. R. VAN DER VAART who was kind enough to test the relationship between our surfaces and the Laplace equation.

So

$$(3) \quad \frac{c-c'}{J} = R = \frac{\int n(v) \cdot dv}{2\pi k \cdot \int m(u) \cdot du}.$$

However this condition is not complied with. Accordingly the function $f(u,v)$ can not be split up into a function of u and a function of v . So the method used in the following is not correct from a mathematical point of view, but approximate. If the condition described is satisfied, equation (3a) resulting from this method (see below) reduces to equation (3), as one can easily see by replacing $f(u,v)$ in (3a) by $m(u)/n(v)$.

Differentiating (2b) with respect to u we find

$$\frac{dJ}{du} = 2\pi k \cdot f(u,v) \cdot \frac{dc}{dv}$$

or

$$\frac{dc}{dv} = \frac{1}{2\pi k} \cdot \frac{1}{f(u,v)} \cdot \frac{dJ}{du}.$$

Acting as if dJ/du did not depend on v we find on integration

$$c-c' = \frac{1}{2\pi k} \cdot \frac{dJ}{du} \cdot \int_{-\infty}^{\sqrt{r^2-a^2}} \frac{dv}{f(u,v)},$$

whence

$$\frac{dJ}{du} = 2\pi k \cdot \frac{c-c'}{\int_{-\infty}^{\sqrt{r^2-a^2}} \frac{dv}{f(u,v)}}.$$

If $c-c'$ were independent of u it would follow that

$$J = 2\pi k \cdot (c-c') \cdot \int_a^{+\infty} \frac{du}{\sqrt{r^2-a^2} \int_{-\infty}^{\sqrt{r^2-a^2}} \frac{dv}{f(u,v)}}$$

and that

$$(3a) \quad R = \frac{c-c'}{J} = \frac{(2\pi k)^{-1}}{\int_a^{+\infty} \frac{du}{\sqrt{r^2-a^2} \int_{-\infty}^{\sqrt{r^2-a^2}} \frac{dv}{f(u,v)}}}.$$

Now we use this expression as an approximation to R supposing that $f(u,v)$ can be approximated closely enough by a quotient $m(u)/n(v)$.

As

$$\int_{-\infty}^{\sqrt{r^2-a^2}} \frac{uy}{s^2} \cdot \frac{u^2+s^2}{uv+ys} \cdot dv = \frac{uy^2 \cdot \text{angle FMD}}{q^3} + \frac{u^2y}{sq^2}$$

Computation of the diffusion resistance in these systems proceeds as follows.

System I

The appropriate formula for this system is (5) because v varies between finite values (from MH to NH). Thus we have

$$R_I = \frac{\text{angle MBN}}{2\pi k \cdot BH \cdot \log_e \frac{BM \cdot BN \cdot \text{angle MBN} \cdot CH + (BN - BM) \cdot BH \cdot AC}{BM \cdot BN \cdot \text{angle MBN} \cdot AC + (BN - BM) \cdot BH \cdot AC}}$$

Let d be the radius of a circle the area of which equals the area of the stomatal slit in the narrowest part ($\pi d^2 = \pi \cdot \text{half long axis} \cdot \text{half short axis of the ellipse}$), then we have

$$BM = 50, BN = EN = CH = d + 4, AC = \frac{50}{\sqrt{50^2 - (d + 4)^2}},$$

$$BH = \sqrt{(d + 4)^2 - AC^2} \quad (\text{as } HN = CE = AC)$$

$$\text{and} \quad \text{angle MBN} = \text{angle (MBH - HBN)} = \sin^{-1} z,$$

$$\text{wherein} \quad z = \frac{BH(\sqrt{50^2 - BH^2} - HN)}{50(d + 4)}.$$

As d is the only variable in each expression R_I can be computed for various stomatal apertures.

System II

The appropriate formula for this system is (4) because v varies from NK to $-\infty$. Thus we have

$$R_{II} = \frac{\text{angle LNT}}{2\pi k \cdot LK \cdot \log_e \frac{GK \cdot \text{arc LT} + GE \cdot LK}{GE \cdot \text{arc LT} + GE \cdot LK}}$$

Expressing again the various quantities in this equation as functions of d we get

$$LK = \sqrt{d^2 + 8d}, GK = d + 4, \text{arc LT} = (d + 4) \cdot \text{angle LNT}$$

$$\text{and} \quad \text{angle LNT} = \cos^{-1} \frac{-4}{d + 4}.$$

So R_{II} can be calculated as a function of d .

Addition of R_I and R_{II} yields the total resistance of the substomatal cavity (including the lowest part of the stoma) and hence this resistance can be calculated for various stomatal apertures (see fig. 20).

II. CALCULATION OF THE DIFFUSION RESISTANCE IN THE STOMA

The schematic representation of the stomatal slit which we used in this calculation is shown in fig. 23. Four systems can be distinguished

indicated in the figure as III, IV, V and VI, the undermost part of the slit having been included in the substomatal cavity. The measurements approximate as closely as possible to the actual values.

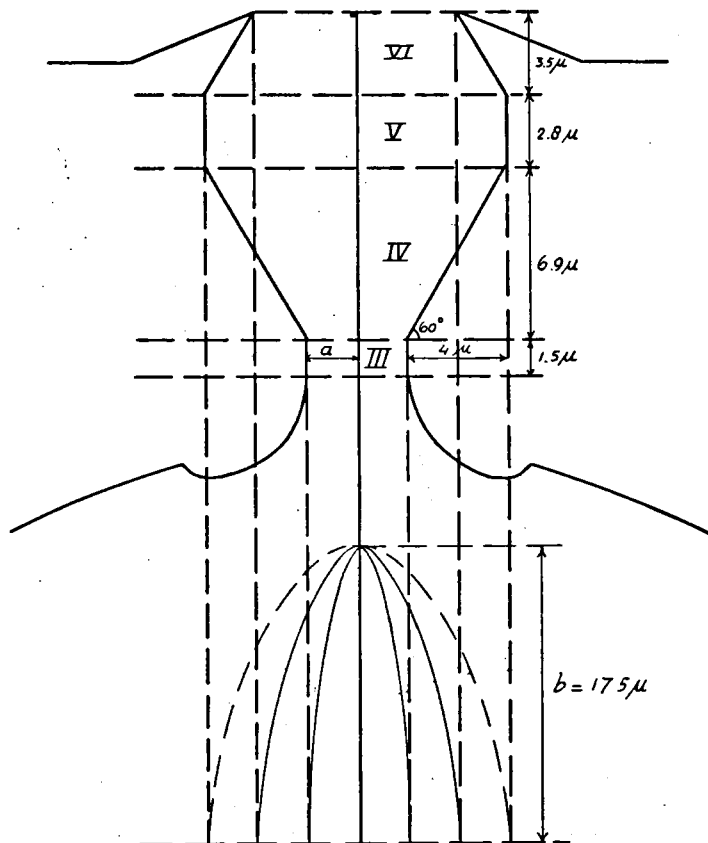


Fig. 23

System III

Here we have

$$R_{III} = \frac{1}{k} \cdot \frac{h_3}{\pi a b} = \frac{1}{k} \cdot \frac{1.5}{3.14 \times 17.5 \times a}.$$

System IV

In estimating the resistance in this system (fig. 24) we may proceed in the following way.

As an approximation let us suppose that c depends on h only (h represents the length of the perpendicular to the basal plane) and so the surfaces of equal vapour concentration to be flat and perpendicular to the axis of the stomatal slit, then we can write

$$i = -k \cdot \pi a b \cdot dc/dh$$

or

$$dc = \frac{-i}{k \cdot \pi b} \cdot \frac{dh}{a_h} = \frac{-i}{k \cdot \pi b} \cdot \frac{dh}{a + h \cdot \cot \alpha}.$$

Integration of c with respect to h (h varying from 0 to $(a' - a) \cdot \tan \alpha$) yields

$$\begin{aligned} c - c' &= \frac{-i}{k \cdot \pi b} \int_{(a' - a) \cdot \tan \alpha}^0 \frac{dh}{a + h \cdot \cot \alpha} \\ &= \frac{i \cdot \log_e(a'/a)}{k \cdot \pi b \cdot \cot \alpha}. \end{aligned}$$

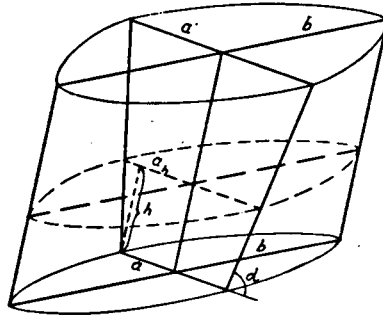


Fig. 24

Thus the diffusion resistance in this system amounts to

$$R_{IV} = \frac{\log_e(a'/a)}{k \cdot \pi b \cdot \cot \alpha} = \frac{\log_e(a+4)/a}{k \times 3.14 \times 17.5 \times 0.58}.$$

Some loss of accuracy results from the use of the approximation for the shape of the surfaces of equal vapour concentration. The extent of this depends on the size of angle α and as in this case its minimal value is 60° deviations will not be large.

System V

Here we have

$$R_V = \frac{1}{k} \cdot \frac{h_s}{\pi(a+4)b} = \frac{1}{k} \cdot \frac{2.8}{3.14 \times 17.5 \times (a+4)}.$$

System VI

Applying to this system the same formula as was developed for system IV we find

$$R_{VI} = \frac{\log_e(a'/a'')}{k \cdot \pi b \cdot \cot \alpha} = \frac{\log_e(a+4)/(a+2)}{k \times 3.14 \times 17.5 \times 0.58}.$$

The algebraical sum of these four resistances gives the total resistance in the stoma for a given value of a (see fig. 20).

III. CALCULATION OF THE DIFFUSION RESISTANCE WITHIN A VAPOUR SHELL OF LIMITED SIZE

The shape of the surfaces of equal vapour concentration extending over a perforated septum will be very complicated from a mathematical point of view. As an approximation we used the schematical representation shown in fig. 19.

The formula of BROWN and ESCOMBE for the resistance of a vapour shell (cf page 258) must be adapted to meet the special case where the size is limited. The following method may be used.

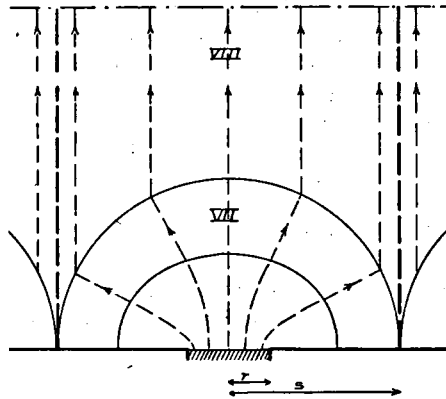


Fig. 25

Surfaces of equal vapour concentration (fig. 25) at a distance of say $5r$ from the evaporating surface (r = radius of this surface) may be regarded as spherical which implies the equality of the vapour concentration gradient at all points of these surfaces. Thus we have

$$i = -k \cdot O \cdot dc/ds = -k \cdot 2\pi s^2 \cdot dc/ds$$

(s = radius of the surface considered).

Integration of c with respect to s (s varying from s' to $+\infty$) gives the fall in vapour concentration and thus the resistance between this surface and the surface at infinity

$$c = \frac{-i}{k \cdot 2\pi} \int_{+\infty}^{s'} \frac{ds}{s^2} = \frac{1}{k} \cdot \frac{i}{2\pi s'}$$

therefore

$$R' = \frac{1}{k} \cdot \frac{1}{2\pi s'}$$

Reducing the resistance in the vapour shell of unlimited size by this amount we get the resistance in the shell of limited size (system VII)

$$R_{VII} = \frac{1}{k} \cdot \left(\frac{1}{4r} - \frac{1}{2\pi s'} \right)$$

The actual value of s' depends on N = number of pores (stomata) per cm^2 according

$$\pi s'^2 = 1/N$$

and the quantity r is related to a by the equation

$$\pi r^2 = \pi(a+2)b = 3.14 \times 17.5 \times (a+2),$$

r being the radius of a circle the area of which equals the area of the stomatal opening at the end of the slit.

Here the supposition prevailed that the formula for the vapour shell resistance over a circular evaporating surface equally holds for an elliptical surface of the same area. According to STEFAN (1881) deviations will not be large as long as the eccentricity of the ellipse is small. At narrow stomatal slits this requirement is not complied with, but in this case the resistance in the shells is only a small fraction of the total resistance, so the inaccuracy introduced will be negligible.

Further it might be questioned whether the thickness of the still air layer (system VIII) should not be reduced by $2/3$ of the height (s') of the vapour shells. In our experiments, however, this correction could be omitted on account of its smallness ($\pm 2.5\%$).

The value of the resistance in the micro vapour cups at various stomatal apertures is given in fig. 20.

IV. THEORETICAL ANALYSIS OF THE EXPERIMENTS ON MODELS BY SIERP AND SEYBOLD (1929)

In the experiments which they made on the evaporation through multiperforate septa SIERP & SEYBOLD used brass boxes covered by perforated thin brass sheets. The diameter of these boxes amounted to 45 mm, their height to 21 mm and the thickness of the brass sheets to 20μ . These sheets had a perforated area of 20×20 mm. The total area of the pores was constant (3.14 mm^2), but the radius of the pores varied from 1000μ to 5μ (boxes I—V). Another box (Q_4) had a cover without pores, but with a square opening of 20×20 mm.

These boxes were filled with water up to 7 mm below the cover and allowed to evaporate under a bell-glass under which P_2O_5 (at the bottom) maintained a constant gradient of vapour concentration. The evaporation power of a box was measured by its decrease in weight after a given time.

Fig. 4 shows the results obtained by the authors (drawn from table 3, page 249), the abscissa representing the diameter of the pores, the ordinate the evaporation power of the box in question in relative units. The evaporation power of the additional box Q_4 is taken as 1.0.

The authors tested the theoretical analysis of these results based on the formulae of BROWN & ESCOMBE and their interpretation was that the theoretical and the experimental data did not agree. From this they concluded that these formulae had no practical value especially for pores of stomatal size.

This conclusion appears to be unfounded. The authors took the evaporation power of the box containing the largest pores as a unit of reference and expressed the other ones in terms of it. However, the greatest deviations are to be expected from the largest pores as in this case the macro vapour cup and the micro ones can no longer be treated as separate systems. So this lack of agreement is not surprising.

How closely indeed the actual and calculated values can agree will be shown for some of their experiments.

When no filter paper was used four diffusion resistances were placed between the evaporating surface and the free (i.e. circulating) air, viz:—

1. The resistance between the evaporating surface (area = $\pi \times 2.25^2 = 16 \text{ cm}^2$) and the perforated part of the brass sheet (area = 4 cm^2).

Simplifying matters by taking an average value of $\sqrt{4 \times 16} = 8 \text{ cm}^2$ for the area of the cross section of this part we compute the following resistance

$$R_1 = \frac{1}{k} \cdot \frac{0.7}{8} = \frac{0.088}{k}.$$

2. The resistance in the pores which had the constant value of

$$R_2 = \frac{1}{k} \cdot \frac{0.002}{0.0314} = \frac{0.064}{k}.$$

3. The resistance in the micro vapour shells under and over each pore. We will leave out of account the limited size of these shells because of their relatively great mutual distance. Doing so we compute their resistance as

$$R_3 = \frac{1}{k} \cdot \frac{1}{N} \cdot \frac{1}{2r}$$

(N = total number of pores in the sheet,
 r = radius of pores).

From this formula we get the following values of this resistance for the several boxes:—

Box I ($N = 1, r = 1 \text{ mm}$)	$R_3 = k^{-1} \cdot 5$
Box II ($N = 400, r = 0.05 \text{ mm}$)	$R_3 = k^{-1} \cdot 0.25$
Box III ($N = 1600, r = 0.025 \text{ mm}$)	$R_3 = k^{-1} \cdot 0.125$
Box IV ($N = 10000, r = 0.010 \text{ mm}$)	$R_3 = k^{-1} \cdot 0.05$
Box V ($N = 40000, r = 0.005 \text{ mm}$)	$R_3 = k^{-1} \cdot 0.025$

4. The resistance in the macro vapour shell (still air layer) extending over the whole perforated area.

As conditions of still air will have been realized very closely under the bell-glass use of BROWN & ESCOMBE's formula seems to be justified

$$R_4 = \frac{1}{k} \cdot \frac{1}{4s} = \frac{1}{k} \cdot \frac{\sqrt{3.14}}{8} = \frac{0.221}{k}$$

(s = radius of circle the area of which equals the area of the perforated part of the sheet).

The diffusion resistance of the additional box Q_4 consists of the resistances R_1 and R_4 only.

Now taking the evaporation power of box Q_4 as a unit we can compute the evaporation power of the other boxes (I—V) by the formula

$$E = \frac{R_1 + R_4}{R_1 + R_2 + R_3 + R_4}.$$

Thus we find the following values

Box I	$E = 0.06^*$
Box II	$E = 0.50$
Box III	$E = 0.62$
Box IV	$E = 0.73$
Box V	$E = 0.78$

In fig. 4A these results are compared with the experimental data (taken from table 3, page 249). The agreement appears to be rather close.

Computing the ratio Q_4/IV and Q_4/V we find 1.37 and 1.28 respectively, whereas the authors record

$Q_4/IV = 1.29$ (table 3, page 249) and 1.39 (mean value from tables 5—8),

$Q_4/V = 1.32$ (table 3, page 249) and 1.20 (table 8, page 252).

Similarly calculating the ratio between the evaporation power of box Q_1 (square opening 1×1 cm) and box IVa (same number and size of pores as box IV, but on an area of 1×1 cm) we get 1.18, whereas SIERP & SEYBOLD actually found a ratio of 1.26 (table 3, page 249) and 1.20 (page 253). The theoretical values of the ratios Q_4/Q_1 and IV/IVa are somewhat lower (11 % and 22 % respectively) than the experimental ones (table 3, page 249).

When wet filter paper was attached to the lower side of the septum three resistances only are to be taken into account, viz:—

1. The resistance in the pores (R_2) which has the same value as in the first case.
2. The resistance in the micro vapour shells (R_3). As these shells are now present at the upper side of the pores only this resistance amounts to half the value it had in the first case.
3. The resistance in the macro vapour shell (R_4) having again the same value as above.

The diffusion resistance of box Q_4 now consists of resistance R_4 only.

Consequently the relative evaporation power of boxes I—V is given by the formula

$$E = \frac{R_4}{R_2 + R_3 + R_4}.$$

* Strictly speaking our formula for E is less correct for these large pores (cf page 291), so not too great a value should be set on this number.

Thus we find

Box I	$E = 0.08^*$
Box II	$E = 0.54$
Box III	$E = 0.64$
Box IV	$E = 0.71$
Box V	$E = 0.74$

In fig. 4B these results are compared again with the experimental data (taken from table 11, page 255). The agreement is very close indeed.

Comparison of the theoretical and experimental values of the ratios Q_1/IVa , Q_4/Q_1 and IV/IVa yields in this case

	theoretical value	experimental value (table 11, page 255)
Q_1/IVa	1.20	1.29
Q_4/Q_1	2.00	2.20
IV/IVa	1.71	2.08

In the main the lack of agreement between theory and experiment is considered to be much too small to justify the authors' doubt about the practical value of BROWN & ESCOMBE's principles for pores of stomatal size.

V. THEORETICAL ANALYSIS OF THE EXPERIMENTS ON MODELS BY HUBER (1930)

HUBER attacked the problem of evaporation through perforated septa by studying the influence of pore number at constant pore size on the one hand and of pore size at constant pore area on the other. For that purpose he used the following perforated metal sheets (see table I).

The evaporating surface consisted of wet filter paper attached to the lower part of the septum. Evaporation took place into the free air of a room.

TABLE I
Perforated septa used by HUBER

Pore size (= O)	Diameter of pores (= $2r$)	Number of pores (= N)	Perforated area (= P)	Relative area of pores (= A)	Thickness of septum (= d)
1 cm ²	11.3 mm	1-4-9-16-25-36-49-64	100 cm ²	0.01-0.04-0.09-0.16-0.25-0.36-0.49-0.64	0.6 mm
1 mm ²	1.13 mm	25-100-400-625-1090-1600-2500	100 cm ²	0.0025-0.01-0.04-0.0625-0.109-0.16-0.25	0.13 mm
2000 μ ²	50 μ	400-3600-6400-10000	4 cm ²	0.002-0.018-0.032-0.05	0.02 mm
80 μ ²	10 μ	2500	1 cm ²	0.002	0.02 mm

* See note on page 292.

Relative evaporation rates were determined using as a base of reference the evaporation power of a septum with a central opening of the same area as the perforated part of the septum in question.

The results are shown in fig. 6 the abscissa representing the relative pore area, the ordinate the relative evaporation power.

The question arises as to whether these results can be explained quantitatively on the principle of consecutive resistances.

Three diffusion resistances are to be taken into account, viz:—

1. The resistance in the pores amounting to

$$R_1 = \frac{1}{k} \cdot \frac{d}{N \cdot O}.$$

2. The resistance in the micro vapour shells. Using the formula for shells of limited size we get

$$\begin{aligned} R_2 &= \frac{1}{k} \cdot \frac{1}{N} \left(\frac{1}{4r} - \frac{1}{2\pi s} \right) = \frac{1}{k} \cdot \frac{1}{N} \left(\frac{1}{4r} - \frac{1}{2\pi \sqrt{P/\pi N}} \right) \\ &= \frac{1}{k} \cdot \frac{1}{N} \left(\frac{1}{4r} - \frac{\sqrt{A}}{2\pi r} \right). \end{aligned}$$

3. The resistance in the macro vapour shell (still air layer) extending over the whole perforated area. As in the free air of a room conditions of still air will not be realized sufficiently to justify the use of BROWN & ESCOMBE's formula we must write

$$R_3 = \frac{1}{k} \cdot \frac{a}{P}$$

(a = thickness of hypothetical still air layer).

Thus the total resistance is computed as

$$\begin{aligned} R_t &= R_1 + R_2 + R_3 \\ &= \frac{1}{k} \cdot \left(\frac{d}{N \cdot O} + \frac{1}{4r \cdot N} - \frac{\sqrt{A}}{2\pi r \cdot N} + \frac{a}{P} \right) \\ &= \frac{1}{k} \cdot \left(\frac{d}{A \cdot P} + \frac{\pi r}{4A \cdot P} - \frac{r\sqrt{A}}{2A \cdot P} + \frac{a \cdot A}{A \cdot P} \right) \\ &= \frac{1}{k} \cdot \frac{1}{4A \cdot P} (4d + \pi r - 2r\sqrt{A} + 4a \cdot A). \end{aligned}$$

Leaving out of account the thickness of the septum we compute the resistance of the reference septa as

$$R_r = \frac{1}{k} \cdot \frac{a}{P}.$$

So the relative evaporation rates are given by the formula

$$\begin{aligned} E_{\text{rel}} &= \frac{a/P}{(4d + \pi r - 2r\sqrt{A} + 4a \cdot A)/4A \cdot P} \\ &= \frac{4a \cdot A}{4d + \pi r - 2r\sqrt{A} + 4a \cdot A}. \end{aligned}$$

All quantities in this formula are known with the exception of a . The drawback is that this quantity a can be computed only from the experimental data themselves. However, the result of this computation can be made plausible on grounds to be discussed.

The experimental relative evaporation rates of the sheets indicated in italics of table I were substituted in the formula for E_{rel} to calculate a . Thus we found $a = 1$ cm for the sheet with a perforated area of 100 cm^2 ($O = 1 \text{ mm}^2$) and $a = 0.3$ cm for the sheet with a perforated area of 4 cm^2 ($O = 2000 \mu^2$).

The resistances in the adhering air layer then become $0.01/k$ ($1 \text{ mm}^2\text{-septum}$) and $0.075/k$ ($2000 \mu^2\text{-septum}$). According to STEFAN's diameter law in perfectly still air the ratio between these resistances would be 1 to 5, whereas in strong wind their ratio would approach to 1 to 25, so it may be seen that the ratio 1 to 7.5 is not unlikely for the prevailing conditions.

The relative evaporation power of the $1 \text{ mm}^2\text{—}$ and $2000 \mu^2\text{—}$ septa at varying pore number and consequently varying pore area as calculated with the aid of the mentioned values of a have been plotted graphically in fig. 6 (dotted lines). Because our formula is not valid for the largest pores as in this case the macro vapour shell and the micro ones can no longer be treated as separate systems, the $1 \text{ cm}^2\text{-septum}$ were not included in the calculation.

There appears to be a very close agreement between the shape of the theoretical and experimental curves, though there are some numerical differences.

The large value (0.6) HUBER found for the relative evaporation rate of the $10 \mu\text{-septum}$ can not be accounted for unless we assume the adhering air layer to be of an unplausible thickness. Possibly interfering effects (capillary attraction of water by the pores?) are responsible for the discrepancy.

VI. CALCULATION OF THE CORRECTION FOR THE NUMBER OF STOMATA PER cm^2

In still air only a fraction of the total diffusion resistance is inversely proportional to the number of stomata per cm^2 , viz the sum of the resistances of the substomatal cavity, of the stomata and of the micro vapour shells.

Putting this sum (computed for $N = 1625$ = the average number of stomata per cm^2 in our experiments and for a given stomatal aperture) = R_s and putting the resistance in the still air layer per $\text{cm}^2 = R_e$ we have

$$R_t = R_s + R_e$$

wherein R_t = total resistance per cm^2 for $N = 1625$ and for the aperture concerned.

For a leaf with N' stomata per cm^2 the total resistance per cm^2 for the same stomatal aperture becomes

$$R'_t = (1625/N') \cdot R_s + R_e$$

Consequently

$$\frac{R'_t}{R_t} = \frac{(1625/N') \cdot R_v + R_c}{R_t} = \frac{T}{T'},$$

wherein T = transpiration rate reduced to $N = 1625$ and T' = empirical transpiration rate for N' stomata per cm^2 .

Thus

$$T = T' \cdot \frac{(1625/N') \cdot R_v + R_c}{R_t}.$$

The value of R_v , R_c and R_t can be read from fig. 20 for any stomatal aperture, so T can be computed.

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