

**MEDEDELINGEN LANDBOUWHOGESCHOOL  
WAGENINGEN • NEDERLAND • 72-3 (1972)**

**LEAF DIFFUSION RESISTANCE TO WATER  
VAPOUR AND ITS DIRECT MEASUREMENT**

**I. INTRODUCTION AND REVIEW  
CONCERNING RELEVANT FACTORS AND METHODS**

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*(Received 20-X-1971)*

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391-3

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# 1. INTRODUCTION

## 1.1. GENERAL REMARKS

During recent years the interest in the diffusion of water vapour from leaves in a canopy has increased. For example the definite influence of the leaf diffusion resistance on canopy evaporation forms a point of controversy. LEE (1967, 1968a, 1968b) thinks that a crop may not be seen as a passive wick. IDSO (1968) and VAN BAVEL (1968) have opposed this opinion for well watered crops. In favour of LEE's standpoint GARDNER (1970) recently stated that stomatal resistance would seem to be the single most useful measurement for evaluation of the water factor in agroclimatology. The controversy may be removed only by studying simultaneously evaporation from a complete canopy and stomatal behaviour within the canopy.

The study of the canopy climate may be helpful as an intermediary for these and other problems, such as those related to plant diseases control and growth studies. Therefore plantphysiologists, entomologists, phytopathologists and ecologists are also interested in a more quantitative knowledge of stand climate (Comp. WADSWORTH, 1968).

The qualitative influence of leaf diffusion resistance on the aerial microclimate of crop canopies and forest stands is now well documented (e.g. PHILIP, 1964; WAGGONER and REIFSNYDER, 1968; WAGGONER et al., 1969). For a fuller quantitative approach more experiments are needed. This article is intended to review literature and to discuss problems and methods which are of relevance to this experimental approach.

## 1.2. THE CLIMATE OF PLANT STANDS

In the very last chapter of one of his personal contributions to an old and well known handbook of climatology, GEIGER (1930) mentioned already the main influences plants exert on the climate near the earth surface. The physical properties and the shape of a canopy surface are highly different from those of the bare soil. Moreover the exchange ratios are influenced by the presence of the plants. Finally within the plant cover a special aerial microclimate is formed. However, in the twenty years following this publication only few investigations were made on the microclimate of crop stands, some more in forest stands (GEIGER, 1950). Although in the United States some topics in micro-meteorology were relatively late discovered to be of interest (SCHILLING et al., 1946), in relation to agriculture important work was done quite early. This however included mainly studies on frost protection, wind protection, the influences of soil mulches and some evaporation studies, and no special studies of stand climate (Comp. WANG and BARGER, 1962). Interesting measurements of climatic

factors within canopies were made in India already in 1932 (RAMDAS, 1962) and reviewed by RAMDAS (1946, 1951) and GADRE (1951).

Much more investigations within the plant cover are reported from the period 1950–1960 (e.g. PENMAN and LONG, 1960; GEIGER, 1961; VAN WIJK and DE WILDE, 1962; TANNER 1963b). It was stated in the review by VAN WIJK and DE WILDE, covering literature up to 1960 included, that in the course of this period more emphasis was given to a physical approach. In stead of the rather descriptive nature of the foregoing investigations one now used for example heat balances, water balances and the physics of transport phenomena. The design and use of specific micrometeorological instrumentation was also increased.

The first attempt to a more integrated physical explanation of the genesis of crop microclimate was made, as far as the author is aware, by PENMAN and LONG (1960). They used part of their observations and experience of the preceding ten years. From 1960 onwards so many research articles, books and reviews have appeared that no attempt for a review will be made here. The situation at the moment (Comp. UNESCO, in press) is that, more than ever before, the study of the canopy microclimate is integrated in a study of what is called the soil-plant-atmosphere continuum (e.g. preliminary PHILIP, 1957; SLATYER and MCILROY, 1961; more comprehensive e.g. COWAN, 1965; PHILIP, 1966; MILLINGTON and PETERS, 1969; BERGER, 1970; DENMEAD, 1970; GARDNER, 1970; SHAWCROFT and LEMON, 1970). Consequently measurements of soil parameters, plant parameters and climatological parameters are often needed simultaneously (BEGG et al., 1964).

There is also a strong tendency towards the collection of existing knowledge and the obtaining of new data for the building of growth models (e.g. DE WIT, 1965; DE WIT and BROUWER, 1968; WAGGONER, 1969; DE WIT, BROUWER and PENNING DE VRIES, 1970). Meteorological submodels of the canopy climate are to be incorporated in these plant community models (LEMON, 1970). For this purpose, among others, attempts are made to simulate crop microclimate (e.g. PHILIP, 1964; WAGGONER and REIFSNYDER, 1968; WAGGONER et al., 1969; STEWART and LEMON, 1970; MILLER, 1970). Simulation is also hoped to be useful in the near future to help calculating the insect microclimate in an integrated approach to diseases control (e.g. PENMAN and LONG, 1960).

### 1.3. SIMULATION, STOMATA AND EXPERIMENTS

In trying to design such a micrometeorological submodel our aim was to simulate the profiles of temperature and humidity within a corn crop (DE WIT et al., internal report). Inputs of the model are firstly values of temperature and vapour pressure at the top of, or somewhere above, the canopy and at the soil surface. Secondly one needs net radiation, wind speed and turbulent diffusion coefficient(s) (for example from wind speed data at different heights) at the top of the crop, and soil heat flux. Thirdly one makes use of measurements, or

calculations based on canopy architecture, of the extinction of net radiation. Canopy wind speed data and values for turbulent diffusion coefficients within the vegetation have also to be used as an input. The model is of a kind which has been mentioned by PHILIP (1966) as a one dimensional- two parameter type. In such models it is necessary to look at the sources for heat and water vapour, which means at the energy and mass balances of leaf surfaces. The leaf diffusion resistance plays an important part in these balances.

For a test of our model we made use of reported measurements in corn canopies (e.g. BROWN and COVEY, 1966). From the first results it became apparent that small changes in the vertical canopy profile of stomatal resistance (at each height averaged over the horizontal plane) were of enormous influence on the aerial canopy climate as characterized by the profiles of temperature and humidity (Fig. 1). This is in accordance with results of other preliminary models (WAGGONER and REIFSNYDER, 1968; WAGGONER et al., 1969). Therefore we started to study the field measurements of stomatal resistance.

The problems of transport through the stomata and the leaf boundary layer in the field are far from solved (INOUE, 1970). It is therefore worthwhile, also again in relation to growth models and evaporation studies, to try to make a submodel of stomatal behaviour (PENNING DE VRIES, in press). Field data are necessary for the testing of such models. The same applies to the micro-meteorological submodels as described above, where stomatal resistance may be used either as a test or as an input. We plan to use it as an input to our model. As a choice for apparatus had to be made and an idea was to be obtained of problems we could come across, in the following parts of this article factors and methods are reviewed which are of importance to the set up, performance, and interpretation of such measurements.

At first a few summarizing remarks on stomatal behaviour are made and after that the vapour concentration at the liquid surface and the partitioning of leaf internal diffusion resistance to water vapour over different parts of the stomata are discussed. Further some other factors of possible influence on diffusion will be dealt with. These are the resistance of the boundary layer adhering to the leaf, the diffusion coefficient to be used, the temperature and its differences within a leaf. Finally apparatus is reviewed for measuring stomatal resistance directly in the field, with emphasis on the WALLIHAN leaf diffusion resistance meter, its use and modifications. Our modification of this instrument will be described in a following paper.

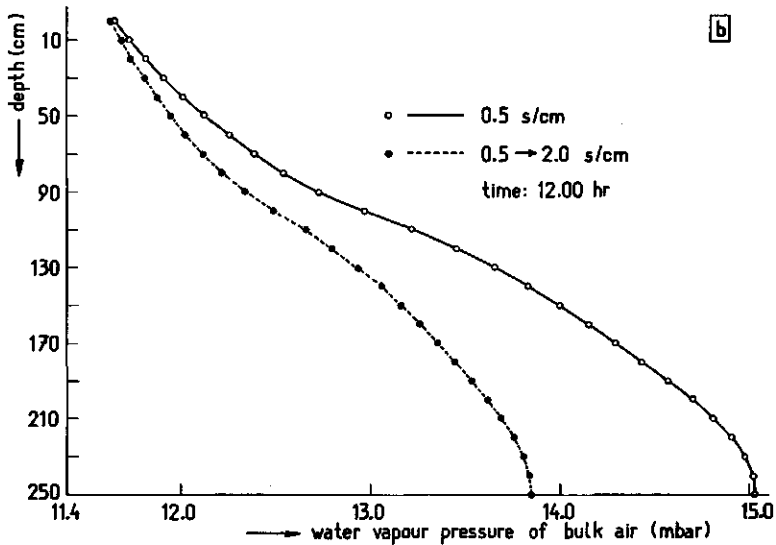
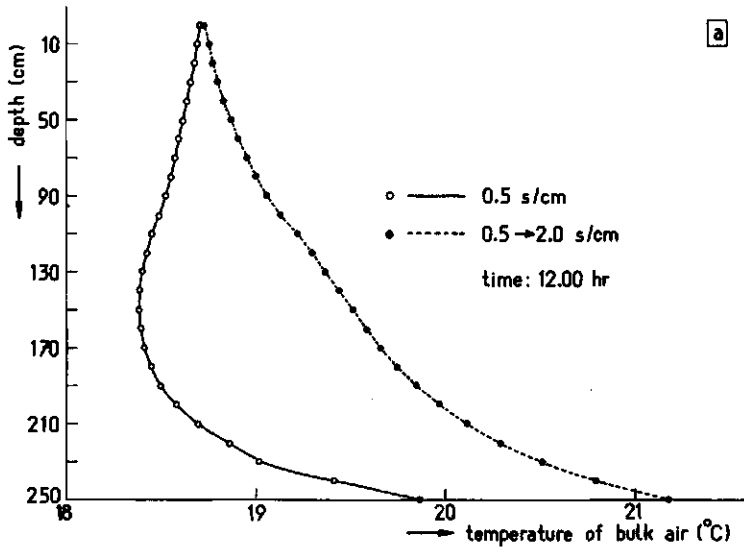


FIG. 1. Temperature (a) and water vapour pressure (b) profiles within a corn canopy. Full curve for a constant stomatal resistance throughout the canopy. Dashed curve for a stomatal resistance increasing linearly with depth into the canopy. The profiles come from a computer run with a program by J. GOUDRIAAN (unpubl.), which is an extended form of the model mentioned in the text (C. T. DE WIT, C. J. STIGTER and J. GOUDRIAAN, internal report).

## 2. THE BEHAVIOUR OF STOMATA

Several recent authoritative texts do exist on stomatal behaviour in general (MEIDNER and MANSFIELD, 1968; MILTHORPE, 1969; ZELITCH, 1969) and several others on the specific diffusion and resistance aspects (BANGE, 1953; LEE and GATES, 1964; WAGGONER and ZELITCH, 1965; LEE, 1967). In early literature many confusing misinterpretations are to be found about the influence of stomatal resistance on vapour exchange. In the latter papers quoted above many of these misinterpretations are discussed thoroughly from a physical point of view and corrected.

The present author agrees with the mentioned critics and no attempt will be made to review their opinions. Only an underlining should be made of their warn against constructions using the principle of interference of vapour streams from neighbouring pores, as incorrect reasoning still occurs (COOK and VISKANTA, 1968). Recent examples of other important misinterpretations regarding the existence of a low overall vapour pressure in the stomatal cavities and the occurrence of vapour streams of any importance within the mesophyll will be discussed in an other part of this article.

For interpretation of leaf diffusion resistance measurements, plant physiological literature on stomatal behaviour is (for the time being) somewhat less relevant. A few summarizing remarks will be made only.

It is still a matter of clear controversy which are the exact mechanisms responsible for the influence stomata are able to exercise. Under field conditions the CO<sub>2</sub> content of the substomatal cavities is often held responsible in many species for a state of opening or closing (e.g. RASCHKE, 1965; SLATYER, 1967a), when water is not a limiting factor in the soil (nor in the leaf under too heavy transpiration). The strong influence of light on this CO<sub>2</sub> content, by photosynthesis, has drawn attention to the connection between stomatal opening and illumination (e.g. KUIPER, 1961; EHRLER and VAN BAVEL, 1968; KANEMASU and TANNER, 1969; TURNER, 1969, 1970; STEWART and LEMON, 1969).

In his review ZELITCH (1969) gives a long list of arguments, derived from experiments, which indicate that internal CO<sub>2</sub> concentration plays *no* important role in the normal opening and closing of stomata. In any case, he argues, apart from the well known effects of closing of stomata in the light at very high CO<sub>2</sub> concentration no reasonable biochemical explanations have yet been suggested for other CO<sub>2</sub> effects in dark or light. On the other hand in the mentioned review evidence for light induced biochemical processes, which influence the osmotic potential of the guard cells relative to the adjacent epidermal cells, is given. ZELITCH believes in the existence of an exchange possibility of potassium ions between guard cells and adjoining epidermal cells. MILTHORPE (1969) on the contrary thinks water to be the only material which freely moves between these cells. The views of ZELITCH have got support in recent considerations and experiments of HOPMANS (1971).

A special influence of blue light on the opening mechanism has also been reported (RASCHKE, 1967; MEIDNER and MANSFIELD, 1968). However its influence within a canopy is not clear. The effect of temperature remains difficult to evaluate (BOSIAN, 1968; MEIDNER and MANSFIELD, 1968) although RASCHKE (1970) claims to have collected more pertinent information now from his recent experiments.

Apart from these influences well known endogeneous rhythms and short period fluctuations of different kinds (e.g. HOPMANS, 1968, 1971; KREITH and WHITE, 1970; RASCHKE and KÜHL, 1969) make the interpretation and measurement of stomatal behaviour still a difficult and troublesome matter. On the field appearance of the latter effects little exact information does exist at the moment (BROWN and ROSENBERG, 1970; SCHENK and STIGTER, 1971; STIGTER, 1970).



### 3. LEAF INTERNAL DIFFUSION RESISTANCE TO WATER VAPOUR

#### 3.1. GENERAL CONSIDERATIONS

When a water vapour molecule has overcome the surface forces of the liquid water in the mesophyll cell walls of the plant it moves towards regions with lower concentrations. When the stomata of the leaves are open and the outside air contains less water vapour molecules per unit volume compared with the concentration at the evaporating surface, the way out will be via internal leaf spaces and the stomata. The latter ones are normally seen as pure mechanical obstructions (resistances) to vapour flow.

Due to the equivalence from a macroscopic point of view it is convenient to use for the exchange process of water vapour the electrical model of Ohm's law:

$$\Delta e = I \times R \quad (1)$$

Here the electrical potential difference is replaced by the water vapour concentration (= density) difference  $\Delta e$  (the difference in absolute humidity) in for example grams<sup>1</sup> per cubic centimeter<sup>1</sup>; the electrical current is replaced by the vapour flow density,  $I$ , in grams per square centimeter per second and the electrical resistance is replaced by an equivalent quantity  $R$ , which is a measure for the resistance against diffusion of water vapour, in seconds per centimeter (Fig. 2).

Some authors prefer to emphasize the diffusional aspects of the phenomenon and want to see equation (1) still as an engineering form of FICK's diffusion law:

$$I = \frac{D}{L} \times \Delta e \quad (2)$$

Now  $D$  is the temperature dependent molecular diffusion coefficient and  $L$  is a so called effective length. This effective length  $L$  is the length of still air, at the temperature of the system, equivalent with either a geometrically more complicated diffusion path (internal leaf spaces, stomata) or with a different path length along which the transport coefficient ( $D$ ) differs from the pure molecular value (external boundary layer, see below).

It is true that for a consideration of what happens microscopically in these transport phenomena of gases the diffusional point of view gives more insight. For example only a detailed look at the diffusion process can make clear what happens at the entrance and exit openings of the stomatal pores. There the lines of equal vapour concentrations (isopsychres, seen as a transverse section through surfaces of equal concentration) have forms different from those more inwards or outwards from the leaf surface. The isopsychres more outside the leaf finally become parallel to its surface (Fig. 3), the more inside are influenced by the alignment of the vapour sources. The phenomena in between the first

<sup>1</sup> In this paper the cm and the g are used as legal units in the SI.

FIG. 2. Resistances to water vapour diffusion in and over a leaf.

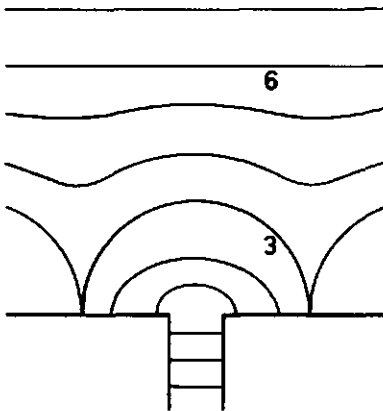
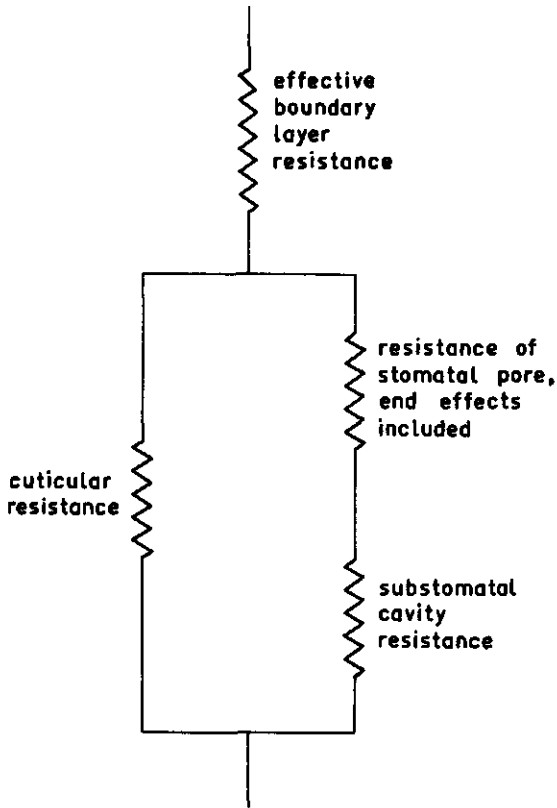


FIG. 3. Transverse section of three dimensional water vapour pressure (or concentration) field, so called isopsychres, at the outer side of a stomatal pore. No frontier is given between the leaf boundary layer and the turbulent bulk air. Resistance from the leaf surface up to curve 3 is called the (external) end effect.

isopsychres so influenced and the geometrically lower and upper ends of the stomata are called the end effects (Fig. 3, 4). They may be calculated from simple geometrical expressions (PARLANGE and WAGGONER, 1970). With the more diffusional form (2) in mind, where appropriate, we prefer in this text to talk about resistances (1). It is only when we should need a connection between such resistances and hydraulic resistances in the liquid phase in the leaf, for use in a soil-plant-atmospheric model, that we would encounter any trouble (PHILIP, 1966).

It is important to point out that we are dealing below with resistances of a unit of homogeneous leaf surface, with the restriction in mind that the differences, over one side of a leaf, between upper and lower side and from leaf to leaf, even at one height in a crop, can't be ignored in calculations or measurements (comp. MORESHET et al., 1968a; MORESHET et al., 1968b; PERRIER, 1968). Secondly we know that our resistances are to be localized between the vapour concentration 'potential' at the outer frontier with the turbulent bulk air outside the leaf and the concentration at the curved capillary surfaces within the walls of the mesophyll cells. This means that for the first concentration we take in our model a time average as well as a place average over a small height (in the air in the canopy, where the unit leaf surface is found) and we assume this mean value to exist at part of the outer frontier of the boundary layer of the leaf concerned. Therefore we must speak of an effective boundary layer resistance (or an effective length in (2)). When we are interested in the real vapour concentration profile over the leaf this is of course not permitted because of the existence of a transition layer instead of a frontier and the differences in its thickness over the leaf (e.g. DE PARCEVAUX, 1961; SLATYER, 1967a). Just because the real nature of the boundary layer outside the leaf is not clear, the true physical interpretation of the effective resistance or length under all conditions remains somewhat obscured.

It has been made clear in several classical texts (comp. SLATYER, 1967a) that the resistance  $R$  of a leaf is formed by the normally high cuticular resistance, parallel to the series resistances of stomatal cavity and stomatal pore (end effects included, PENMAN and SCHOFIELD, 1951), with finally the effective boundary layer resistance in series with the resultant of the others (Fig. 2). The complete description of the details of overall leaf resistance has been given already many times (e.g. HOLMGREN et al., 1965; MORESHET et al., 1968a; JARVIS and SLATYER, 1970; DE PARCEVAUX and PERRIER, 1970). So only remarks pertinent to an understanding of operation and calibration of a measuring device to be described later on will be made. Interference of the device with the situation to be measured will also be considered.

In the methods involved a vapour stream  $I$  (1) is sensed by clamping a small chamber, where humidity is measured, on the leaf (see final part of the article). Therefore actual  $\Delta e$  during the measuring period has to be known to measure  $R$  correctly. Although the findings of others (e.g. WALLIHAN, 1964; KANEMASU et al., 1969; MORROW and SLATYER, 1971a, 1971b) will have to be verified under our own experimental conditions, it is supposed for the present that pure

mechanical reactions of the stomatal system on the actions of measurement in the field can be avoided (at least during the measuring period). Therefore especially misinterpretations in  $\Delta e$  have to be considered.

### 3.2. THE CONCENTRATION AT THE LIQUID SURFACE

The problem of the real vapour concentration at the mesophyll walls was certainly not ignored. With physical arguments this concentration was supposed to be equal to the saturated one belonging to leaf temperature (MILTHORPE, 1961; SLATYER, 1966a, 1967a).

Very recently, however, JARVIS and SLATYER (1970) threw doubt on the assumption that this is true under all conditions. It is well known that it is not the curvation of capillary water surfaces in the cell walls which may give a drop of any importance in the saturation vapour concentration. It now appeared in their study also unlikely that 'incipient drying', i.e. a growing diffusional resistance because of withdrawal of the capillary surfaces inwards (e.g. COWAN and MILTHORPE, 1968b) under heavy evaporation, did occur. JARVIS and SLATYER were also able to conclude that neither a normal lowering of leaf water potential nor any local accumulation of osmotically active solutes could be a reason for their measured cell wall resistances. Therefore they suggest a significant source of hydraulic resistance to liquid flow, across the outer and denser layers of the cell walls, to be of influence on the surface water potential. This will result in a lower water vapour concentration than the saturated one at the same temperature, as may be seen from the thermodynamic relationship connecting water potential and water vapour concentration at the cell solution / leaf air interface (e.g. PHILIP, 1966). Of course more knowledge about the physical character of the hydraulic resistance involved will make its interpretation less doubtful.

The authors remark that the effect of this passive (apparent) hydraulic resistance, under their experimental conditions with CO<sub>2</sub> free air, will be much smaller under normal outdoor conditions. However, the relative leaf water content, as found by some authors (KANEMASU and TANNER, 1969a; review by SHAWCROFT and LEMON, 1970) to be critical for stomatal closure amounts 85 → 90% RWC. Combining this with the estimated drop of the saturation concentration at the mesophyll walls, as given for cotton under such conditions by JARVIS and SLATYER, still a drop in the vapour concentration of about 10% might occur without any closing of the stomates. If soil water is not limiting this might happen under very high evaporation only ( $> 4 \times 10^{-6}$  g/cm<sup>2</sup>s). Under more normal evaporation ( $< 4 \times 10^{-6}$  g/cm<sup>2</sup>s, e.g. BROWN and COVEY, 1966) in most cases no more than a 2 to 3% reduction was estimated and in some cases it was even negligible. Talking about a cell wall resistance therefore remains doubtful in these latter cases (for mesophytes). Of course as soon as the stomata are starting to close, the evaporative demand becomes smaller and the effect described above will disappear completely.

It is suggested here that the measurements on maize of SHIMSHI (1963), under limiting soil water conditions but with a very high external humidity ( $\approx 90\%$ ), form an example of the same (apparent) hydraulic resistance. He measured a maximum drop of 7% in the vapour concentration under such conditions, with wide open stomata and high turbulence of the air surrounding the plant.

A better known but less important effect, which also results in a surface water vapour concentration smaller than the saturated one at the surface temperature, results from stress conditions because of a dry soil. This gives, even at a leaf water potential of  $-50$  bars, a drop in the vapour concentration of less than 4% (SLATYER, 1967a).

In measurements the latter effect would be especially of influence when  $\Delta e$  is small during the period of measurement, as the drop is constant and will not be influenced by short changes in evaporative conditions. The former effect should confuse measurements if the (apparent) hydraulic resistances change during the measuring period. If the measuring device does not (or only slightly) alter the evaporative conditions, this resistance is measured in the sensing of a lower  $I$ . If the evaporation is clearly different during the measuring period one of the following consequences may arise. Either the 'hydraulic resistance effect' may be induced or enlarged by the measuring device, which gives a measured  $R$  which is too high. Either this effect is made smaller or cancelled out by the application of the device, which gives a  $R$  too small compared with the natural situation. No field measurements of stomatal resistance reported so far have taken into account the possible existence of the effects mentioned.

### 3.3. RESISTANCE OF SUBSTOMATAL AND INTERCELLULAR SPACES

A second point of interest, related to the above and sometimes quite confusing in the existing literature, is the relative humidity in the intercellular and substomatal spaces and the partitioning of stomatal resistance over the resistance in the pore itself and in the substomatal cavities.

What we have to investigate is, given the total  $\Delta e$ , as mentioned, under a specific situation, what are the relative values of intermediate vapour concentrations at both ends of the stomata. Fig. 4, one of the fine figures of BANGE (1953, Fig. 17) showing the geometry of diffusion from different sources, directly shows that within the leaf we have to talk about a three dimensional potential field. Thus the definition of one relative humidity, or one uniform gradient of relative humidity, in the stomatal cavity is impossible. One sees from the isopsychres of the same figure that the cells nearer the stomatal pores must make a greater contribution to evaporation if the vapour pressure at the walls is and remains the same everywhere and if the evaporation sites are located directly at the geometrical boundary between the cell and internal air.

When such apparent 'hydraulic resistances' as treated above could build up in (parts of) cell walls nearer the pores, because of a high demand, of course their contribution to evaporation will decrease to values equal to those of cell walls

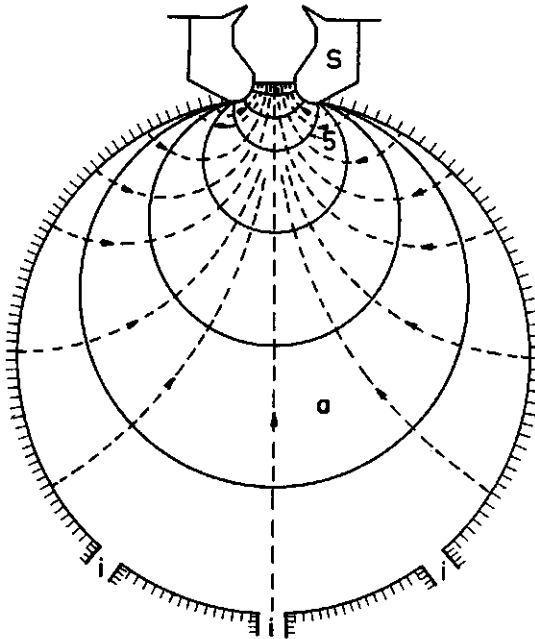


FIG. 4. Transverse section of schematical three dimensional water vapour pressure field (isopsychres), with flow lines, within a substomatal cavity (a). One of the guard cells is marked s, intercellular spaces are marked i. Resistance from curve 5 upwards to the geometrically lower end of the stoma is called the (internal) end effect. After BANGE (1953).

at larger distance. Consequently the total flux will then be reduced and the distances between the isopsychres will increase, compared with those in Fig. 4 near sites where these extra resistances occur.

As to the resistance of the intercellular spaces, at least under isothermal conditions (see also below), the following reasoning does apply. It is unlikely that they make any significant contribution because of the distance between the isopsychres near these sources, provided the schematical distribution of evaporation sources as given in Fig. 4 is approached in reality. From BANGE's transverse section through a *Zebrina* stoma this seems for example to be correct, from transverse sections for leaves of alfalfa and corn as given by ANDREW (1968) this distribution also does seem a very good approach. An indirect result from the above mentioned recent publication of JARVIS and SLATYER (1970) also reveals a strong indication that the sum of intercellular and substomatal space resistance to water vapour diffusion almost entirely consists of the resistance of substomatal cavities.

This is in contrast with an earlier conclusion by SLATYER (1967a). He considered measurements on cotton leaves by JARVIS et al. (1967). They measured an open-stomata resistance of  $\approx 4$  s/cm (for both surfaces added in series) and a resistance to  $N_2O$  - diffusion through the leaf from one side to the other of  $\approx 3$  s/cm. This was erroneously (in the opinion of the present author) taken as an indication of a high internal resistance against water vapour flow, as the open-stomata resistance comes from a diffusion *from* the leaves and the other figure from a diffusion *through* the leaves. In the first case the vapour sources

are *internal* ones. The evidence, with all proper reserve suggested by SLATYER in his description, from an explanation of differences in light intensity influences on stomatal aperture and stomatal resistance, is indeed not high. These differences may be better explained from two- or three- dimensional analyses of the stomatal pore (WAGGONER and ZELITCH, 1965; WAGGONER, 1966).

It follows from this kind of analyses that a relatively high potential may be supposed to exist on, for example, the equipotential curve marked 5 in Fig. 4. Under normal external relative humidities (> 40%) one easily calculates a minimum relative humidity there of 96% (temperature or pressure influences excluded), under the maximum percentual influence of the substomatal cavity, i.e. under windy conditions (LEE and GATES, 1964, see also below).

In connection with this, attempts to assign from experimental results a much lower relative humidity somewhere in the substomatal cavity under quite normal conditions are suspicious. They have been made for example by THUTT (1938, 1939) and more recently by LAUE et al. (1968). In all these experiments, however, no leaf temperatures were measured and no energy balances could therefore be set up for the leaves. This was more or less appreciated by the former author (THUTT, 1939) but the latter ones failed to take the difference in temperature between the leaf and its aerial environment into account. One sees (Table 1) from the values taken from their table 2, that such differences in temperature must have been present. Bringing their leaves at an air temperature of 15°C from a high to a somewhat lower relative humidity indeed increased the transpiration. Bringing these same leaves at an air temperature of 25°C from a lower to a higher relative humidity did however also increase the transpiration.

Differences found in the mentioned publications between different plants under the same experimental conditions may easily have been due to differences in radiation absorption capacity, stomatal behaviour etc. They are of influence on the energy balance of these single leaves. Using the values for transpiration as given by LAUE et al. (1968) and calculating the energy transpired one has an entrance to diagrams such as made by GATES (1970, p. 245). They give for a certain resistance value and for different air temperature and humidity combinations an idea of the temperature difference between leaf and air. When accepting as an approximation the overall diffusion resistance to be 3 s/cm, as in this diagram of GATES, one finds for the case of *Nicotiana rustica* L. at 25°C in

TABLE 1. Figures from table 2 of LAUE et al. (1968) indicating higher transpiration values at higher relative humidity values, erroneously attributed by the authors to differences in inter-cellular and substomatal relative humidity. No leaf temperatures were measured but could be calculated to amount lower and higher than air temperatures respectively in one evaluated case (bold type figures, see text).

	<i>Nicotiana rustica</i>				<i>Brassica napus</i>			
Temp. (°C)	15	15	<b>25</b>	<b>25</b>	15	15	25	25
R.H. (%)	79.1	74.8	<b>47.7</b>	<b>55.9</b>	79.1	74.8	47.7	55.9
Transp. (10 <sup>-3</sup> g/cm <sup>2</sup> h)	4.7	4.9	<b>10.4</b>	<b>13.8</b>	5.2	9.6	10.3	12.8

the left hand case in table 1, a leaf temperature 2.5°C lower than the air and in the right hand case one of 2.5°C higher than the air.

For different overall resistances, of course, different absolute values should have been found. This kind of analysis however explains the wrong conclusion from the cited experiments of low relative humidities in the substomatal and intercellular spaces. We are therefore bound to conclude that with the restrictions given above the resistance of the leaf to water vapour diffusion will lay almost completely in the stomatal pore, end effects included.

### 3.4. RESISTANCE OF THE STOMATAL PORE

Accurate calculation of the resistance of stomata would be possible when at each moment the geometrical shape in three dimensions would be known. This means that we see the stomatal systems as multipore membranes, and their changes as step-functions in time, as an approach to their dynamic behaviour.

Finally the use of end corrections was shown to be necessary from mere diffusion theory (e.g. PENMAN and SCHOFIELD, 1951; BANGE, 1953). The mathematical expressions involved, with which we will deal in a following paper on apparatus and calibration, show that these corrections may be substantial at wide apertures. They do arise from the resistance against diffusion of the 'micro vapour cups' over the ends of the pores (Fig. 3, curve 3; Fig. 4, curve 5). It was originally suggested intuitively by BANGE that the complete resistance between the geometrical pore end and the air layer with uniform vapour pressure in the horizontal (Fig. 3, curve 6) was in these vapour cups. In a thorough mathematical derivation by PARLANGE and WAGGONER (1970) this was recently confirmed to be almost exact for interstomatal distances existing in nature. They proved this to be independent of stomatal shape, by making use of the 'interference concept' for the vapour streams of neighbouring stomata in the region below curve 6 (Fig. 3) only. This interference concept therefore has done its job and can be definitely abandoned as was shown also by the measurements and calculations of LEE (1967).

For most agricultural crops minimum values of total stomatal pore resistance per unit leaf surface (one side only), under normal soil and environmental conditions measured in the field, are normally between 0.3 s/cm and 2 s/cm (LINACRE 1966, 1967a; GATES, 1968; COWAN and MILTHORPE, 1968a). The lowest values ever reported were of the order of 0.1 s/cm in freshly irrigated sorghum (EHLER and VAN BAVEL, 1968). However, MONTEITH and BULL (1970) suggest lack of temperature equilibrium in the measuring instrument to be the reason for such low values. Much higher values have been reported for other species (GATES, 1968). Age of the leaves or special circumstances, as dry spells in the past, may have an influence on minimum values under normal conditions.



### 3.5. RESISTANCE OF THE CUTICULA

As the partitioning between parallel resistances (Fig. 2) is not important in our model and procedure, no special attention will be given here to cuticular resistance. Low values reported are from 5 s/cm to 15 s/cm (MILTHORPE, 1961; HOLMGREN et al., 1965), but normally values of 25 to 50 s/cm are measured. Such resistances are equivalent with a stomatal pore of a diameter of something like 0.1  $\mu\text{m}$ , which is about one percent of a mean full opening value.

## 4. SOME OTHER FACTORS OF POSSIBLE INFLUENCE ON DIFFUSION

### 4.1. AIR LAYER RESISTANCE

The last resistance encountered by the water vapour molecules is to be found in the air layer 'adhering' to the leaf. Again its resistance may be calculated from diffusion when its effective length is known. This boundary layer effect is directly determined by the motion properties of the bulk air, which may be from completely at rest (theoretically) via more or less idealized laminar and turbulent wind tunnel circumstances up to the highest scale of turbulence encountered outdoors.

At one end of this scale, the indoor still air (without too strong radiation sources), the theoretical value, using STEFAN's law (e.g. MEIDNER and MANSFIELD, 1968) for a (leaf)disc of  $d \simeq 10$  cm is about 16 s/cm for 1 cm<sup>2</sup>, from

$$R = \frac{\pi d}{8D} \quad (3)$$

This must be seen as an 'end effect' for a whole leaf disc. This value was already found to be too high by PENMAN and SCHOFIELD (1951), because of the ever existing motion of slow air currents. A value of somewhat more than 6 s/cm is for the same case found from their often quoted formula:

$$R = \frac{0.4 d^{0.6}}{D} \quad (4)$$

In practice however, even this appears to be too high a value, which may be appreciated from the literature investigations of KUIPER (1961) and LINACRE (1966) and the measurements of KUIPER (1961), LINACRE (1967a) and LEE (1967). From their independent but equal results the highest value encountered in special experimental compartments, with surfaces of the same dimensions ( $\simeq 10$  cm), can be set at 4 s/cm, reducing to between 2 and 3 s/cm in a normal work room without any special (induced) form of circulation. This is in accordance with recent observations of very slight air currents (10 cm/s and 30 cm/s) to be very effective in increasing transfer from broad artificial leaves in a wind tunnel (VOGEL, 1970) and with our own observations during calibration performances.

At the other extreme, which interests us more regarding field experiments, we have to consider the turbulence in the air layers within a canopy. Here recently new insights have been gained. PHILIP (1966) already doubted the relevance of laminar wind tunnel experiments to transfer processes around a leaf in the canopy. Free stream turbulence, the mutual interactions of streams around the leaves and the possibilities of bending and flutter were mentioned as differences between tunnel and field. PARKHURST et al. (1968) found that forced convection heat transfer in a wind tunnel was increased generally less than 20%

by the presence of other branches and leaves and about 5% because of 'oscillations'. HUNT et al. (1968) supposed that apart from geometrical surface properties it was essentially the scale or intensity of turbulence experienced by leaves in the field that makes exchange in the canopy different from (idealized) wind tunnel experiments. They used arguments comparable to those of PHILIP for an explanation of their low boundary layer resistances, encountered at the large leaves in a field of sunflowers. Similar results were found in snap beans by KANEMASU et al. (1969). Their values were used by STEWART and LEMON (1969) as an extrapolation to field conditions of their own wind tunnel experiments with two leaves upwind from a test leaf. They calculated from KANEMASU's measurements for a leaf width  $d$  of the order of 5 cm:

$$R_{\text{boundary}} = 0.6 \sqrt{d/u} \quad (5a)$$

where  $u$  is a measured wind velocity. For a leaf of about 10 cm the slope of  $R_{\text{boundary}}$  against  $(d/u)^{1/2}$  was found to be only 0.43 s<sup>1/2</sup>/cm. These values are 45% and 33% of even the lowest values hitherto supposed to be the most representative for leaves in the open (MONTEITH, 1965). However, PARLANGE and WAGGONER (Private communication by Dr. P. E. Waggoner) believe from their experiments this value of MONTEITH to be still more representative. In that case (5a) becomes:

$$R_{\text{boundary}} = 1.3 \sqrt{d/u} \quad (5b)$$

For wind speeds in the order of 100 cm/s values of the boundary layer resistance for leaves of something like 5 cm width are of the order of 0.2 s/cm (5b). This is somewhat higher than the values of HUNT et al. (1968) but in agreement with the lowest values reported by LINACRE (1966). STOUTJESDIJK (1970) recently reported the boundary layer resistance to be from 10 to 30 per cent of the overall resistance, under normal outdoor conditions, for leaves of some production crops, tropical weeds and plants from Savanna vegetation. Referring to the values of stomatal resistance given earlier (order of 1 s/cm) this is found to be in accordance with the values calculated above for  $R_{\text{boundary}}$ .

As to the suggestion of high turbulence intensity within a canopy new evidence, in support of older results (UCHIJIMA and WRIGHT, 1964), was recently collected by LUXMOORE et al. (1970) and PERRIER et al. (1970). They found very high turbulent intensities, higher than even directly above the crop, in row sown soybeans. This demonstrates, as they state, the importance of micro-scale turbulence in determining exchanges between plant leaf and lower atmosphere. Of course differences because of morphology and stand structure may occur as is shown by PERRIER et al. (1970). Their turbulent intensities increase with depth in the soybean canopy and they quote turbulent intensities in a corn canopy (UCHIJIMA and WRIGHT, 1964), that just decrease with depth. One might suggest that the increase of the turbulence intensity was due to the fact that the crops were sown in rows. However, the same turbulent intensities, be it with appreciably less overall air movement (wind speed), were measured when the canopy over the rows was closed (MILLINGTON and PETERS, 1969b). This

suggests that also in a relatively open structure which is more or less isotropic, as a corn crop sown with equal spacing in two perpendicular directions or hexagonally, high turbulence intensities do occur. This apart from the effect of 'sealing' of a dense easily bending crop as wheat, which may give rise to the building up of 'hot' and 'damp' spots (PENMAN and LONG, 1960), which are not easily to reconcile with high turbulent intensities.

The skewed frequency distributions of wind velocities (PERRIER et al., 1970) and the suggested almost omnidirectional air movements within the not sealed canopy make the possibility of determination of exchange coefficients in the turbulent air from usual wind speed measurements highly questionable.

The conclusions derived above give also again support to the supposed importance of stomatal resistance in the exchange process of water vapour from leaves in the field, the external resistance being in most cases smaller than hitherto often accepted.

One other possibility of vapour exchange in the field which is sometimes suggested (BERNBECK, 1924; POORE, 1965; SLATYER, 1967a), is the existence of substantial internal air movement in the leaf air spaces, by through blowing or bellows (pumping) action of fluttering leaves, or influence of other pressure differences across amphistomatous leaves. WOOLLEY (1961) tried to verify the existence of these processes for corn leaves but found them to be negligible. The extremely low influence of pressure fluctuations, from gustiness of the wind, on vapour exchange from the soil (FUKUDA, 1955) does support these results indirectly. It suggests that apart from pumping by mechanical actions in leaf movement other pressure differences will have no influence. Therefore the process of exchange is considered to be completely diffusional up to the outer edge of the effective boundary layer, when no extreme radiation loads during spells of extremely low wind speeds are concerned.

#### 4.2. VALUE OF THE DIFFUSION COEFFICIENT

As was put forward by MILTHORPE and PENMAN (1967) and COWAN and MILTHORPE (1968a, 1968b) diffusion through narrow pores differs from free diffusion at the same temperature. This phenomenon of wall influences on the diffusion may be seen as a kind of SMOLUCHOWSKI-KNUDSEN effect (CARMAN, 1956). With an (equivalent) throat diameter of 20  $\mu\text{m}$  the correction seems to be zero; at 10  $\mu\text{m}$  it may be in the order of 10%, at 3  $\mu\text{m}$  in the order of 20%. The use of too high values for the diffusion coefficient in calculation of stomatal resistance from geometry may have been one reason for persistent believe in relatively high substomatal or cell wall resistance; calculations did always show lower resistances than measurements. Of course this smaller diffusion coefficient is measured as a higher  $R$  by sensing a smaller  $I$  (1).

A smaller factor with the same effect was recently dealt with by PARKINSON and PENMAN (1970). The fact that a net outflow of water vapour from the stomata along its partial pressure gradient is not coupled with a net inflow of

air because of the 'no air flow' boundary condition at the mesophyll walls is responsible for a correction. To make the theoretical balance correct a compensating mass flow of air out of the leaf to bulk air should assist outward diffusion of water vapour, which makes the following correction on calculated resistances necessary:

$$R_{\text{corr}} = R_{\text{calc}} P / (P - \bar{p}) \quad (6)$$

with  $P$ , total atmospheric pressure and  $\bar{p}$ , partial pressure halfway the partial pressure gradient. Of course this correction is temperature dependent, amounting at its maximum about 3% at 40°C and a difference of 80% in relative humidity between mesophyll and ambient air. At room temperature the error is under the same conditions only about 1%.<sup>2</sup>

A last remark concerns the temperature dependence of the diffusion coefficient. It is sometimes ignored that  $D$  changes about 10% over 15°C difference in ambient temperature (LIST, 1963). Especially the temperature in that part of the leaf where the vapour flow resistance (and by the way the residence time of the vapour molecules) is highest determines the value to be taken. This means that, if high temperature differences should exist between guard cells, epidermal layer or parenchymatic tissue, different temperatures should have to be taken for the determination of  $D$  and the evaluation of the saturated vapour pressure at the mesophyll walls in different parts of the leaf.

#### 4.3. TEMPERATURE WITHIN THE LEAF

Internal temperature differences and their effects depend on the physical processes of reflection, transmission, absorption, scattering and back radiation of radiative energy, on cooling processes by convection and evaporation and on development of internal vapour concentration fields.

The major part of the solar radiation load is absorbed by the pigments in the parenchymatic tissue of the leaf, and an other much smaller part (in the near infra red) by all watery tissue (e.g. GATES, 1970). Taking into account the scattering at the air-water interfaces, as pictured by GATES (1970), and the quite even distribution of the pigments over the leaf, radiation absorption will be quite evenly distributed over the inner parts of the leaf too. Important temperature gradients are not induced in this way. The transparent outer (epidermal) cells, with their cuticula, absorb less radiation and are responsible for the net back radiation in the far infra red, integrated over a depth from a few  $\mu\text{m}$  to a few tens of  $\mu\text{m}$ 's (IDLE, 1968; PERRIER, 1970), and for the first instance reaction on convective cooling (or heating). We have also seen that the evaporation sources are likely to lay in that parts of the leaf which are near (one or both of) the leaf surfaces, at least when 'hydraulic resistances' in the flow from cell to cell and from within the cell into the outer walls are small. Therefore, if temper-

<sup>2</sup> It is shown in the same publication that the effect can't be ignored for photosynthesis calculations.

ature differences exist it is likely that they will be with their cooler end at the outer layer(s) of the leaf.

No investigations do exist which have evaluated temperature differences between the inner and outer parts of amphistomatous leaves. In view of the difference of thermal conductivity of water and air (0.60 and 0.025 J/s m °C respectively at room temperature) and the probability that liquid water is present in the epidermical cells also nearly right up to the surface (SLATYER, 1967a), one may suppose that the temperature gradients are not steep within the leaf. This apart from the overlying waxy materials of the outer part of the cuticular walls. Of course temperature gradients may be steeper over the still air boundary layer.

It has been suggested from theoretical considerations by LINACRE (1964) and by MILLINGTON and PETERS (1969a) that temperature differences over (thick) hypostomatous leaves may be important. The latter authors even suggest influence on transpiration from a leaf by internal vapour diffusion due to such temperature differences. The only way of measuring adequately temperature differences over two sides of a leaf in the field is certainly by infrared detection instruments. Especially those not integrating many plant surfaces (e.g. TANNER, 1963a) but only part of a leaf surface (e.g. FUCHS and TANNER, 1966; STOUTJESDIJK, 1966) would be useful here. No such measurements have been reported in the recent excellent review by GATES (1968). Reviews and reports on leaf temperature experiments (LINACRE, 1964, 1967b; STOUTJESDIJK, 1970) also make no reference to such measurements. The only investigations found by the present author are those of PERRIER (1968). He *calculated* for symmetric (i.e. amphistomatous, with no differences between upper and lower side) leaves, perpendicular to the solar rays and not thicker than 0.5 mm, temperature differences smaller than 1°C and for such asymmetric leaves (no evaporation at the upper side) maximum differences of 1.5°C, depending of course on stomatal opening and convectional situations. For asymmetric leaves of thicknesses from 0.5 to 1.5 mm temperature differences of 1°–6°C were calculated.

Two objections may be raised to these interesting calculations. A value of 0.15 J/s m °C was used for the thermal conductivity of the tissue, which is only a quarter of that for water at the same temperature. Secondly all net radiation was supposed to be absorbed at the leaf surface. Both assumptions tend to overestimate the temperature differences. However, the same author has also *measured* temperature differences over leaves. He found them to be always smaller than 1°C between surfaces of thin leaves (< 0.5 mm) but from 2° to 6°C at asymmetric thicker leaves (from 1 to 1.5 mm). His phosphorescence method of temperature measurement, which needed a 20 µm coating of the leaves by crystals, is claimed to be hardly of influence to heat and mass exchange nor to any other leaf property. Change in the surface temperature would therefore be no more than 0.5°C. However, the value for the thermal conductivity of leaf tissue, used in PERRIER's calculations, was obtained from the temperature differences measured with this method. This justifies some hesitation to accept PERRIER's results quantitatively. Therefore the present author thinks the

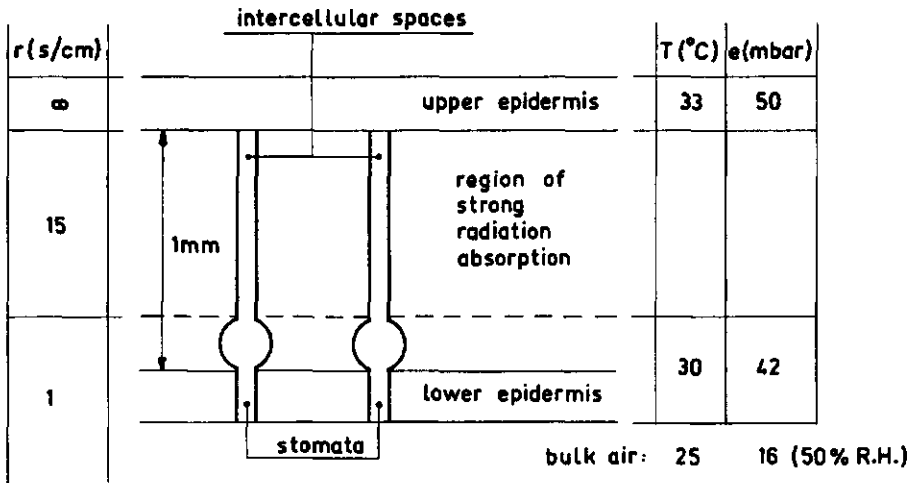


FIG. 5. Schematic diagram of a hypostomatous leaf of medium thickness. The upper epidermis is supposed to have no cuticular transpiration. An example of possible resistance partitioning is given in the left hand column ( $r$ ), an example of possible mean temperatures and resulting saturated vapour pressures (instead of concentrations) is given in the right hand columns. An extreme situation with low external air speed and high radiation load has been chosen, however with open stomata.

schematic example of Fig. 5 to give a more correct idea of the maximum influence of temperature differences within hypostomatous leaves on saturated vapour pressure partition.

#### 4.4. INTERNAL VAPOUR PRESSURE FIELD BECAUSE OF A TEMPERATURE DIFFERENCE

For our situation of Fig. 5 we have to look at the internal resistances of a leaf. In this situation a resistance measured by  $\text{N}_2\text{O}$ -diffusion through 200  $\mu\text{m}$  thickness of cotton mesophyll tissue, being 3 s/cm (JARVIS et al., 1967), may now correctly be used as an approximate value. The leaf being estimated 1 mm thick, the internal resistance has therefore been taken in Fig. 5 to be 15 s/cm. Reasons for such a high resistance are the mean dimension of internal air-spaces, for example in cotton estimated to be smaller than 2  $\mu\text{m}$  (JARVIS and SLATYER, 1970), tortuosity of the vapour path (only schematically drawn in Fig. 5) and a reduced diffusion coefficient (wall influences).

Because of this relatively high resistance the isopsychres will be, in the diagram of Fig. 5, almost parallel to the leaf surface as far as intercellular spaces are concerned. This is in contrast to the isothermal situation where the isopsychres, following this schematic diagram, would be almost perpendicular to the leaf surface. However, in both cases the distances between isopsychres in

the intercellular spaces are so large that the gradients are very small compared with those in the substomatal cavity. Consequently the flow field in these substomatal cavities, such as given in Fig. 4, is not influenced.

So only in such cases that internal resistances are not high there may be any influence on transpiration from temperature differences over a leaf. We believe therefore to have shown the suggestion of MILLINGTON and PETERS (1969a) mentioned above to be improbable under normal situations in the field. The same arguments as used above apply to the calculated differences up to 7°C between centre and border of a not too small leaf (PERRIER, 1968). This can also be of influence only when connections of very low diffusional resistance do exist laterally in the leaf.

Finally again the same kind of arguments applies to suggestions of lateral transport (WALLIHAN, 1964) when differences in evaporation over one side of a leaf are induced by a measuring device. This is an important conclusion derived from the theory dealt with above, regarding field measurements of leaf diffusional resistance.

The second conclusion in this respect is that a change in the alignment of internal vapour concentration fields after clamping an apparatus on the leaf will not influence the transpiration (so the resistance) measured. This equally applies to induced evaporation conditions at the back side of the leaf part measured. Only the direct or indirect (by conduction) temperature change at the measured surface changes the actual transpiration. For this latter effect it is good to know that the thermal time constant of a leaf amounts indoors about 50 seconds or more. This may be calculated by methods from heat transfer theory in fair agreement with empirical evidence (LINACRE, 1967a).



## 5. APPARATUS FOR MEASURING STOMATAL RESISTANCE DIRECTLY

### 5.1. THE CHOICE OF A SUITABLE TYPE

The review given above has emphasized points which will become of importance in design, calibration and use of a small measuring chamber to detect the vapour stream diffusing from the leaf in the field. We may now start to review shortly relevant methods which have been used for measuring transpiration from single plants or leaves.

In the laboratory some measuring systems have been developed which indeed sense the real vapour stream from leaves in their indoor condition directly. One may distinguish between closed and open systems. In the former the sensing element is in the same enclosure as the plant (parts), in the latter the air passing these plant parts is sensed elsewhere (comp. SLATYER and SHMUELI, 1967).

The laboratory measurements in an open system are difficult to extrapolate to field conditions. The whole instrumental system is quite complex and modifies heavily the natural leaf environment (e.g. GAASTRA, 1959; BIERHUIZEN and SLATYER, 1964; PARKINSON, 1968). The closed system, as independently improved by rapid sensing of water vapour by DECKER and WETZEL (1957) and ASHBY (1957) originally met many objections even in laboratory use. This method, however, was modified for field use by GRIEVE and WENT (1965). Some of the objections against the closed system method (SLATYER and SHMUELI, 1967; SHIMSHI et al., 1965) were experimentally met by GRIEVE and WENT. Nevertheless the disturbance of especially the temperature regime (i.e. the energy balance) of the leaf is in most cases too severe to be ignored. The principle of the method has been independently used by WALLIHAN (1964) to develop a measuring device for stomatal resistance in stead of actual transpiration in the field, to which we will refer in due course.

Many objections have been raised against the use of methods requiring severing techniques or weighing whole plants. Although recently TAYLOR and GATES (1970) met some of these by combination with energy budget techniques, their field use remains cumbersome. Especially profiles of evaporation within a canopy in the course of time can not be obtained in this (indirect) way.

The different kinds of heat budget methods form an other indirect way. One observes the energy balances of two leaves or at two positions of one leaf. The leaves are not detached from the plants in their natural conditions and disturbances or modifications of the direct environment of the leaf are as small as possible under the differences of heat budget mentioned. However, at least one energy balance has to be induced artificially. This makes it also difficult to measure profiles throughout the canopy with these methods. Moreover these methods (e.g. IMPENS et al., 1967; STOUTJESDIJK, 1970; DE PARCEVAUX and PERRIER, 1970) finally yield values for the ratio of total resistance to transpiration and resistance of the unmodified boundary layer. The latter one or the

stomatal resistance has to be determined separately for obtaining the needed value of total resistance.

Because of the problems mentioned above determination of evaporation per unit leaf surface under natural conditions in the field is almost impossible. Therefore separate measurement of the resistance of stomata has become a goal in demand. As in the field the stomatal resistance is normally more important than the boundary layer resistance (as we have seen before in the present paper) this is a highly promising and reliable approach. We have also stated already that such a determination implies the assumption that when evaporation is now changed on purpose by the detecting device, stomatal resistance is not affected.

Well known state of the art reviews on measuring stomatal resistance directly by a wide variety of not always quantitative methods do exist (SLATYER and SHMUELI, 1967; BARRS, 1968; MEIDNER and MANSFIELD, 1968). With our purpose of many measurements in canopies in mind, it has no sense to consider laborious methods which need a lot of measurements on leaves and in the ambient air throughout the vegetation. For example DE PARCEVAUX and PERRIER (1970) made their heat budget method also appropriate for direct measurement of stomatal resistance. They studied for this purpose the kinetics of temperature of leaves under different budgets. The temperature measurements involved of two neighbouring places of one leaf, one with an extra induced radiation load, make quick profile measurements again quite difficult. Only infra red thermometry would make the method valuable for our purposes but the experimental difficulties were not yet met by the mentioned authors. Results of error calculations were also mentioned to be not yet very favorable.

Therefore in the following only diffusion methods will be dealt with here, with in mind that some viscous air flow porometers are sometimes suitable for field use (BIERHUIZEN et al., 1965; WILLIAMS and SINCLAIR, 1969). It remains a problem that the measured values are not always readily converted into diffusive resistances (WAGGONER, 1965; JARVIS et al., 1967). Moreover the natural diffusion path is not followed and with hypostomatous leaves other problems are involved. Cobalt paper measurements, which are sometimes listed under diffusive flow methods, will not be dealt with.

Some of the diffusion methods make use of the diffusion of other gases than the water vapour released by the plant itself (hydrogen, nitrous oxide, argon). None of them can be conveniently used in the field for our purpose. Again an objection against the nitrous oxide method (SLATYER and JARVIS, 1966) and the radioactive labelled argon method (MORESHET et al., 1968b), which seem not to damage any physiological process, is the inclusion of the internal resistance from one side of the leaf mesophyll to the other, as discussed earlier.

We therefore finally will deal with more recent diffusion methods. They are the most quantitative methods available for determining stomatal resistance. They make use of direct sensing of the water vapour coming from inside the leaf along its natural internal pathways. The vapour is finally carried to a sensor through a modified but constant boundary layer. Compared with the original environment the boundary layer resistance may have increased (still air between

leaf and sensor, which is now more or less within an extended boundary layer) or may have remained of the same order (artificially agitated air between leaf and sensor). The 'boundary' resistances left may be experimentally eliminated by measuring their value over saturated surfaces of known temperature, and subtracting them from the values of field measurements.

In fact all sensing methods hitherto used in open or closed laboratory systems, that are thermocouple psychrometry (e.g. SLATYER and BIERHUIZEN, 1964), infra red gas analyzing of samples (e.g. DECKER and WETZEL, 1957) or electrical hygrometry (e.g. ASHBY, 1957; GAASTRA, 1959; WALLIHAN, 1964; GRIEVE and WENT, 1965; ROGERS, 1965) may be used. Especially the latter one has many advantages as the troubles of wicks and water supply in psychrometry and storage of field samples in some forms of spectroscopic hygrometry are avoided.

## 5.2. THE WALLIHAN LEAF DIFFUSION RESISTANCE METER, ITS USE AND MODIFICATIONS

As mentioned earlier GRIEVE and WENT (1965) tried to measure evaporation in the field by sensing the water vapour directly. They used a small lucite chamber in which a leaf or part of it could be tightly held (Fig. 6). The change in electrical resistance with moisture content of a sensor element of LiCl-salt was used for detection. The speed of uptake, and by the way the speed of change in electrical resistance, is a measure of the rate of evaporation from the leaf. The time between the reaching of two fixed resistance values is taken as a measure for this transpiration.

To be sure that the environmental conditions did not change intolerably GRIEVE and WENT used hygrometric elements of the mentioned type with small sensitivity ranges. These elements had to be selected each time in adaptation to the moisture conditions of the bulk air. The authors concluded from experimental evidence that in measurements of 30 seconds in full sunlight, original temperature and moisture conditions in the leaf environment did not change very much. Indeed BIERHUIZEN (1965) cited an experiment under comparable conditions in which problems of changing the environment became too severe

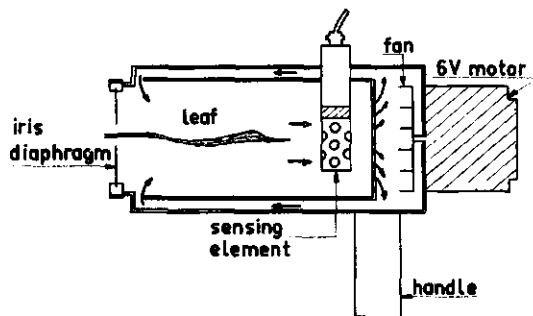


FIG. 6. Humidity sensing compartment. The arrows indicate direction of air movement. After GRIEVE and WENT (1965).

to be ignored. From the figures given by GRIEVE and WENT one may conclude that air temperature had in their experiments become at least one degree Celsius higher after 30 seconds. As regards leaf temperature we could remark that it will not be extremely different from air temperature as a result of the circulation in the measuring device. So it is questionable whether the original leaf temperature is retained during the measurement. An objection to severe modification of the boundary layer conditions is relevant if the original air surrounding the leaf was relatively still. This seems often not to be the case in the greater part of a canopy under normal wind conditions, as discussed earlier.

Apart from these considerations it is evident that a change in the energy balance of the leaf does occur (which may be interpreted as a 'glass house effect' of the lucite chambers). Therefore corrections in the form of back extrapolations in time would always be necessary to obtain an accurate idea about the evaporation of the leaf in its original environment from this kind of experiments. As concluded earlier the direct measurement of stomatal resistance is more useful.

It was therefore interesting to find out that independently from the above WALLIHAN (1964) used a small acrylic chamber, not surrounding the leaf but clamped onto it (Fig. 7). In this instrument the vapour flow was sensed by the same kind of LiCl-element (again of a range selected in correspondence with the ambient relative humidity). No ventilation was applied in the small chamber. The chamber air was dried before each measurement. The aim of this author was to have a (relative) measure of stomatal aperture under different conditions of interest outdoors, the cuticular resistance being estimated with closed stomates.

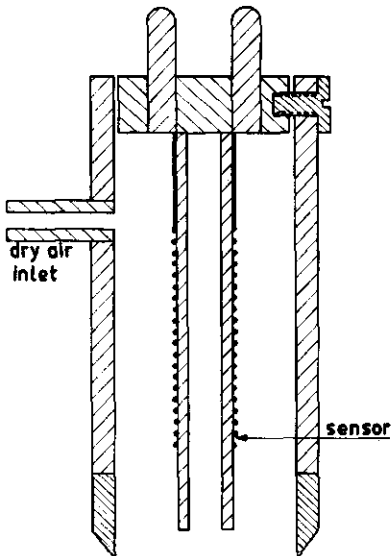


FIG. 7. WALLIHAN leaf diffusion resistance meter.  
After WALLIHAN (1964).

This preliminary work has been continued by several workers, resulting in a great number of modifications. A lot of differences do exist between them. We were in need of a choice which made accurate control in the laboratory as well as in field use possible. Moreover it is desirable to know whether differences from plant to plant, leaf to leaf, side to side and place to place of a leaf within the canopy are actual differences, i.e. not brought about by fluctuating influences or bad interpretation of the device. This is the more pressing as the literature is not of the same tenor regarding such differences and the actual values to be found in the field. Therefore the different modifications will be described here shortly and are summarized concerning their most important features in table 2. On this basis we designed our own type, which is being tested and calibrated at the moment.

The first modification was published by VAN BAVEL (1964) and VAN BAVEL et al. (1965). The most salient feature of these publications is the observation, with the instrument, of stomatal cycling. They used only one narrow range sensor (table 2) and tried to calibrate WALLIHAN's apparatus with diffusion paths of known length.

In such a calibration dummy resistances (against water vapour diffusion) of known value are placed between saturated blotter paper and the opening of the chamber holding the sensor. The transient times between two fixed electrical sensor resistances are now measured and a calibration curve of transient times against (dummy) leaf resistance is constructed (comp. Fig. 8). If the dummy resistances are correct replacements for the leaves the transient times measured in the field, under the same temperature conditions, are directly related to diffusion resistance values of the leaves concerned.

Five other modifications of this type have been constructed. DJAVANCHIR (1970) copied the VAN BAVEL arrangement but correctly used teflon instead of acrylic plastic for the chamber material. Teflon gives less problems with water vapour adsorption and absorption (and subsequent release) of the chamber walls. Moreover he made thorough calibration investigations on the effect of temperature. Different overall instrument temperatures and temperature differences between evaporating surface and the sensor chamber were found to be of high influence on calibration curves. This has been confirmed by MEIDNER (1970) and in the papers of MORROW and SLATYER (1971a, 1971b), which appeared during the preparation of this manuscript.

Two modifications were developed by STILES (1970), as reported originally by PENMAN (1966) and recently more completely by STILES (1970) and MONTEITH and BULL (1970). The main difference with the former types was the use of flat sulfonated polystyrene sensors. These sensors do only absorb a trace of the water entering the chamber in contrast to the LiCl-types which absorb very much water vapour. The first modification of STILES (1970) contains two of the mentioned sensors perpendicular to the evaporating surface, to make the chamber very small and therefore appropriate for application on narrow leaves. The second one has one sensor at the end of a small cylinder (MONTEITH and BULL, 1970). Another variant, inspired by the latter, was constructed by MEID-

NER (MEIDNER and MANSFIELD, 1968; MEIDNER, 1970) making the flat sensor movable within a long cylinder.

The last two constructions mentioned, the one used by MONTEITH and BULL and the one by MEIDNER, facilitate an analytical mathematical description of the diffusion of water vapour into the chamber and of the change of concentrations near the sensor. They make use, as did VAN BAVEL (1964) first, of dummy resistances for calibration, as described above, in the form of cylinders of different lengths with the same diameter as the opening of the chamber. MEIDNER by moving his sensor up and down in the cylinder, MONTEITH and BULL by placing different resistance cylinders between the chamber opening and the evaporating surface.

In the types described before, those of WALLIHAN (1964), VAN BAVEL (1964) and DJAVANCHIR (1970), the big LiCl-sensors were parallel to the cylinder walls (Fig. 7). Mathematical treatment of this situation is almost impossible. This disadvantage was removed by KANEMASU et al. (1969) which made in their modification of the WALLIHAN type the opening of the chamber in the wall of the cylinder. In this way there was only a very small layer of air between the evaporating surface and the almost parallel sensor surface. When the measuring period, depending on the choice of the fixed resistance values between which the transient time is measured, is held short enough FICK'S law may be applied to this situation (Eq. 1, 2).

The same holds true for the situation of a thin membrane or plate with very small holes, imitating the leaf resistance, set between a free evaporating surface and the opening of the chamber. In this way KANEMASU et al. obtained the straight line in their calibration plot (Fig. 8). They argued (without taking the absorption of the sensor into account) that replacing the pore-type resistance plates by the cylindrical tubes, as used by other authors, would change the calibration curve.

Diffusion into cylinders is with the initial and boundary conditions of these

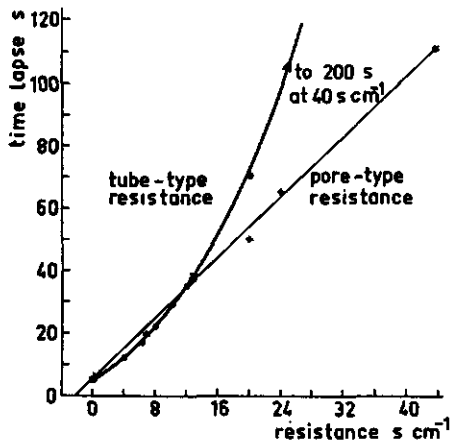


FIG. 8. Comparison of calibration curves obtained from tube-type and pore-type resistance elements. From KANEMASU et al. (1969).

experiments a non-stationary diffusion process and there is now a 'capacity' between evaporating surface and sensor. Diffusion theory gives a parabolic relation between time lapses and resistances (see Appendix 1). The latter ones may be expressed as a path length of normal stationary diffusion of water vapour into still air (1 cm length  $\approx$  4 s/cm). The experiments of KANEMASU et al. (1969) with tube-type resistances confirmed their point of view. It is shown in Appendix 1 that theoretically taking absorption of the sensor into consideration the results of KANEMASU et al. remain valid.

A consequence of the above is that calibrations with long tubes may not be used in combination with subsequent measurements on leaves (which have pore-type resistances).

This is not only true for the apparatus with LiCl-type sensors but also for the type of MONTEITH and BULL (1970). These latter authors beautifully used a solution of the diffusion equation for non-stationary diffusion into a one-dimensional semi-infinite composite medium for a mathematical description of their cylindrical apparatus (with extension tubes). This solution was adapted to their actual measuring device. They introduced an upper boundary condition of complete insulation at the sensor (diffusion is zero). We give part of their calculation, together with some comments, in Appendix 1.

MONTEITH and BULL calibrated their apparatus with pore-type resistances too and the values found in this way were not in agreement with the former ones (Fig. 9). Therefore they thought them to be wrong. However, the arguments as used by KANEMASU et al. (1969) – as described above – do also apply to their measurements. A comparison of the results of MONTEITH and BULL with the results of KANEMASU et al. (see Fig. 8 and 9 and Appendix 1) show a striking correspondence. It would therefore be worthwhile to recalibrate the interesting modification by MONTEITH and BULL with porous plates such as used for example by LEE (1969).

One more problem with the situation of long tubes under temperature differences remains the possibility of free convection, shortening the transient times in an uncontrolled way. The differences as reported in table 2 between

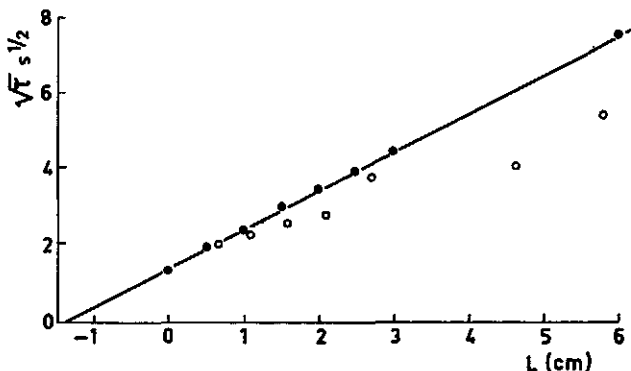


FIG. 9. Relation between square root of transit time ( $\sqrt{t}$ ) and path length ( $L$ ) for two calibrations. Black points give measurements with brass extension tubes and open points measurements with perforated plates. From MONTEITH and BULL (1970).

standard practices of measurements (as to the drying operation used and the shading of the leaf during measurements) find also their causes in different appreciation of temperature and convection problems encountered.

Appreciating these problems SLATYER (1966b, 1967b) as early as 1966 brought a fan into the (quite large) chamber to make, like GRIEVE and WENT (1965) did earlier, the leaf temperature more equal to the air temperature. Moreover the porometer becomes more sensitive. Our own experience sofar throws doubt on the equalness of temperature under all conditions. Modifications have been used by KAUFMANN (1968) and SLAVIK (1970), and by TURNER et al. (1969: to be able to introduce pine needles into the cup). Finally a modification for use on narrow leaves was made by BYRNE et al. (1970), who used also a different calibration method. They bring a certain amount of saturated air of known temperature into their chamber at a rate at which their sensor, of the quick and much absorption type, does not seem to show any overshoot.

They calibrated their sensor at one temperature only. It became apparent however from the most recent publication on the ventilated type of the leaf diffusive resistance meter, by TURNER and PARLANGE (1970), that of course also for the ventilated type calibration is absolutely necessary at different instrument temperatures. The analysis given by the last mentioned authors is the most thorough one hitherto published on the ventilated modification, be it true that their chamber was especially designed for the pine needle measurement. Adsorption and absorption at the wall may have had influence, as the publications of MORROW and SLATYER (1971a, 1971b) and our own experience point out. It still has to be investigated what the influence for this type of instrument is of calibration under a series of temperature differences between source and measuring chamber (sensor).

One, last problem remains the calibration of the ventilated meter only by porous membranes. Failures in this method may have been the reason for the far too low values reported by SLAVIK (1970), although TURNER and PARLANGE claim to have obtained confirmation by this method of their special and interesting calibration performance with which we will deal elsewhere. Their only example cited is however not completely convincing. The influence of a known high pore-type resistance on their calibration curves will also have to be investigated experimentally. It will therefore deserve special attention in our measurements. In our modification of the resistance meter we have tried to make use of the many experiences gathered during recent years by the above mentioned authors. We will also try to add some more evidence to the usefulness of this type of instrument, which has been emphasized repeatedly over recent years to be of high value to research now and in the near future (e.g. MONTEITH, 1968; BARRS, 1968; MILTHORPE, 1969; BERGER, 1970).



TABLE 2. Most important features of modifications of the WALLIHAN leaf diffusion resistance meter. Sequence of authors has been chosen after the time of final results published.

Authors	Ventilation	Calibration	Temperature measurements	Leaf shaded during meas.	Drying operation	Humidity range (approx.)
1. WALLIHAN (1964)	no	no	outside the chamber near the leaf.	one minute before and during meas.	before clamping	variable
2. GRIEVE and WENT (1965)	yes	no	air temp. within the chamber (no routine)	no	no drying	variable
3. VAN BAVEL (1964)	no	by tubes	not emphasized but possible.	not reported	before clamping	14-27% R.H.
VAN BAVEL et al. (1965)						
4. SLATYER (1966b, 1967b)	yes	not reported	chamber air temp. (leaf temp. possible)	not reported	not reported	not reported
5. KANEMASU et al. (1969)	no	by tubes and by membranes	air temp. within the chamber.	a few seconds before and during measurements	presumably before clamping	14-27% R.H.
6. BYRNE et al. (1970)	yes	by injection	air temp. within the chamber.	not reported	after clamping	Mid range
7. TURNER et al. (1969)	yes	by membranes	chamber air temp. (leaf temp. possible)	not reported	clamping before	11% R.H.
TURNER and PARLANGE (1970)		and by a 'two sensor method'				20-30% R.H.
8. KAUFMANN (1968)	yes	by membranes	presumably chamber air temp.	not reported	presumably after clamping	30-34% R.H.
SLAVIK (1970)						
9. DJAVANCHIR (1970)	no	by tubes	chamber air temp. leaf temp. and air temp. within the chamber.	yes	before clamping	not reported
10. STILES (1970) I (narrow leaves)	no	not reported	as in 11	as in 11	as in 11	as in 11
11. STILES (1970) II	no	by tubes and by membranes	cup temp. near the leaf.	no	after clamping	55-85% R.H.
MONTEITH and BULL (1970)		by membranes	near the leaf.	yes	clamping before	
12. MEIDNER and MANSFIELD (1968)	no	by tubes (built in)	leaf temp. and air temp. within the chamber.	yes	before clamping	55-85% R.H.
MEIDNER (1970)						

## 6. SUMMARY

Relevant factors and methods are discussed and a literature review is given regarding the direct measurement of leaf diffusion resistance to water vapour, with emphasis on field measurements. After an introduction on leaf resistance and canopy climate a few summarizing remarks are made on the behaviour of stomata. In two subsequent chapters the components of the diffusion resistance and the factors which may (apparently) influence its value, as measured by a suitable device, are discussed. Emphasis is laid on what happens within the leaf. A consideration of the external resistance within canopies has been added. Finally a suitable apparatus for vertical profile measurements within a canopy, the WALLIHAN leaf diffusion resistance meter, is discussed. Existing modifications are reviewed and some calibration conditions for different types are dealt with. A theoretical derivation of the fact that calibration with pore-type resistances is necessary, is added in an Appendix.

## 7. ACKNOWLEDGEMENTS

I am highly indebted to Prof. Dr. Ir. C. T. DE WIT, head of the department of theoretical production ecology, and to Prof. Dr. Ir. J. SCHENK, head of our department of physics and meteorology, for stimulating suggestions and for thorough and very useful criticism on a draft form of the manuscript. Dr. P. E. WAGGONER from the Connecticut Agricultural Experiment Station at New Haven was so kind to read the manuscript and to give some valuable comments. I mention thankfully the discussions on some of the subjects dealt with above with my colleagues Ir. J. GOUDRIAAN, from the theoretical production ecology department, and Dr. F. A. BOTTEMANNE from this laboratory.

I acknowledge gratefully consent from authors and/or publishers for reproduction of the figures 4, 7, 8 and 9.

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## 9. APPENDIX 1

For a mathematical description of diffusion into their measuring device, MONTEITH and BULL (1970) made use of diffusion theory for a one dimensional semi-infinite composite medium (see CRANK (1956), p. 39). For comparison with the case of KANEMASU et al. (1969) we derive their results along a somewhat different way.

A well known solution for the case of diffusion along the vertical positive  $z$ -axis from a surface  $z = 0$ , held for  $t \geq 0$  at a constant concentration  $c_0$ , into a semi-infinite medium of uniform properties reads:

$$c = c_0 \operatorname{erfc} (z/\sqrt{4 Dt}) \quad (7)$$

To apply this approach to the finite calibration cylinders we must extend this formula to a series of complementary error functions (CRANK, 1956, p. 14). As a boundary condition at the sensor for the case of MONTEITH and BULL we may introduce complete insulation, since the absorption by their sulfonated polystyrene sensor is negligible in this connection. If we localize the position of the sensor at  $z = L$  and if we abandon all terms of the series except for the first two the concentration at  $z = L$  can be written as:

$$c = 2 c_0 \operatorname{erfc} (L/\sqrt{4 Dt}) \quad (8)$$

with  $dc/dz = 0$  at  $z = L$ .

We assume neglect of all terms but the first two permitted for

$$c_0 \operatorname{erfc} (2L/\sqrt{4 Dt}) < 0.1 c_0 \quad (9)$$

Tables of the  $\operatorname{erfc}$  show (see e.g. CRANK (1956), p. 326) the argument to have to obey in this case:

$$2L/\sqrt{4Dt} > 1.2 \quad (10)$$

from which follows:

$$t < 0.7 L^2/D \quad (11)$$

In our case of diffusion of water vapour in air into cylinders of length  $L$  (in cm) this means that approximately

$$t < 2.8 L^2 \quad (12)$$

This condition is satisfied in the experiments of MONTEITH and BULL (Fig. 9).

If for different calibration cylinders the time  $t$  is measured to obtain a certain fixed concentration  $c$ , at the sensor plane, we can see from (8) that a linear relation must occur between  $L$  and  $\sqrt{t}$ . Simple algebra shows the same kind of relation to be true for time differences between two fixed concentrations and  $L$ . This was completely confirmed by the experiments of MONTEITH and BULL (see Fig. 9). Only a small correction to  $L$  appears to be necessary to account for the

non-zero depth of the measuring cup (distance between entrance and sensor).

The calibration procedure of KANEMASU et al. can be treated mathematically along the same lines. In their case, contrary to MONTEITH and BULL, the sensor absorbs an important part of the vapour that arrives at  $z = L$ . Therefore we introduce as an approximation a new boundary condition:  $c = 0$  at  $z = L$  (i.e. all vapour is absorbed).

Again we can describe the concentration  $c$  as a function of time  $t$  and place  $z$  by a series of complementary error functions. MONTEITH and BULL state that the concentration of vapour in the cup for this case would tend to decrease linearly from the value for saturated air in the plane of the source to a value close to zero in the plane of the detector. This, however, would only be true for a stationary situation. Taking again only the first two terms of the now alternating series of complementary error functions into consideration, condition (9) and therefore condition (12) have to be true for this case too. It is to see from the values in Fig. 8 that the points of the parabolic curve satisfy this condition (12).

For this case it is interesting to calculate the mass of vapour,  $M_t$ , that is absorbed in the sensor after a time  $t$ . We therefore have to integrate the flux:

$$M_t = - \int_0^t D \left( \frac{dc}{dz} \right)_L dt \quad (13)$$

Introducing (7) in (13) and multiplying by two because we take two terms of the series into consideration gives:

$$M_t = \frac{4Dc_0}{\sqrt{\pi}} \int_0^t \frac{e^{-L^2/4Dt}}{\sqrt{4Dt}} dt = 2c_0 [\sqrt{4Dt/\pi} e^{-L^2/4Dt} - L \operatorname{erfc}(L/\sqrt{4Dt})] \quad (14)$$

One sees from (14) that if  $M_t$  is constant, a fixed relation exists between  $L$  and  $t$ . As transient times between two fixed electrical resistance values of the sensor are measured we work always with a fixed amount of water absorbed by the sensors (apart from problems of time constants of the sensors). Therefore indeed  $M_t$  has to be constant for the measurements of KANEMASU et al. In the graphical representation of KANEMASU et al. the quantity  $L$  is replaced by the diffusional resistance ( $R = L/D$ ). This, however, does not violate the relation derived, as  $D$  is a constant.

Taking into account a small correction for the distance between source and sensor, one calculates from points of the curve in Fig. 8 that  $M_t$  is indeed quite constant. Deviations for high time lapse values can easily be ascribed to the very rigorous approximations that were applied in the derivation of (14). Therefore the measurements of KANEMASU et al. have now a theoretical base also for the case in which the sensor is taken into account.

As to the points of Fig. 8 and 9 which are measured with pore-type resistances the following reasoning applies. For the case of KANEMASU et al. we may see the situation as approximated by two fixed concentrations,  $c_0$  and 0, over a thin

layer of air. Therefore FICK's law does apply here, as is confirmed by the straight line in Fig. 8. For MONTEITH and BULL's case the points have to deviate from their straight line in Fig. 9 more and more when a bigger part of the total resistance is formed by pore-type resistances. This is confirmed by their measurements and makes it indeed necessary to recalibrate their device.