C.J. Stigter

Department of Physics and Meteorology, Agricultural University, Wageningen, The Netherlands

The epidermal resistance to diffusion of water vapour: an improved measuring method and field results in Indian corn *(Zea mays)*

Centre for Agricultural Publishing and Documentation

Wageningen - 1974

ISBN 90 220 0543 7

The author graduated on 21 November 1974 as Doctor in de Landbouwwetenschappen at the Agricultural University, Wageningen, the Netherlands, on a thesis with the same title and contents.

Abstract

Stigter, C.J. (1974) The epidermal resistance to diffusion of water vapour: an improved measuring method and field results in Indian corn *(Zea mays)*. Agric. Res. Rep. (Versl. landbouwk. Onderz.) 831, ISBN 90 220 0543 7, (vi) + 25 p.
Also: Doctoral thesis, Wageningen.

The resistance of the epidermis of the leaf to diffusion of water vapour can be measured most accurately in the field by closed diffusion porometers. It was possible to overcome the problems related to calibration and to dynamical use of a LiCl humidity sensor in the porometer. The dynamic behaviour could be represented by one calibration volume provided a special measuring scheme is applied. Presence or absence of device influence on the opening situation of the stomata is demonstrated. Measurements on corn leaves yielded permitted clamping times of 1½ to 2 minutes. All sunlit places of corn leaves, sampled throughout a dense crop on a moist soil, showed on the average a basic equality in resistance. Sampling shaded places separately this equality was also found in the average reaction of resistance to different light density levels.

Symbols

D = diffusion coefficient of water vapour in air (s/m^2)
d' = Penman and Schofield's equivalent diameter of funnel-shaped holes (m)
d_m = mouth diameter of the holes in the porous membranes (m)
d_t = throat diameter of the holes in the porous membranes (m)
e_ℓ = absolute humidity at the (artificial) evaporating surface (kg/m^3)
e_p = absolute humidity within the porometer (kg/m^3)
I = water vapour flux density (kg/m^2s)
K = slope of lines in the resistance/transient time diagrams (m)
ℓ = length of the holes in the porous membranes (m)
n = number of holes per unit of surface for the porous membranes
Q = ratio of long and short transient times
R_ℓ = (dummy) leaf diffusional resistance for water vapour (s/m)
R_m = porous membrane resistance for water vapour (s/m)
R_p = porometer diffusional resistance for water vapour (s/m)
S_p = surface of the porometer entrance opening (m^2)
T = temperature (K)
t = time (s)
t_f = time of passage of second fixed electrical resistance of humidity sensor (s)
t_i = time of passage of first fixed electrical resistance of humidity sensor (s)
V_p = air volume of the porometer during measurements (m^3)
V_t = calibration volume of the porometer (m^3)

Introduction

Science has become a production factor of continuously increasing importance. It is no longer a mere search for scientific truth. Application of science therefore implies directing the use of production forces. Directing the bulk of production forces to satisfy the exorbitant needs of powerful minorities seems at least selfish. It becomes even intolerable when scientific potential and results of scientific research are used to maintain and strengthen the dominant position of such minorities. Then the application of science becomes an accessory to the suffering of a majority of mankind. Hence no scientist can deny his direct responsibility in relation to the problems and crises of today's world *as a whole* and consequently he should work on bridging the gap between his science and its participation in solving *these* problems and crises.

Based on these premises the science of physics can also be used in many fields, although most physical research is not yet involved in solving the most urgent problems. We chose to tackle problems related to the growth of more and better food and to take part in bridging the mentioned gap by promoting agricultural or environmental physics. The physicist who makes this choice has to provide the scientists working in agricultural research with physical knowledge in a form that is closely tied to the fields of application concerned. This task does not, however, relieve him of his responsibility with regards to the choice of problems to attack.

Agricultural science tries to use and extend our knowledge for a better production of food. Also *within* this scientific field priority criteria have to be defined. As an important *external* criterion, those research projects deserve priority that are closely geared to an improvement of the opportunities of food production and to a distribution of products that are based on promotion of social justice, both on a world scale and a local scale. As an *internal* priority criterion, research that suc-

ceeds in integrating existing knowledge from various fields, for a synthetical approach to improve our understanding, contributes most to the practice of better production.

The latter criterion is fully met by research that tries to increase our insight into crop growth processes by the construction of simulation models of plant growth. Such models are based on quantitative relationships describing processes and the models are provided with relevant information collected and integrated from many disciplines. Our laboratory, that does research in environmental physics (Schenk et al., 1973), came into contact several years ago with the Department of Theoretical Production Ecology of our University. This department works on construction of growth models (e.g. de Wit et al., 1970). This contact resulted in a project of collection of meteorological and related field data. These data are being used as input and check of output of the micrometeorological or crop climatological submodels of the growth models.

After preliminary assistance in constructing the submodel, the most important part of our work was the design of instruments adapted for spatial measurements inside and above the chosen crop of Indian corn (*Zea mays* L.). The first results with a preliminary model (Stigter, 1972) pointed to the important conclusion, also drawn by Monteith (1973) in his recent textbook, that the main limitation of microclimatic models is ignorance about spatial changes of the epidermal resistance of leaves in a canopy. Monteith added that the spatial changes had seldom been measured with accuracy. Therefore we paid special attention to exploration of canopy leaf resistance to water vapour and its direct measurement by relevant sampling *throughout the crop*. Our work on these subjects has been reported in detail in three publications (Stigter, 1972; Stigter et al., 1973; Stigter and Lammers, 1974).

The first publication is a literature review and discusses relevant factors and methods for the measurement of leaf diffusion resistance to water vapour. Thorough attention was paid to field measurements. Emphasis was laid on what might happen inside the leaf. Possible side effects of attaching a measuring device onto the leaf were considered. A short review of existing methods indicated that diffusion porometers are potentially the most reliable instruments for measuring canopy resistance

profiles. Existing modifications were finally compared and their problems reviewed.

In the second publication we report on design and calibration of an improved diffusion porometer. From literature reports published during our research it appeared that the accuracy of the existing types was much lower than earlier supposed. This was in accordance with our results. We discussed how to cope with the difficulties and outlined a pertinent theory. Special attention was given to a new calibration method. A new measuring strategy was introduced. A chapter on the automatic self-timing circuit in use, mainly written by two colleagues, the electronic engineers J.Birnie and B.Lammers, was added.

The third publication reports on the use of the improved diffusion porometer and deals first with the independent determination of the diffusion resistance of dummy epidermes for calibration. Their use in comparison measurements with the porometer and in checking the field measuring strategy is demonstrated. Some experiments in growth chambers and field results in Indian corn are reported. Thorough attention is given to any possible influence of the apparatus on the resistance to be measured and to the methods of sampling. The use of the measured canopy profiles in simulation models is discussed. The results in this third article prove the importance of a reliable measuring method as discussed in the second article and the need to know what may happen with leaf and stomata (as dealt with mainly in the first article of the series).

Whereas a preliminary review of some results has been given recently (Stigter, 1974) this publication is a full summary of the most important results obtained in improving the measurement of epidermal resistance. It will mainly deal with the improved device and with some of the field results obtained in sampling Indian corn. For more details than reported here the publications shortly reviewed above should be consulted.

Materials and methods

Theory of a suitable instrument

For measuring directly the epidermal resistance to diffusion of water vapour, the closed diffusion porometer is the most promising instrument. The vapour flux, as it diffuses from the mesophyll cell walls through the epidermis of the leaf, is detected directly. Changes in the two concentration potentials will certainly produce differences in the vapour flux density between the situation before and after clipping of the instrument onto the leaf. Such changes have to be incorporated in the detection. The boundary layer resistance over the leaf, which acts in series with the leaf epidermal resistance to be measured, will change also. This again modifies the existing flux density. But again such differences can be taken into consideration. However, it is important to prevent modification of the flux density by changes in functioning of the stomatal system during the measurement.

As to the potential at the leaf side, which is formed by the vapour concentration at the sources inside the leaf, temperature of the measured leaf part is nearly always a sufficient determinant. For the potential at the porometer side and for the modified boundary layer, the measuring method must be considered in more detail.

The principle is simple. The porometer consists of a small cup containing a humidity detector (Fig. 1). For several reasons electrical humidity sensors are normally preferred. The device is clamped onto a leaf, and then the initially low absolute cup humidity, preferably made spatially uniform by a little fan, increases. The transpiration rate is determined by the leaf resistance but also by the new diffusion resistance of the boundary layer (= porometer). The rate is also determined by the new leaf temperature, which has to be constant over the measuring period and by the (changing) absolute humidity in the cup. The rate of change of this absolute cup humidity is itself determined by the transpiration rate. Ideally it is indicated directly by the rate of decrease of

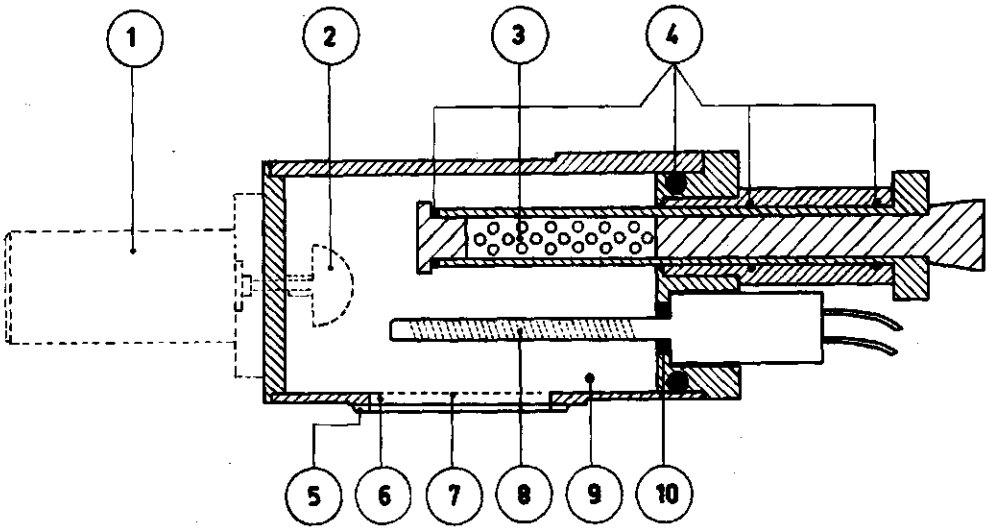

Fig. 1. The Wageningen Laboratory of Physics and Meteorology diffusion porometer. Cross-section through the central longitudinal axis of the cylindrical cup (V_p = 39.9 ± 0.2 cm^3). The material used is polypropylene. 1. motor; 2. fan; 3. silica gel holder, which may be moved into and out of the cup; 4. O-rings for sealing; 5. rubber sealing fringe around the sensor cup opening; 6. sensor cup opening (2.03 ± 0.01 cm^2); 7. perforated membrane for suppression of turbulent exchange between cup air and ambient air; 8. humidity sensor (length 4 cm, diameter 3 mm); 9. thermistor; 10. luting material to fix the sensor.

electrical resistance of the humidity sensor. The time needed for a fixed decrease of sensor electrical resistance (between two fixed points of the log-linear part of its calibration diagram of electrical resistance against relative humidity) is now taken as a measure for leaf diffusion resistance. Cup air temperature has to be measured because of the temperature dependence of the sensor calibration curves. After each resistance measurement the cup air is dried to its original starting point. To cancel out starting-up effects this point is a good deal higher in electrical resistance (drier) than the two fixed values used in the measurement.

What happens with the absolute humidity in the cup during a measurement is expressed by:

$$\frac{d\, e_p\,(t)}{dt} = \frac{S_p}{V_p} I\,(t) \qquad (1)$$

which can be approximated as:

$$\frac{d\, e_p\,(t)}{dt} = \frac{S_p}{V_p}\ \frac{e_\ell - e_p(t)}{R_\ell + R_p} \qquad (2)$$

If all parameters are constant, integrating Eq. (2) between the two times t_i and t_f, at which the fixed electrical resistance values are passed, gives:

$$t_f - t_i = \Delta t = \frac{V_p}{S_p}\,(R_\ell + R_p)\,\ln\frac{e_\ell - e_p(t_i)}{e_\ell - e_p(t_f)} = K\,(R_\ell + R_p) \qquad (3)$$

If the sensor takes up a negligible amount of water for indication, it would be sufficient to obtain R_p by a measurement with the porometer over a saturated surface of known temperature. K, being different for each combination of evaporating surface and cup temperatures, is known in theory. R_p being determined in this way, unknown R_ℓs could be obtained by measuring transient times Δt.

The diffusion porometer in practice

The method as described in the former section was found to be troublesome in practice. Because most causes of this remained obscure, a thorough investigation of the instrument behaviour was necessary. From our research three main reasons were indicated. Firstly awareness of sensor properties was insufficient. Therefore an explanation of a series of anomalies in behaviour remained impossible. Secondly some calibration methods appeared to be incorrect. Thirdly porometer wall materials were used that with their own short time absorption and adsorption properties influenced the processes that took place in cup and sensor. We found that the much used perspex was inferior and that teflon and polypropylene were appropriate. We preferred polypropylene.

For calibration it is necessary to have dummy resistances that imitate leaf epidermal resistance correctly, from the point of diffusion theory. Therefore pipes of different length for imitating R_ℓ or injection of saturated water vapour, as reported in the literature, are bound to fail as calibration methods. Dummy resistances preferably consist of multipore membranes from which the resistance can be calculated from pore

number and dimensions or can be determined independently from evaporation measurements. We used commercially available nickel multipore membranes, provided with holes with a circular axial cross-section. We proved that the formula for resistance to diffusion through such membranes, as adapted by Penman and Schofield (1951), gives very accurate results. This modified formula is:

$$R_m = \frac{4\ell}{\pi(d')^2 nD} + \frac{1}{2d'nD} + \frac{1}{2d_t nD} \qquad (4)$$

with

$$d' = \sqrt{d_t \sqrt{d_t d_m}} \qquad (5)$$

The results obtained with Eq. (4) were compared for 14 different membranes with improved results from simple evaporation experiments with receptacles sealed by the membranes. Some results, for membranes finally used for calibration, are given in Table 1.

Porometer measurements with a series of (correct or incorrect) dummy R_ℓ have been common practice for calibration. The slope K and the intersection R_p from an assumed straight line relationship, Eq. (3), were then used as calibration factors, mostly without further calculations from this slope. Comparable to what has been shown above to be valid in theory, each combination of sensor (cup) temperature and surface temperature yielded its own calibration line. Later observations, in accordance with ours, even showed these calibration lines to alter in the course of time. This

Table 1. Values, for calibration membranes, of calculated resistances by Penman and Schofield's formula and measured resistances. The latter ones are obtained from evaporation experiments and improved by mutual comparison using the porometer.

Membrane type	Calculated resistance (s/cm)	Measured resistance (s/cm)
20 T VERO	6.10 ± 0.35	5.70 ± 0.10
15 T VECO	5.55 ± 0.25	5.45 ± 0.10
30 T VECO	2.75 ± 0.10	2.75 ± 0.10
30 R VECO	1.35 ± 0.10	1.50 ± 0.10
125 T VECO	0.50 ± 0.02	0.55 ± 0.25

makes thorough calibration in such a way already unmanagable. The number of calibration measurements needed would at least be reduced by having leaf and cup in the field at the same temperature. But firstly inevitable deviations from this condition introduce appreciable errors. Secondly the required artificial shadowing of sunlit leaf parts prior to each measurement enhances the risk of a change in stomatal opening conditions before the end of the measurement. It appeared therefore worthwhile to study this calibration in more detail.

Taking measurements over our calibration membranes we obtained indeed straight lines such as line 1 in Fig. 2. By calculating a volume, V_t, from the slopes, using Eq. (3), much higher values than the actual volume V_p of 40 cm^3 were found. The volumes measured became higher each consecutive day of measuring under identical conditions (Figs. 2 and 3). Changing the cup temperature yielded relations between volumes and temperatures as given in Fig. 3. But changes in evaporating surface temperature, with the other conditions unchanged, did not influence V_t (Fig. 2). No two sensors showed the same behaviour in the course of time.

Making use of what was found in the literature on LiCl sensors, as used in our porometer, and doing complementary investigations, we could explain the behaviour as described before from the following sensor properties:

- an absorption of water vapour which is not negligible in comparison with V_p,
- a time lag between actual humidity in the cup and indication by the sensor,
- changes of this response time and of calibration in the course of time (ageing effects),
- a temperature dependence of the response time,
- an insensitivity of the response time to the rate of transpiration into the cup,
- a mere dependence of the response time on the *constant amount* of absorbed water per unit of (relative) humidity change in the cup.

If the amount of absorbed water per unit change of humidity and not the rate of change of humidity determines sensor indication, the two main aspects are clear. The straightness of the lines in Fig. 2, dynamical sensor properties included, can be understood from the apparent constancy of the amount absorbed. The result is one V_t for different resistances, and so for different transpiration rates. Then it is no longer surprising

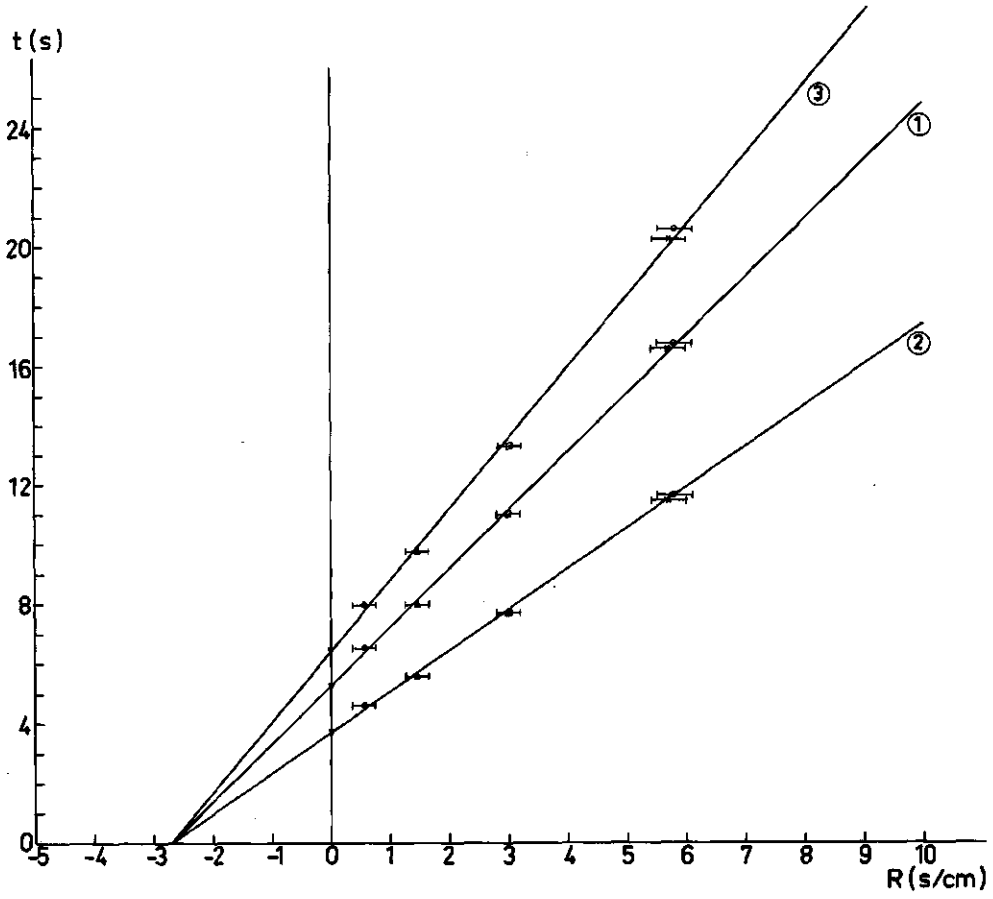

Fig. 2. Line 1 represents a calibration, after six weeks of intensive sensor use, with cup and surface at about 27°C, giving a V_t of 213 cm^3. Line 2 represents a calibration made on the same day as line 1, with the same cup temperature but with the surface now at about 31°C, giving a V_t of 212 cm^3. With cup and surface both at 27°C, lines with a slope such as line 2 were found when this sensor was still hardly used, with a V_t of about 140. The calibration marked 3, with V_t = 272, under the same temperature conditions as line 1, was made after five months in which periods of intensive use were succeeded by periods of storage under dry conditions.

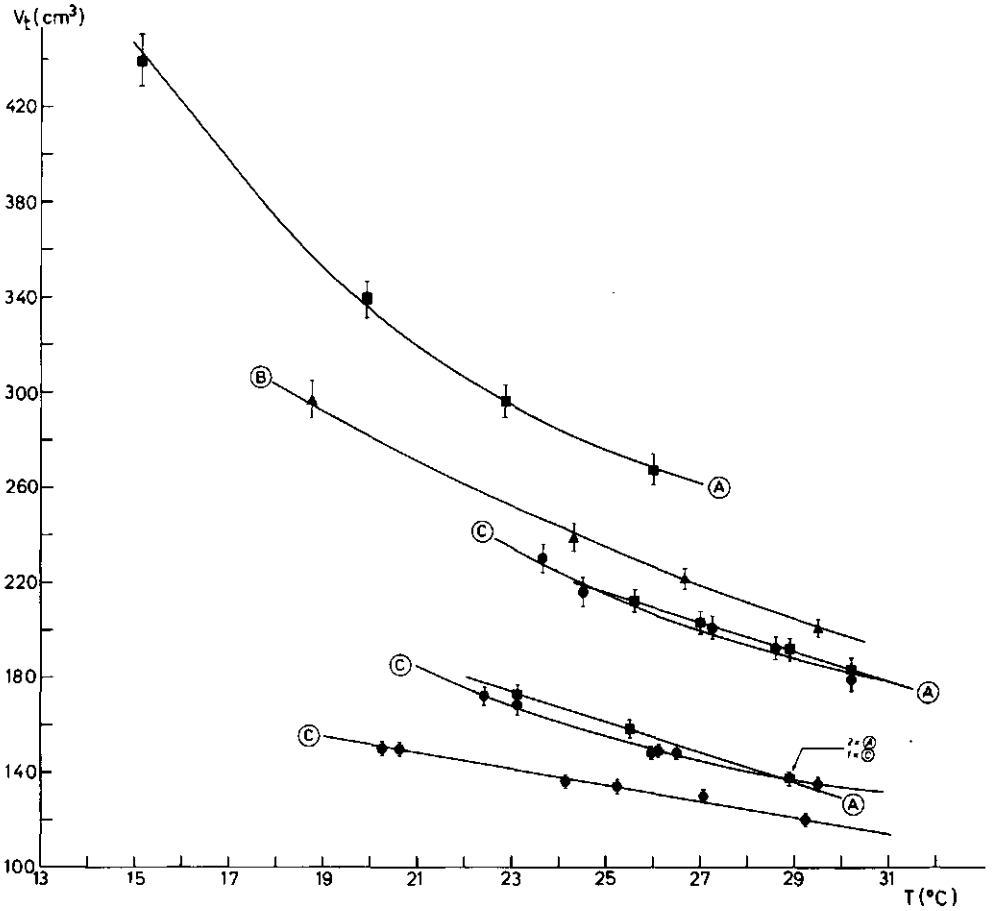

Fig. 3. The relation of V_t with temperature in the course of time for three sensors. Sensor A: lowest straight line in the first week of its use, second straight line one month (of intensive use) later, upper curve after five months of alternate intensive use and storage. Sensor B: only the curve after half a year of use in preliminary investigations and testing of other calibration methods, succeeded by half a year of dry storage. Sensor C: straight line in the first week of its use, lower curve after one month of intensive use, upper curve after eight more months of dry storage with occasional usage. Curves such as the last two and B may, of course, also be approximated by two straight lines. The figure illustrates clearly the individual character of the sensors. This does, however, in no way invalidate the calibration method. Note: near the point of intersection of the lowest A-line and the lower C-curve we have accidentally three measuring points, two equal ones on A and one on C.

that surface temperature also has no influence. This very important fact was confirmed by a series of measurements such as shown in Fig. 2, lines 1 and 2, resulting in the same V_t. So our calibration method makes it possible to measure sunlit leaf parts directly.

The R_p values, determined from the intersections with the abscissa of the lines in Fig. 2, could be almost completely deduced from calculations of turbulent transport processes taking place in the cup. Finally to obtain consistent results we found it absolutely necessary to have the water distribution within the sensor stabilized, for about two minutes, before each measurement. This distribution must be the same, before each measurement, at the starting point of the starting-up period prior to the passage of the first electrical resistance. Therefore the use of the same fixed starting point was an indispensable condition for calibration and subsequent field use. With this scheme all ageing effects of the sensor could be found back in the change of V_t in the course of time. Determination of the course of this (apparent) calibration volume was therefore sufficient to cope with the troubles experienced.

The best measuring procedure was the following. When a whole day of measurements in the field was planned, a V_t and a R_p were determined the day before with two or more dummy R_l values at at least two cup temperatures. This was repeated the day after the field measurements. A mean V_t curve from the two calibrations was used for the day inbetween, when the field measurements were taken. If the relationship between V_t and temperature (Fig. 3) was no longer a straight line, the last occasional determination of the course of V_t with temperature was used to bring a curve through the calibration points. The form of this relationship changed only slowly in the course of time (Fig. 3). This measuring scheme was shown to be valid by using a series of known dummy resistances in an imitation of a field trial.

Field experiments

Precautions in the field

In the field careful attention was paid to two factors that are often neglected. These are the accurate measurement of the temperature of the leaf parts concerned and the possible influence of the porometer on stomatal opening during the measurement.

Because of the importance of good e_ℓ-measurements it is necessary to assess accurately the (internal) leaf temperature. It was found most suitable to measure the temperature on the leaf side opposite to that used for resistance measurement. A special construction held the leaf thermistor insulated from the porometer clamp. Slight pressure of two springs on the thermistor touching the leaf and a construction that averages the temperature of a part of the surface to be measured and keeps the thermistor wires also at leaf temperature, facilitated the attainment of the actual leaf temperature. The thermal time constant of this construction, when used on a leaf, was about 4 seconds. It was proved that the leaf time constant was even less, under our conditions. Hence for transient times Δt of 10 seconds or more, we could use the temperature read directly after passage of the second fixed electrical resistance. For the shortest measuring times observed (of the order of 5 seconds), the thermistor could be read once more after the passage of a third fixed electrical resistance, which we introduced for this and other purposes.

The introduction of a third electrical resistance made it possible to measure two transient times. For a short transient time we made use of an apparent change of only 1.5% relative humidity in the cup, from about 20% relative humidity upwards. For a long transient time we used the whole linear part of the earlier mentioned equilibrium diagram, amounting to 6.5% of apparent change in relative humidity from the same value upwards. Thus the long transient time included the short one. We

found that V_t, representing the dynamical characteristics of the measurement, was almost the same for long and short transient times.

It can be seen from Eq. (3) that the ratio Q of long and short transient times must theoretically be constant, at fixed temperatures, as long as R_ℓ is the same for both transient times. It is easy to determine Q in the laboratory under controlled temperature conditions and with dummy R_ℓ values, that remain constant over the measurement. This procedure simply formed part of the calibrations. The Q predicted, between 3.5 and 4.5 in our experiments, can now be used for immediate information on what happens in the field. Under identical temperature conditions and no water stress, a difference between the predicted and the measured Q is a direct indication that at least after the short transient time something happened to the opening status of the stomata. As it could be argued that our device can only cause closing of the stomata, a too high Q indicates influence from the device.

We measured small deviations from the theoretically expected value of the constant Q, notably for the combination of low V_t and low R_ℓ. The reason could only be a small inconsistency, for this combination, in the determination of R_p. We found that this must be because the porometer diffusion processes did not completely obey Fick's law on which the derivation of Eq. (3) was based. However, this nowhere invalidated the use to be made of Q.

Influence on the stomata

An example of the prediction capability of Q is given in Table 2. It contains a series of consecutive measurements on upper and lower sides of fully sunlit parts of corn leaves. We used here measuring places near the top of big leaves, not far from the central vein, in a 1-m high crop on a moist soil. For this measurement series we used a sensor with a low V_t and because of the ideal radiation conditions the R_ℓ values were small. Because of the resulting small short transient times and the proved absence of device influence on the results, the same measurement series was used to test the field performance of the temperature measuring system dealt with.

It follows from Table 2 that no significant influence of the device was present during clamping times of half a minute. For studying clamping

Table 2. For these 20 consecutive measurements, with a mean arithmetical resistance of 2.25 s/cm, the mean ratio between long and short transient times was found to be 3.61 ± 0.04 at 27.5°C mean cup temperature. From calibrations the day before and the day after the measuring day we expected at this resistance and this temperature 3.64 ± 0.04.

Short time (s)	Ratio	Leaf side	R_ℓ (s/cm)	Short time (s)	Ratio	Leaf side	R_ℓ (s/cm)
5.34	3.60	U	2.00	6.22	3.60	U	2.70
5.64	3.57	L	2.15	5.46	3.65	L	2.65
5.90	3.64	U	2.65	5.15	3.55	U	1.95
5.70	3.64	L	2.45	4.80	3.59	L	1.85
5.61	3.61	U	2.20	4.57	3.56	U	1.65
6.64	3.65	L	3.15	4.47	3.60	L	1.65
6.35	3.60	U	2.75	5.20	3.62	U	2.25
5.08	3.59	L	1.90	5.04	3.63	L	2.15
4.93	3.61	L	1.65	4.69	3.60	U	1.70
7.57	3.60	U	3.50	5.10	3.64	L	2.10

times *with* a possible influence of the device on the opening situation of the stomata, measurements with a sensor with high V_t on leaves with a relatively high R_ℓ are needed. Because of the variability involved an appreciable number of such measurements have to be made. In 1972 we used five days of measurement for this purpose. After correction for a supplementary variation in Q because of capriciously changing light conditions on these days, we collected measurements with large *long* transient times and correct Q and measurements with a too high Q. From comparison of these long transient times we learned that in the morning clamping times of about 2 minutes were permitted without device influence on the resistance. In the afternoon permitted clamping time became about 1.5 minutes. This meant that for a correct measurement we could use up *short* transient times of about half the permitted clamping times, the starting-up period being about as long as the short transient time concerned. Most measurements needed clamping times between 10 and 60 seconds, if the porometer was provided with a sensor with a relatively low V_t. Under the light conditions concerned, no difference in susceptibility to closing influences could be detected between leaf parts throughout the canopy.

Resistance profiles in corn

We wanted to use our field epidermal resistance observations for calculation of the effective resistance of different crop layers in a dense corn crop. For the total vapour flux from the total leaf surface in the layer, resistances of different leaf parts are, of course, parallel resistances, each in series with the boundary layer resistance concerned. Therefore *harmonic* means are preferred. To study the spread of resistance of our 2-cm^2 samples of leaf surface, we looked at frequency distributions over the *arithmetical* means of a sufficient number of equivalent measurements. Each measurement takes 2.5 to 3 minutes, including the time needed for recovery of the sensor. So, for studying differences throughout a crop, no unknown trends of resistance with time should exist over the period to be averaged.

In accordance with existing evidence, our first measurements already showed that on moist soil the average resistance of a corn leaf was highly correlated with light density over the leaf surface. The most interesting kind of relationship, that between absorbed light in the wavelength regions responsible for stomatal action and the diffusion resistance, has never been determined. To obtain such a relationship with any reliability would be extremely difficult. Therefore cancelling out the light factor by sampling would seem a good approach. Because of the difference in their relative contribution, the best choice for a dense crop like ours is to study sunlit leaf parts and shaded leaf parts separately. Variability in resistance within these two categories for a certain crop layer is now supposed to be due to differences in stomatal functioning under identical light density and to differences in light density, stomatal geometry and effective surface measured.

With systematical sampling of sunlit corn leaf parts, averaging out the above random factors, we found no basic differences in resistance between any of the sunlit leaf parts throughout our complete corn crop on the moist soil. Some indication for a slight deviation from this rule in the lowest crop layer investigated may be attributed to the frequent occurrence of intermittently illuminated leaf parts deeper in the canopy and to penumbral effects.

The same approach to shaded leaf parts, again sampling heavily three different crop layers, yielded the following results. For each layer again no significant difference in average resistance was observed between any

Table 3. Epidermal resistances R_ℓ (s/cm) of a unit of leaf surface determined as harmonic means of N_{tot} measurements on sunlit places for three different crop layers under high light density over the crop. Abbreviations: Su = sunlit leaf part, U = upper leaf side, L = lower leaf side, H = highest crop layer (> 1.75 m), M = middle crop layer (between 1 m and 1.5 m), Lo = lowest crop layer (< 0.75 m), To = top part of a leaf, Mi = middle part of a leaf, Ba = base part of a leaf.

		N_{tot}	R_ℓ	N_{tot}	R_ℓ	N_{tot}	R_ℓ
Su U H	To + Ba	14	2.25	36	2.20	73	2.30
	Mi	22	2.15				
Su L H	To + Mi	14	2.55	37	2.45		
	Ba	23	2.40				
Su U M				24	2.30	48	2.10
Su L M				24	1.90		
Su U Lo				13	2.60	23	2.70
Su L Lo				10	2.75		

Table 4. Epidermal resistances R_ℓ (s/cm) of a unit of leaf surface, determined as harmonic means of N_{tot} measurements on shaded places for three different crop layers under high light density over the crop. Abbreviations as in Table 3. Sh = shaded leaf part.

		N_{tot}	R_ℓ	N_{tot}	R_ℓ	N_{tot}	R_ℓ
Sh U H				33	6.95	65	6.70
Sh L H				32	6.45		
Sh U M				67	9.10	132	8.75
Sh L M	To + Ba	33	7.80	65	8.45		
	Mi	32	9.25				
Sh U Lo	To + Mi	33	15.65	61	14.30	125	16.25
	Ba	28	13.00				
Sh L Lo	To + Mi	32	16.55	64	18.65		
	Ba	32	21.35				

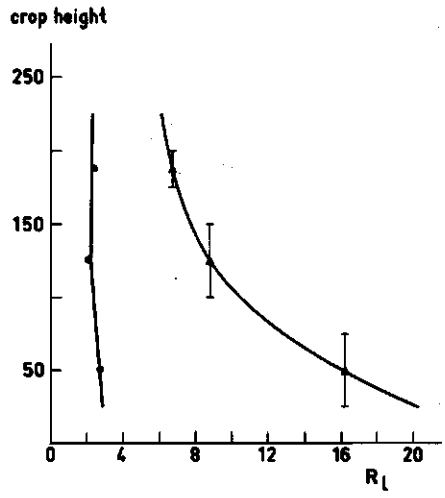

Fig.4. Change of harmonic mean resistance (s/cm) of a unit leaf surface with crop height (cm), under high light densities over the crop. Circles indicate sunlit leaf parts and triangles represent shaded leaf parts. The vertical lines through the points on the right curve indicate the layer effectively sampled.

place on a leaf, either at the top, middle or base part of a leaf, or at the lower or upper side. The average resistance became much higher in deeper layers. This increase could, of course, be attributed to the diffuse light extinction in the canopy (e.g. Monsi et al., 1973). The harmonic means for a unit of leaf surface are given in Fig. 4. Examples of partitioning over different leaf sides and different leaf parts at one side of a leaf, as far as assessed by our sampling method, are given in Tables 3 and 4 as averages over several days. Differences left between leaf parts can be mainly attributed to extremes in the frequency distributions, which are not given here.

Introduction of well-known distribution patterns of sunlit and shaded leaf area at each height in the crop (e.g. de Wit, 1965) completes the calculation of resistance profiles for the simulation model of crop climate.

The basic equality of leaf parts throughout our corn crops being assessed, the sampling of this crop for whatever purpose can take this knowledge into account. This may decrease appreciably the number of measurements that have to be made.

Discussion

Our porometer is an improvement on the types originally proposed by Wallihan (1964), Van Bavel (1964) and Grieve & Went (1965). The most important research on this type of instrument was done by Kanemasu et al. (1969), Monteith & Bull (1970, including work of Stiles) and Turner & Parlange (1970). The alarmingly laborious determination of slopes in the resistance/transient time diagrams was discussed by Meidner (1970) and more thoroughly investigated by Morrow & Slatyer (1971). Our work (Stigter et al., 1973) was an extension of this research (see Chapter *materials and methods)*. We used the very important results of Kobayashi (1960) on LiCl sensor behaviour. We checked the dummy resistances for calibration in two ways. By using an extension of Penman & Schofield's *theory* (1951) and by improving on *experiments* of Lee (1967).

Recently semi-open porometers have been used (Beardsell et al., 1972; Parkinson & Legg, 1972). They use humidity sensors to measure the equilibrium humidity in air inside or leaving the cup. A gas stream enters the cup with a fixed humidity. We believe that in field work the disadvantage of gas supplies and waiting periods for equilibrium outweigh the problems of using the sensor dynamically. This is certainly so with the LiCl sensor where the dynamical properties can now be represented by only one calibration constant, V_t. In the review of diffusion methods (Stigter, 1972) we objected to porometer methods making use of diffusion of a gas, other than water vapour, *through* the leaf. Measuring the two parallel resistances of the upper and lower leaf side in series is one main objection; comeasuring the mesophyll (or parenchyme) resistance is another. The latter resistance was found to be high for Indian corn in a study by Dupaigne & Louguet (1971). Both objections equally apply to the viscous flow porometer, a still much used method. It was recommended again recently by Downey et al. (1972) as of use if calibrated against a diffusion porometer. We believe that the only advantage of this method, the possibility of a high amount of samples per unit of time, does not outweigh its disadvantages for many purposes.

Indeed for the closed diffusion porometer the only useful improvement still to be made is the suppression of the waiting time before each measurement. No reports have been published as yet on humidity sensors or other detectors combining the advantages of the LiCl sensor with a less problematic hysteresis behaviour.

Our prototype was built for use on corn leaves. No principal differences exist in application of this porometer on other leaves. The value of the porometer volume, V_p, is not of fundamental importance and may be made as small as allowed by mixing, drying and thermistor and sensor geometry. Small leaves would make it necessary to lower S_p, which yields higher Δt values. If these were to come into conflict with permitted clamping times, due to influence of the device on the stomatal opening of the leaves concerned, Δt can be made lower by adapted choices for the starting point of the starting-up periods and for $e_p\ (t_f)$.

Only a rough comparison of our field results with scarce comparable literature on field data can be made. It has no sense to compare absolute resistance levels, even for one species such as corn, as so many variables are involved relating genetic differences and differences in the growth conditions and their history. Moreover the measuring methods used and the required number of measurements are too often insufficiently checked. Our aim has been to explore crop epidermal resistance by averaging out existing variability within a certain layer (Stigter & Lammers, 1974). This would make it possible to study crop resistance *at the vapour sources* (e.g. Philip, 1964) without, as mentioned earlier, the problems of obtaining additional information on stomatal geometry and density, (absorbed) light densities of different wavelengths and water status of leaf, plant and soil. It is evident from earlier considerations (Stigter, 1972) and the measurements of Turner (1973), Turner & Begg (1973) and Ritchie (1973) that, under our climatological conditions and with a moist soil, neither leaf water status nor soil water status will influence stomatal resistance in corn. Results of Čatský et al. (1973) on irrigated corn do not correspond with this evidence. They are, however, very difficult to explain if no (previous) stress phenomena did occur in the crop (cf. also Lemon et al., 1971). Sampling under low soil or low leaf water-potential may yield different results. Turner's research on corn also clearly indicated that no senescence effects on resistance exist as long as no visible yellowing of leaf parts is present. This is confirmed by our measurements.

With regard to observed diurnal resistance trends on sunny days (e.g. Turner, 1973), we have no indications that there were important trends in the crop between the beginning and the end of our measuring periods (cf. also Downey et al., 1972).

Corn is often supposed to be an example of at least approximative symmetry between adaxial and abaxial epidermis (De Parcevaux & Perrier, 1973). This can, however, differ between varieties (Heichel, 1971). No statistically significant differences were observed in resistances of sunlit leaf parts between the two leaf sides throughout an *open* corn crop by Turner (1969). The same applied to their reaction on changes in illumination occurring in this crop (Turner & Begg, 1973). We also observed this lasting symmetry in resistance in the sense that for all the illumination levels studied in the layers of our *dense* corn crop the average resistances of both sides were equal. The reports of Čatský et al. (1973) again do not always agree with these results but, apart from genetic differences and stress, problems with the calibration method of their diffusion porometer and their sample method may be involved. Proper field investigations on differences in resistance over one side of a corn leaf were not found in the literature. Application of somewhat comparable sample procedures have only been reported recently in dense *Sorghum* by Brun et al. (1973). They did, however, not separate sunlit and shaded leaf parts. Their final conclusion is that to obtain the crop resistance in dense canopies all leaves on the plant have to be included in the measurements. Objections can be made, however, to their way of calculation of such a canopy resistance.

The work of Brun et al. is an example of the role the diffusion porometer and relevant field sampling are able to play in the still unsolved problem of potential crop transpiration (e.g. Lee, 1967; Shepherd, 1972). The kind of simulation models to which our work has been related will take part in the solution. To predict real water use and crop productivity, field measurements of epidermal resistance will be of much help (Comp. Waggoner, 1969; Sceicz et al., 1973; Čatský et al., 1973). Interesting work related to improving food production has been carried out by plant breeding research, although up till now plants have not been bred for potential production. Gifford & Musgrave (1973) recently stated that if the breeder is to be able to utilize photosynthetic variability to advantage, work is required to sort out environmental and genetic sources of

variability of stomatal resistance in the field. An example of this was given by Loomis et al. (1971) mentioning the interest in the sorting out of genetic and environmental sources of variability in light-saturated net photosynthesis, where determination of CO_2 uptake is involved. Exploring the effect of genetic changes in epidermal resistance seems, however, to be a difficult job (Wilson, 1972). Field measurements are important for these problems. The diffusion porometer will therefore certainly play an important role in the near future in plant physiological research on these and other problems related to exchanges between a leaf and its natural environment.

Acknowledgments

The organization of the project incorporating the work reported here required the close co-operation of many people. The results would never have been obtained without the valuable assistance of my colleagues ir. J. Birnie, ing. B. Lammers and mr. A.E. Jansen (and his co-operators), responsible for electronic design, electronic construction (and research assistance) and mechanical construction work, respectively. Fine co-operation in the very early stages of simulation model construction with ir. J. Goudriaan, of the Department of Theoretical Production Ecology, led to my choice to put emphasis on leaf resistance. During preparation of the project, field work and calculation of the results, many members of our department always assisted skillfully when they were needed. I acknowledge therefore gratefully the co-operation of dr. F.A. Bottemanne, mr. W.C.A.M. Hillen, mr. P. Jansen, mr. T. Jansen, ir. J.G. Lengkeek, mr. J.W. Vaags, mr. B. Verhaaf, mr. A.D. Welgraven and mr. N.A. Zaki, B.Sc. The same applies to the undergraduate students messrs. H.B.M. van der Ham, L. van der Neut and D. Verwaart. I am very thankful to dr.ir. E.G. Kloosterman and his staff, from the university agricultural experiment station in Flevoland, for making it possible for us to carry out the bulk of the field research in their corn fields. Finally I am highly indebted to prof.dr.ir. J. Schenk, head of our Department of Physics and Meteorology, and to prof.dr.ir. C.T. de Wit, head of the Department of Theoretical Production Ecology, for appreciable help during preparation of the publication by supplementing the contents and improving presentation of the results.

References

Bavel, C.H.M. van, 1964. Measuring transpiration resistances of leaves. Water Conservation Laboratory Report No. 2, 30 pp.

Beardsell, M.F., P.G. Jarvis & B. Davidson, 1972. A null-balance diffusion porometer suitable for use with leaves of many shapes. J. appl. Ecol. 9 (3): 677-690.

Brun, L.J., E.T. Kanemasu & W.L. Powers, 1973. Estimating transpiration resistance. Agron. J. 65: 326-328.

Čatský, J., P. Chartier & A. Djavanchir, 1973. Assimilation nette, utilisation de l'eau et microclimat d'un champ de mais. IV. Evolution diurne de la résistance stomatique et du déficit de saturation des feuilles; conséquences sur la fixation du CO_2. Ann. agron. 24(3): 287-305.

Downey, L.A., R.N. Anlezark & W.A. Muirhead, 1972. Construction, calibration and field use of a rapid-reading viscous flow porometer. J. appl. Ecol. 9(2): 431-437.

Dupaigne, F. & P. Louguet, 1971. Étude de la transmission des mouvements stomatiques d'une partie à l'autre de la feuille de *Zea mays* au moyen d'une méthode porométrique utilisant la diffusion de l'hydrogène à travers la feuille. Physiol. Vég. 9 (1): 129-136.

Gifford, R.M. & R.B. Musgrave, 1973. Stomatal role in the variability of net CO_2 exchange rates by two maize inbreds. Aust. J. biol. Sci. 26: 35-44.

Grieve, B.J. & F.W. Went, 1965. An electric hygrometer apparatus for measuring water vapour loss from plants in the field. Unesco Arid Zone Research Series, Vol. 25: 247-257.

Heichel, G.H., 1971. Stomatal movements, frequencies and resistances in two maize varieties differing in photosynthetic capacity. J. exp. Bot. 22: 644-649.

Kanemasu, E.T., G.W. Thurtell & C.B. Tanner, 1969. Design, calibration and field use of a stomatal diffusion porometer. Plant Physiol. 44: 881-885.

Kobayashi, J., 1960. Investigations on Hygrometry. Pap. Met. Geophys., Tokyo 11: 213-338.

Lee, R., 1967. The hydrologic importance of transpiration control by stomata. Wat. Resour. Res. 3: 737-752.

Lemon, E., D.W. Stewart & R.W. Shawcroft, 1971. The sun's work in a cornfield. Science, N.Y. 174: 371-378.

Loomis, R.S., W.A. Williams & A.E. Hall, 1971. Agricultural productivity. Ann. Rev. Plant Physiol. 22: 431-468.

Meidner, H., 1970. A critical study of sensor element diffusion porometers. J. exp. Bot. 21: 1060-1066.

Monsi, M., Z. Uchijima & T. Oikawa, 1973. Structure of foliage canopies and photosynthesis. Ann. Rev. Ecol. Syst. 4: 301-327.

Monteith, J.L. & T.A. Bull, 1970. A diffusive resistance porometer for field use. II. Theory, calibration and performance. J. appl. Ecol. 7: 623-638.

Monteith, J.L., 1973. Principles of environmental physics. Edward Arnold, London, 241 p.
Morrow, P.A. & R.O. Slatyer, 1971. Leaf resistance measurements with diffusion porometers: precautions in calibration and use. Agric. Met. 8: 223-233.
Parcevaux, S. de & A. Perrier, 1973. Bilan énergétique de la feuille. Application de l'étude des cinétiques de température à la détermination des résistances aux flux gazeux. In: R.O. Slatyer (Editor): Plant response to climatic factors, Proceedings Uppsala Symposium, Ecology and conservation 5: 127-135.
Parkinson, K.J. & B.J. Legg, 1972. A continuous flow porometer. J. appl. Ecol. 9 (3): 669-676.
Penman, H.L. & R.K. Schofield, 1951. Some physical aspects of assimilation and transpiration. Symp. Soc. exp. Biol. 5: 115-129.
Philip, J.R., 1964. Sources and transfer processes in the air layers occupied by vegetation. J. appl. Met. 3: 390-395.
Ritchie, J.T., 1973. Influence of soil water status and meteorological conditions on evaporation from a corn canopy. Agron. J. 65: 893-897.
Schenk, J., C.J. Stigter & F.A. Bottemanne, 1973. Onderzoek op de afdeling Natuur- en Weerkunde van de Landbouwhogeschool. Ned. Tijdschr. Natuurk. 39: 53-56.
Shepherd, W., 1972. Some evidence of stomatal restriction of evaporation from well-watered plant canopies. Wat. Resour. Res. 8 (4): 1092-1095.
Stigter, C.J., 1972. Leaf diffusion resistance to water vapour and its direct measurement. I. Introduction and review concerning relevant factors and methods. Meded. Landbouwhogesch. Wageningen 72-3: 1-47.
Stigter, C.J., J. Birnie & B. Lammers, 1973. Leaf diffusion resistance to water vapour and its direct measurement. II. Design, calibration and pertinent theory of an improved leaf diffusion resistance meter. Meded. Landbouwhogesch. Wageningen 73-15: 1-55.
Stigter, C.J., 1974. Water vapour diffusion porometry for leaf epidermal resistance measurements in the field. In: Proceedings of the International Seminar on Heat and Mass Transfer in the Environment of Vegetation (Dubrovnik). Trans. Int. Cent. Heat and Mass Transfer; in press.
Stigter, C.J. & B. Lammers, 1974. Leaf diffusion resistance to water vapour and its direct measurement. III. Results regarding the improved diffusion porometer in growth rooms and fields of Indian corn *(Zea mays)*. Meded. Landbouwhogesch. Wageningen 74-21: in press.
Szeicz, C., Van Bavel, C.H.M. & S. Takami, 1973. Stomatal factor in the water use and dry matter production by sorghum. Agric. Met. 12 (3): 361-389.
Turner, N.C., 1969. Stomatal resistance to transpiration in three contrasting canopies. Crop. Sci. 9: 303-307.
Turner, N.C. & J.-Y. Parlange, 1970. Analysis of operation and calibration of a ventilated diffusion porometer. Plant Physiol. 46: 175-177.
Turner, N.C., 1973. Illumination and stomatal resistance to transpiration in three field crops. In: R.O. Slatyer (Editor): Plant response to climatic factors. Proceedings Uppsala Symposium, Ecology and conservation 5: 63-68.
Turner, N.C. & J.E. Begg, 1973. Stomatal behaviour and water status of maize, sorghum and tobacco under field conditions. I. At high soil water potential. Plant Physiol. 51: 31-36.
Waggoner, P.E., 1969. Environmental manipulations for higher yields. In: J.D. Eastin et al. (Editors): Physiological aspects of crop yield, American Society of Agronomy, Madison, Wisconsin, Ch. 15: 343-373.

Wallihan, F.E., 1964. Modifications and use of an electric hygrometer for estimating relative stomatal apertures. Plant Physiol. 39: 86-90.
Wilson, D., 1972. Effect of selection for stomatal length and frequency on theoretical stomatal resistance to diffusion in *Lolium Perenne* L. New Phytol. 71: 811-817.
Wit, C.T. de, 1965. Photosynthesis of leaf canopies. Versl. landbouwk. Onderz. 663, 57 p.
Wit, C.T. de, R. Brouwer & F.W.T. Penning de Vries, 1970. The simulation of photosynthetic systems. In: Prediction and measurement of photosynthetic productivity. Proceedings of the IBP/PP Technical Meeting, Třeboň: 47-70.