Diffusive Resistances at, and Transpiration Rates from Leaves in Situ Within the Vegetative Canopy of a Corn Crop[1]

I. I. Impens[2], D. W. Stewart, L. H. Allen, Jr. and E. R. Lemon

Microclimate Investigations, SWC, Agricultural Research Service,
United States Department of Agriculture, and Agronomy Department,
Cornell University, Ithaca, New York 14850

Summary. At several heights and times of day within a crop of *Zea mays,* internal leaf diffusion resistance (r_i) and external boundary layer diffusion resistance (r_a) were evaluated by measuring the temperature of a transpiring and a non-transpiring leaf (simulated by covering both sides of a normal leaf with strips of polyethylene tape), and by measuring the immediate air temperature, humidity and windspeed.

Both r_a and r_i increased with depth into the crop. However, r_a generally was less than 10 % of r_i.

Profiles of latent-heat flux density and source intensity of transpiration showed that transpiration corresponded roughly to foliage distribution (with an upward shift) and were not similar to the profile of radiation absorption.

The data were compared with heat budget data. The 2 approaches yielded quite similar height distributions of transpiration per unit leaf area and total transpiration resistance.

The total crop resistance to transpiration was computed as 0.027 min cm⁻¹. This compares to Monteith's values of 0.017 to 0.040 min cm⁻¹ for beans (*Phaseolus vulgaris* L.), and Linacre's values of 0.015 to 0.020 min cm⁻¹ for turf.

Recently, considerable progress in transpiration studies has been made both in controlled and field environments.

Plant physiologists have considered the vapor phase of transpiration mainly as a boundary-layer problem and described the vapor flux from isolated plants or leaves as a molecular diffusion phenomenon through a barrier of successive resistances.

Micrometeorologists have used either the energy budget or the momentum balance approach to compute the gross diffusivity of water vapor at different heights in a few plant communities.

In the present work the exchange of water vapor was regarded not only from the standpoint of the energy budget, but as a diffusion phenomenon as well. Studies were made directly at leaf surfaces at different heights in a field of corn.

The objectives of this research were to investigate the interaction between and relative importance of plant and atmospheric factors using such concepts as internal leaf resistance, external boundary layer resistance, and leaf wetness.

Theory

A concise description of the theory is adequate for the present paper. A fuller account has been published elsewhere by Impens (10).

Neglecting the minor components of storage of sensible heat and photochemical energy, the energy balance for an individual leaf is given by equation I:

$$\text{net } \phi = Q_h + Q_{ev} \qquad \text{I}$$

in which net ϕ is the net radiation, Q_h the sensible heat and Q_{ev} the latent heat in flux densities (cal cm⁻² min⁻¹).

Assuming similarity for the diffusive resistances to heat and water vapor and assuming the exchange to be uniform over the leaf surface, the following equations apply to the flux density for latent and sensible heat:

$$Q_{ev} = \frac{E_l - e_a}{r_l + r_a} \frac{c_p \rho}{\gamma} \qquad \text{II}$$

$$Q_h = \frac{T_l - T_a}{r_a} c_p \rho \qquad \text{III}$$

where E_l = the vapor pressure in mm Hg at the transpiring surface within the leaf, assumed to be equal to that of pure water at leaf temperature; e_a = the ambient vapor pressure; c_p = the specific heat of dry air in cal g^{-1} $°C^{-1}$; ρ = the density of air in g cm^{-3}; γ = the psychrometer constant which is customarily taken as 0.5 mm Hg $°C^{-1}$; r_l = the leaf resistance in min cm^{-1}; r_a = the air resistance in min cm^{-1}; T_l = the leaf temperature in $°C$; T_a = the ambient air temperature in $°C$.

If we assume the emittance and absorptance of the leaves for long-wave radiation to be equal to 1, then

$$\text{net } \phi = \text{net}\phi_{sh} + \text{in}\phi_{lw} - 2 \sigma T_a^4 \qquad \text{IV}$$

where $\text{net}\phi_{sh}$ = the absorbed short-wave radiation; $\text{in}\phi_{lw}$ = the incoming thermal radiation from above (atmosphere, other leaves) and from below (underlying leaves, soil surface); σT_a^4 = the reradiation from the surface of the leaf according to Stefan-Boltzmann's law.

Combining equations I, II, III, and IV the heat budget for a normal transpiring leaf may be written

$$\text{net}\phi_{sh} + \text{in}\phi_{lw} - 2 \sigma T_{l_1}^4 = \frac{T_{l_1} - T_a}{r_a} c_p \rho +$$

$$\frac{(E_{l_1} - e_a)}{(r_l + r_a)} \frac{c_p \rho}{\gamma} \qquad \text{V}$$

and for a non-transpiring leaf

$$\text{net}\phi_{sh} + \text{in}\phi_{lw} - 2 \sigma T_{l_2}^4 = (T_{l_2} - T_a) \frac{c_p \rho}{r_a} \qquad \text{VI}$$

The subscripts ($_1$) and ($_2$) refer to a normal and a non-transpiring leaf respectively.

If both leaves have an identical exposure with the same geometrical form, then one may assume the transpiring and non-transpiring leaves absorb the same amount of energy. Thus equations V and VI may be combined to give

$$T_{l_2} - T_{l_1} = 2 \sigma \frac{r_a}{c_p \rho} T_{l_1}^4 - T_{l_2}^4) +$$

$$E_{l_1} - e_a) \frac{r_a}{\gamma(r_a + r_l)}. \qquad \text{VII}$$

Furthermore,

$$\sigma(T_{l_1}^4 - T_{l_2}^4) \cong 4 \sigma T^3 T_{l_1} - T_{l_2})$$

$$\cong h_r (T_{l_1} - T_{l_2})$$

$$\cong \frac{c_p \rho}{r_r} (T_{l_1} - T_{l_2}). \qquad \text{VIII}$$

h_r is a radiative heat transfer number which for the sake of uniformity is replaced by a radiation resistance, r_r = 0.036 min cm^{-1} at 20°.

Combining equations VII and VIII finally results in

$$(E_{l_1} - e_a) \frac{r_a}{\gamma(r_a + r_l)} = T_{l_2} - T_{l_1} + 2 \frac{r_a}{r_r}$$

$$(T_{l_2} - T_{l_1}) = \triangle T_c, \qquad \text{IX}$$

$\triangle T_c$ being the transpiration cooling in $°C$.

Transpiration cooling as defined here is not simply the difference in measured temperatures of a transpiring leaf and a non-transpiring leaf. It is the expression of the effect of latent heat exchange on the leaf temperatures as distinguished from the other temperature factors of sensible heat and radiative energy exchange. This definition permits expression of the energy transfer due to evaporation in a form similar to sensible heat transfer, since by combining II and IX the latent heat flux is

$$Q_{ev} = \triangle T_c \frac{c_p \rho}{r_a}. \qquad \text{X}$$

Rearranging equation IX gives the leaf resistance as

$$r_l = \frac{[1 - (\triangle T_c \gamma (E_{l_1} - e_a)^{-1}]}{\triangle T_c \gamma (E_{l_1} - e_a)^{-1}} r_a. \qquad \text{XI}$$

Then by knowing leaf and air temperatures, ambient vapor pressure, and external diffusion resistance, it is possible to calculate the leaf transpiration rate and transpiration resistance.

It has been shown (5, 9, 12, 20) that atmospheric boundary resistances calculated from heat transfer theories agreed reasonably well to those determined experimentally (e.g., using wet blotting paper).

The errors that do exist from heat transfer calculations are negligible if one is interested in total resistance ($r_a + r_l$), since under field conditions r_a is usually much smaller than r_l.

Following Pohlhausen's analysis (1, 7) the mean external resistance per unit area is

$$r_a = c_p \rho / 2 \ (Pr^{1/3} \ 0.666 \ Re^{1/2} \ k/L)^{-1}. \qquad \text{XII}$$

The Prandtl number, Pr, for air is 0.72. The Reynold's number, Re, is defined as vL/ν where v is the air velocity (cm sec^{-1}), L is the width of leaf parallel to the air stream and assumed to be 6 cm, and ν is the kinematic viscosity of air (cm^2 sec^{-1}). k is the thermal conductivity (cal cm^{-3} min^{-1} $°C^{-1}$).

For the conditions of this experiment r_a can be described by

$$r_a \cong 0.06 \ v^{-1/2}. \qquad \text{XIII}$$

Materials and Methods

The measurements were performed on August 31, 1965, in a cornfield at Ellis Hollow, Ithaca, New York.

Corn with tassels was about 250 cm high. Profiles of windspeed, air and leaf temperatures, and vapor pressure were measured by simultaneously sampling at 5 levels: 65, 110, 150, 185, and 220 cm above the ground.

Windspeed was obtained with Hastings heated-thermocouple anemometers mounted on a tower at the above-mentioned levels.[3] The electrical outputs were amplified and fed to individual, single-pen recording milliammeters.

An aspirated psychrometer apparatus devised by Brown (2) was used to measure the difference between the wet- and dry-bulb, as well as the dry-bulb temperature (referred to an ice bath) of the air at each of the selected heights.

The leaf temperature-air temperature difference was measured at each of 5 heights with 4-junction, 36-gauge copper-constantan thermopiles. Each of 4 leaf junctions (hot junctions) at a given height was taped to the underside of 2 representative leaves, 1 junction on each side of the midrib. The tape was positioned about 1 cm from each side of a single thermojunction such that there was no obstruction to evaporation or heat transfer at the leaf near the thermojunction. The junction was 0.5 cm long and was in firm contact with the leaf surface.

The 4 air junctions (cold junctions) were positioned a few centimeters below the leaves which served as a shade for the thermojunctions.

A non-transpiring leaf was simulated by covering both sides of a normal leaf with strips of thin polyethylene tape of about 2.5 × 5 cm. 'Dry' leaf temperatures were referred to normal leaf temperatures for the same leaf using a 4-junction thermopile.

Incident short-wave radiation above the crop was measured with an Eppley pyranometer.

Radiation and temperatures were recorded with a 40-channel potentiometric recorder with a print speed of 2 seconds per channel. A 7-minute mean value of all the variables was used at 30-minute intervals.

A few days after the measurements were made, the crop was sampled at 50-cm intervals to determine the leaf area in each layer.

Results and Discussion

Some of the computed data are summarized in table I. First, r_a was computed according to equation XIII. Next, transpiration cooling, ΔT_c, (not tabulated) was computed from equation IX. Then r_l was computed from equation XI, and Q_{ev} from equation X. The r_l values are high, not only when compared to r_a, which could be expected (8, 9, 10, 11, 13, 14, 16 and 22), but even on an absolute scale (fig 1). There is some other evidence in the literature that corn leaves have a higher diffusive resistance to vapor flow than many other crops or vegetable plants; e.g. DeWit and Alberda (6).

The r_l values shown in table I are similar to the ones calculated by Shimshi (21) for corn,

Table I. *Global Radiation above the Corn Crop, ϕ_{sh} (cal cm^{-2} min^{-1}) external boundary layer diffusion resistance, r_a (min cm^{-1}), internal leaf diffusion resistance, r_l (min cm^{-1}) and latent-heat flux density, Q_{ev} (cal cm^{-2} min^{-1}) per unit leaf area with height in the canopy at indicated hours*

| Height (cm)		1200	1230	1300	1330	1400	1430	1500	1530	Mean
	ϕ_{sh}	0.62	0.70	0.24	0.35	0.30	0.43	0.23	0.13	0.375
220	r_a	0.004	0.004	0.005	0.005	0.005	0.005	0.006	0.005	0.0050
	r_l	0.036	0.025	0.051	0.045	0.057	0.051	0.069	0.057	0.049
	Q_{ev}	0.084	0.119	0.030	0.050	0.037	0.078	0.039	0.041	0.064
185	r_a	0.005	0.005	0.006	0.005	0.006	0.006	0.006	0.006	0.0056
	r_l	0.024	0.029	0.066	0.051	0.054	0.049	0.066	0.069	0.051
	Q_{ev}	0.117	0.128	0.047	0.058	0.049	0.079	0.035	0.033	0.068
150	r_a	0.007	0.007	0.008	0.008	0.008	0.008	0.009	0.008	0.0080
	r_l	0.043	0.047	0.092	0.072	0.081	0.072	0.091	0.106	0.076
	Q_{ev}	0.084	0.091	0.035	0.048	0.030	0.050	0.025	0.023	0.048
110	r_a	0.008	0.008	0.009	0.009	0.008	0.009	0.009	0.008	0.0085
	r_l	0.072	0.065	0.104	0.104	0.081	0.091	0.141	0.152	0.101
	Q_{ev}	0.049	0.057	0.024	0.031	0.026	0.041	0.018	0.015	0.033
65	r_a	0.009	0.010	0.009	0.009	0.009	0.010	0.010	0.008	0.0093
	r_l	0.081	0.100	0.216	0.131	0.120	0.101	0.190	0.392	0.167
	Q_{ev}	0.028	0.032	0.013	0.020	0.017	0.022	0.012	0.002	0.018
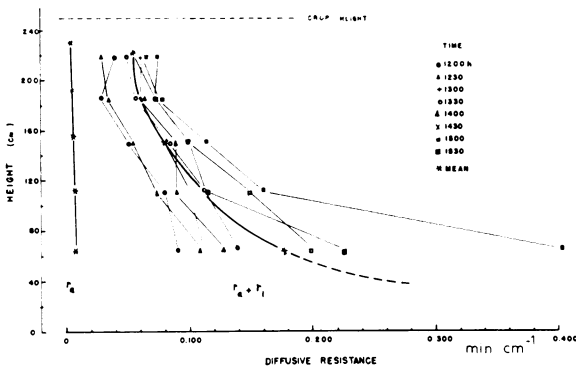
FIG. 1. External, r_a, and total $r = r_a + r_l$, resistances per unit leaf area with height in crop. The r_a values are a mean for the period 1200 to 1530h.

based upon stomatal morphology. Manipulation of his data shows that his values varied with stomatal width, ranging from 0.193 min cm^{-1} for a width of 1.0μ to 0.051 min cm^{-1} for a width of 5.0μ. However, his estimates for external air resistance, r_a, are substantially higher than those reported here, ranging from 0.097 to 0.128 min cm^{-1}.

Even though r_a is nearly twice as high at 65 cm as at 220 cm, this is almost negligible compared to the sharp increase in r_l in the lower half of the crop.

Profiles of latent heat flux density on a unit leaf area basis, $Q_{er}(z)$, are plotted in figure 2. It should be pointed out that the maximum transpiration rates were not from the topmost leaves as one might anticipate. This could be attributed to unfavorable water relationships in the uppermost leaves or to a phenomenon pointed out by Raschke (18,19). By virtue of their smaller size and position at the top of the canopy the uppermost leaves are in the most favorable position to lose heat by convective and radiation transfer. The
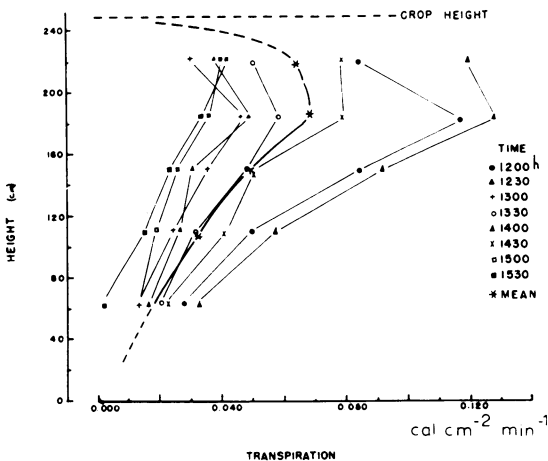

FIG. 2. Latent-heat source profiles on a unit leaf area basis.

effect of higher turbulent transfer at the top in diminishing the vapor pressure gradient through lowering the leaf temperature, and so decreasing E_l, is not fully offset by a concomitant decrease in r_a. Thus the net effect is a lessening of the vapor pressure gradient in greater proportion to the decrease in resistance, r_a, resulting in a decrease in transpiration. This negative effect of windspeed is more pronounced at higher radiation levels, a phenomenon that is reflected in our data.

No attempt was made to analyze the data with respect to the time of day. The fluctuations in solar radiation masked any possible trend in transpiration resistance due to diurnal changes in soil- or leaf-water status. So, for further calculations a mean value of $Q_{er}(z)$ was used.

The source intensity $[Q_{er}(z)\ F\ (z)]$ profile of transpiration in the vegetation canopy (fig 4) was obtained by multiplying the mean flux density of water vapor from leaf to air for each 50-cm layer (fig 2) by the leaf area density (fig 3). Except
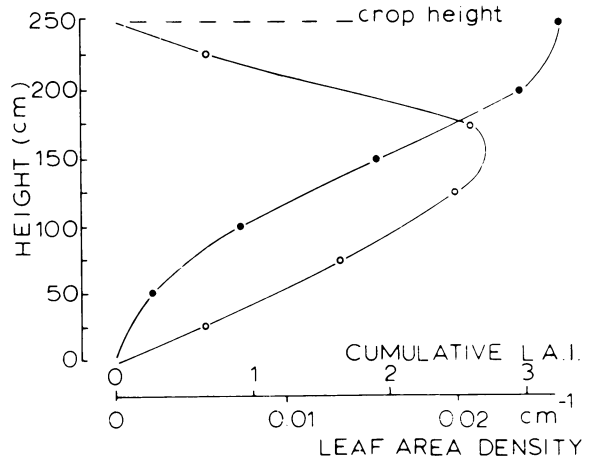

FIG. 3. Cumulative L.A.I. (●), and leaf area density (○) in cm^{-1}.

for a shift upward, the relative strengths of the transpiration sources over the depth of the canopy correspond to the foliage distribution. Denmead (4) also found for a pine forest that the profiles of transpiration sources corresponded roughly to the foliage distribution and were quite dissimilar from the profile of radiation absorption. The temperature profiles in corn from Brown and Covey (3) also show that part of the energy for transpiration in the lower leaves came from sensible heat transfer downward from the middle of the canopy.

Finally, by multiplying the mean leaf-to-air flux density of water vapor for each layer with the leaf area index for that layer, or, in other words, by integrating the flux from leaf to air with respect to height, the vertical flux profile could be constructed:

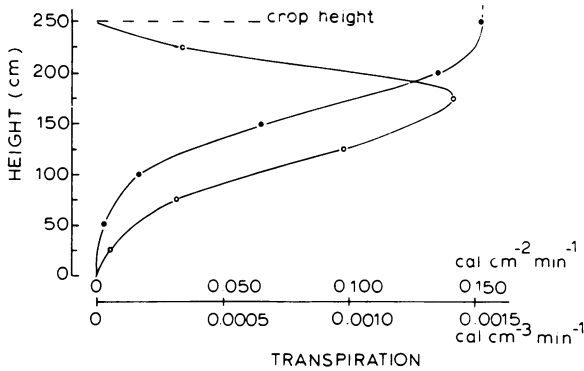$$\int_o^h Q_{er}(z)\ F(z)\ dz \qquad (\text{fig 4}).$$

FIG. 4. Latent-heat flux profile (●) and latent-heat source profile on a plant canopy volume basis (○). August 31, 1965. Mean values: 1200h to 1530h.

Fortunately a study by Brown and Covey (3) provides useful data on transfer processes within a similar cornfield. They used an energy balance method to compute the diffusivities and vertical fluxes of sensible and latent heat in a similar corn crop at the same experimental site.

The data reported here and those of Brown and Covey provide a comparison between the 2 independent and completely different techniques.

The latent-heat source profile values on a unit leaf area basis within the crop are presented in table II. The difference in the absolute values is not surprising in view of the fact that the radiation load during the Brown and Covey study was almost twice as high. However, the similarity in the relative decrease of transpiration with depth in the canopy between the 2 investigations is quite striking. In referring to table III one can see that our transpiration resistance is somewhat higher, especially in the lower part of the crop. This can

be due largely to the difference in leaf area distribution, however. The leaf area density was higher in the uppermost part of the canopy in the 1965 crop.

The relation between the leaf wetness parameter, W in cal cm^{-2} sec^{-1} mb^{-1}, defined by Brown and Covey (3), in terms of various micrometeorological parameters and leaf diffusion resistance, r_i can be written in the following way:

$$W = \frac{1}{r_i} \frac{c_p \rho}{\gamma} \qquad XIV$$

$$r_i \frac{0.0000071}{W} \text{ min cm}^{-1}. \qquad XV$$

A comparison of 1200 to 1500h mean r_i values with height in the crop is given in table III. The same arguments as used in the discussion of table II can be used here.

Assuming that transpiration from one particular leaf is not directly influenced by surrounding plant surfaces, then total crop resistance r_{cr} is given by

$$\frac{1}{r_{cr}} = \sum_{i=1}^{n} \frac{1}{r_i} F_i \qquad XVI$$

where n is the number of layers (here 5), F_i is the L.A.I. for each layer and r_i the mean total resistance $(r_i + r_a)$ per unit leaf area for that layer.

In our experiments we found a mean crop resistance $r_{cr} = 0.027$ min cm^{-1} between 1200 and 1530h. Monteith (17) using an aerodynamic technique found r_{cr} values for beans (*Phaseolus vulgaris* L.) between 0.017 and 0.040 min cm^{-1}, and Linacre (15) using a Penman-type equation found r_{cr} values (with an almost complete predominance of internal

Table II. *Transpiration Per Unit Leaf Area Within a Corn Crop*
Mean 1200 to 1500h values expressed as latent-heat flux densities in cal cm^{-2} min^{-1} and on a ratio basis.

| Height (cm) | Brown and Covey | | Impens et al. | |
	cal cm^{-2} min^{-1}	Ratio	cal cm^{-2} min^{-1}	Ratio
150–200	0.114	1.00	0.063	1.00
100–150	0.082	0.72	0.044	0.70
50–100	0.060	0.52	0.029	0.46
0–50	0.024	0.20	0.010	0.16

Table III. *Leaf Transpiration Resistance, at Different Heights Within a Corn Crop*
Mean values 1200 to 1500h.

| Brown and Covey | | Impens et al. | |
Height (cm)	r_i (min cm^{-1})	Height (cm)	r_i (min cm^{-1})
175	0.050	220	0.048
125	0.060	185	0.048
75	0.075	150	0.071
25	0.139	110	0.084
		65	0.134

resistance) for turf in various places from 0.015 to 0.020 min cm^{-1}.

Literature Cited

1. BOUCHET, R. J. 1964. Evapotranspiration réele, evapotranspiration potentielle et production agricole. INRA, Paris.

2. BROWN, K. W. 1964. Vertical fluxes within the vegetative canopy of a corn field. Interim Report 64-1, DA TASK 1-A-0-11001-B-021-08, by USDA, Agricultural Research Service, in cooperation with New York State College of Agriculture, Ithaca, New York, for Meteorology Department, United States Army Electronics Research and Development Activity, Fort Huachuca, Arizona.

3. BROWN, K. W. AND W. COVEY. 1966. The energy-budget evaluation of the micrometeorological transfer processes within a cornfield. Agric. Meteorol. 3: 73–96.

4. DENMEAD, O. T. 1964. Evaporation sources and apparent diffusitives in a forest canopy. Appl. Meteorol. 3: 383–89.

5. DEVRIES, D. A. AND A. J. VENEMA. 1954. Some considerations on the behaviour of the Piche-evaporimeter. Vegetatio V-VI: 225–34.

6. DEWIT, C. T. AND TH. ALBERDA. 1961. Transpiration coefficient and transpiration rate of three grain species in growth chambers. Meded. 156. IBS, Wageningen.

7. GATES, D. M. 1962. Energy exchange in the Biosphere. Harper and Row Publishers, New York.

8. GATES, D. M. 1964. Leaf temperature and transpiration. Agron. J. 56: 273–77.

9. IMPENS, I. I. Diurnal changes in the internal and external diffusion resistances of upper and lower leaves in a crop of beans. Oecologia Plant. (In press.)

10. IMPENS, I. I. Leaf wetness, diffusion resistances and transpiration rates of bean leaves (*Phaseolus vulgaris* L.) through comparison of "wet" and "dry" leaf temperatures. Oecologia Plant. (In press.)

11. KNOERR, K. R. 1965. Contrasts in energy balances between individual leaves and vegetated surfaces. Inst. of Envir. Sciences. Ann. Tech. Meet., Proceedings.

12. KNOERR, K. R. AND L. W. GAY. 1965. Tree leaf energy balance. Ecology 46: 17–24.

13. KUIPER, P. J. 1961. The effects of environmental factors on the transpiration of leaves, with special reference to stomatal light response. Mededel. Landbhogesch., Wageningen 61: 1–49.

14. LEE, R. AND D. M. GATES. 1964. Diffusion resistance in leaves as related to their stomatal anatomy and micro-structure. Am. J. Botany 51: 963–75.

15. LINACRE, E. T. 1965. Effective diffusion resistances of turf. (In press.)

16. MELLOR, R. S., F. B. SALISBURY, AND K. RASCHKE. 1964. Leaf temperatures in controlled environments. Planta 61: 56–72.

17. MONTEITH, J. L. 1963. Gas exchange in Plant Communities. In: Environmental control of plant growth. L. T. Evans, ed. Academic Press, New York.

18. RASCHKE, K. 1956. Über die physikalischen Beziehungen zwischen Wärmeübergangszahl, Strahlungsaustauch, Temperatur und Transpiration eines Blattes. Planta 48: 200–38.

19. RASCHKE, K. 1958. Über den Einfluss der Diffusionswiderstände auf die Transpiration und die Temperatur eines Blattes. Flora 146: 546–78.

20. ROTH, R. 1961. Konstruktive und Thermodynamische Eigenschaften des Piche-evaporimeters. Arch. Meterol. Geophys. Bioklimatol. Ser. B. 11: 108–20.

21. SHIMSHI, DANIEL. 1963. Effect of soil moisture and phenylmercuric acetate upon stomatal aperture, transpiration, and photosynthesis. Plant Physiol. 38: 713–21.

22. WAGGONER, P. E. AND I. ZELITCH. 1965. Transpiration and the stomata of leaves. Science 150: 1413–20.