

TRANSPIRATION FROM COTTON LEAVES UNDER A RANGE OF ENVIRONMENTAL CONDITIONS IN RELATION TO INTERNAL AND EXTERNAL DIFFUSIVE RESISTANCES

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Summary

Studies on the transpiration of cotton leaves were made under a range of light intensities (3.8, 7.5, 15.0, and 22.5×10^4 erg cm⁻² sec⁻¹), temperatures (30, 35, and 40°C), and humidities (relative vapour pressures ranged from c. 0.4 to c. 0.8) at several low windspeeds, v , ranging from 0.6 to 3.1 cm sec⁻¹.

From these treatments, together with a number of evaporation experiments on wet blotting paper segments cut to standard leaf dimensions, it was possible to calculate the external and internal resistances to diffusive vapour flow from leaf to air. All experiments were conducted under "water non-limiting" conditions.

External resistance, r_e , ranged from 3.5 to 1.6 sec cm⁻¹ from the lowest to the highest windspeed examined. For each windspeed a linear relation between evaporation (E) and vapour pressure difference between the evaporating surface and the bulk air (Δe) was observed. In each case $E/\Delta e$ was proportional to $v^{0.5}$, a relationship frequently found under laminar air flow conditions.

Internal resistance, r_i , was assumed to include a stomatal resistance (r_s) and a cuticular resistance (r_c) connected in parallel. On this basis r_c was found to be 32.3 sec cm⁻¹ and to be independent of environmental conditions. r_s was found to be unaffected by external conditions other than light intensity, but changed from 1.9 to 1.3 to 1.1 sec cm⁻¹ as light intensity increased from 3.8 to 7.5 to 15.0×10^4 erg cm⁻² sec⁻¹. There was no reduction in r_s thereafter.

The results demonstrate the strong dependence of transpiration on r_e under very low windspeed conditions and when light intensity exceeds 7.5×10^4 erg cm⁻² sec⁻¹. Under lower light intensities, however, r_s becomes dominant, and, with windspeeds of the order of 25 cm sec⁻¹, and hence assumed r_e values of <0.5 sec cm⁻¹, transpiration would appear to be primarily limited by r_s at all light intensities.

I. INTRODUCTION

For many years plant physiologists concerned with transpiration studies have attempted to evaluate the anatomical features of the water vapour pathway and so determine the relative magnitude and importance of stomatal and cuticular transpiration, and the physical characteristics of the stomatal regulation mechanism. In general, such investigations have involved the use of viscous flow porometers which, while providing a great deal of information on the stomatal apparatus, have, in a number of cases, not contributed much to a physical understanding of the transpiration process (Stalfelt 1956; Heath 1959). This is partly because the air

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flow induced through the stomatal pores is not by diffusion, as is the case in nature, but by bulk flow, and partly because environmental conditions within the porometer cups have not been readily measurable. In consequence extrapolations of results to natural situations have been qualitative at best.

Because of these objections increased attention has been given recently to the indirect estimation of stomatal and other resistances in the vapour pathway by examining the total vapour transfer away from the effective leaf surface in relation to the vapour pressure gradient from leaf to air.

This procedure was originally used by Brown and Escombe (1900) and subsequently by Maskell (1928), Penman and Schofield (1951), and other workers. Essentially it utilizes a Fick's law relationship for gaseous diffusion through a tube, in response to a concentration gradient, in which the flux is given by the relationship

$$q = u/A = D\Delta c/\Delta z, \quad (1)$$

where q is the diffusive flux of gas (in units such as $\text{g cm}^{-2} \text{sec}^{-1}$), u is the rate of mass flow (in units such as g sec^{-1}) down a tube of cross-sectional area A (cm^2), $\Delta c/\Delta z$ is the concentration gradient down the tube (g cm^{-4}), and D is the coefficient of diffusion of the appropriate gas in air ($\text{cm}^2 \text{sec}^{-1}$).

In the case of evaporation from a wet surface, the flux takes place across a boundary layer which sheaths the surface and in which bulk air flow is laminar in character. Since laminar flow implies that there is no mixing caused by volumes of air moving normal to the direction of bulk transport, vapour can move across such a boundary layer, to the free air beyond, only by molecular diffusion. The thickness, Δz , of this layer is not normally measured in biological experiments and it is convenient to introduce a term, r_a , related to Δz , which describes the resistance of the boundary layer to diffusion. It is defined by

$$q = \Delta c/r_a, \quad (2)$$

so that, from equations (1) and (2),

$$r_a = \Delta z/D, \quad (3)$$

where all previously mentioned terms have the same units as before and r_a is in sec cm^{-1} .

In the case of transpiration from a leaf, however, there is an additional resistance r_l associated with vapour transport from the evaporating sites within the leaf to the leaf surface. In turn this can be partitioned into two main components, one associated with resistances encountered by that part of the total vapour flow which evaporates from the internal mesophyll cell walls and diffuses through the substomatal cavities and the stomatal pores (r_s), and one with the portion which evaporates from the epidermal cell walls and diffuses directly through the cuticle (r_c). Since these two resistances are effectively connected in parallel they are related to leaf resistance, r_l , by the expression

$$\frac{1}{r_l} = \frac{1}{r_s} + \frac{1}{r_c}. \quad (4)$$

At the present time investigators have evaluated these resistances by two main techniques, using either a vapour flow or heat flow approach. In the former (Gaastra 1959; Kuiper 1961) r_a is first calculated from evaporating wet surfaces as similar as possible in surface geometry to wet leaves, so that r_a can be estimated by using a special case of equation (2):

$$E = \Delta c / r_a, \quad (5)$$

where evaporation, E , is in $\text{g cm}^{-2} \text{sec}^{-1}$ and the other terms are unchanged. The experiments are then repeated using actual transpiring leaves and $(r_a + r_l)$ calculated from the expression

$$T = \Delta c / (r_a + r_l), \quad (6)$$

where T is transpiration and the other quantities are in the same units as before. Distinction between r_s and r_c can then be made by repeating the experiments with stomata closed so that $r_l = r_c$.

The alternative approach utilizes the assumption by Raschke (1956, 1960) that the diffusion of heat and water vapour is influenced by the same boundary layer resistance so that a heat transfer equation can be written in a form similar to equation (2) thus:

$$H = c_p \rho (\Delta t) / r_a, \quad (7)$$

where H is net sensible heat transfer in units such as $\text{cal cm}^{-2} \text{sec}^{-1}$, Δt is the temperature difference in degC from leaf to bulk air, c_p is the specific heat of dry air in $\text{cal g}^{-1} \text{degC}^{-1}$, ρ is density of air in g cm^{-3} , and r_a is the external resistance, as before, in sec cm^{-1} . The internal resistances can then be derived using equation (6).

Studies conducted to date have concentrated on situations involving rapid air flow over the leaf (Raschke 1956, 1960; Kuiper 1961; Takechi and Haseba 1962) and have demonstrated that, when the air flow structure is laminar, $r_a \propto v^{0.5}$, where v is wind velocity in cm sec^{-1} . When air flow structure is turbulent, i.e. at Reynolds numbers of the order of 10^5 or greater, $r_a \propto v^{0.75}$ (Martin 1943; Kuiper 1961). Few measurements have been made at very low windspeeds, however, and while it is normally assumed that the $v^{0.5}$ relationship applies in almost still air it was considered desirable to investigate this phenomenon down to windspeeds characteristic of the relatively stagnant air which is frequently found under the uppermost canopy surface of plant communities.

In addition it was desired to examine the relative magnitude of r_s and r_c and to ascertain if there were any effects of light intensity and air temperature other than those which operate through influencing Δc . Associated with these experiments were related investigations into physical aspects of photosynthesis and into the mode of action of transpiration suppressants on both transpiration and photosynthesis (Bierhuizen and Slatyer 1964a; Slatyer and Bierhuizen 1964).

II. EXPERIMENTAL

The transpiration measurements were conducted with a large number of cotton plants (cv. Pope) grown in earthenware pots in a heated, naturally lit

glasshouse. During the experimental period environmental conditions were fairly constant, maximum day temperature ranging from 35–40°C and day length from 14–15 hr. At night minimum temperature was kept at 25°C with artificial heating. The plants were grown at a high level of nutrition and with frequent watering to minimize water stress. They were used for experimental purposes when they had reached a height of 35–40 cm. Measurements were made on one leaf which was selected for size and uniformity using a standard leaf template of 100 cm². In this way the leaf material actually used for each experiment was very similar in geometry and seldom varied more than $\pm 5\%$ in leaf area. Even so leaf area was measured, by tracing the leaf outline and planimentering the enclosed area, and proportional adjustments made. In this paper leaf area therefore means the area of the leaf outline only and not the total area of the upper and lower surfaces (i.e. not twice outline area) as in some investigations. Evaporation measurements were made on pieces of green blotting paper cut to the shape of the standard leaf template.

The experiments were conducted in a leaf chamber in which the temperature, humidity, carbon dioxide concentration, velocity of air stream passing through the chamber, and the incident light intensity could be regulated over quite wide ranges. A detailed account of this equipment has been given elsewhere (Bierhuizen and Slatyer 1964*b*). However, it can be mentioned briefly here that the chamber consisted of an air space 25 cm long by 20 cm wide by 2 cm deep and that the leaf whilst still attached to the plant was inserted through a slot on the long side of the chamber and supported horizontally between two meshes of 0.5-mm nylon fishing line strung 1 cm apart. The air entered at one end of the chamber through a series of pairs of small (0.5 mm diameter) holes drilled in a distributor which extended across the chamber and the air was removed through a similar receptor at the other end of the chamber.

Prior to each experiment the plants were rewatered and then equilibrated for 15–30 min in the temperature-controlled room ($25 \pm 2^\circ\text{C}$) in which the experiments were conducted. They were then arranged on an adjustable platform so that the test leaf projected into the chamber. The other leaves were protected from the extreme heat loads from the light source by semitranslucent paper umbrellas. With the evaporation experiments the pieces of blotting paper were thoroughly wetted before being placed in the chamber. They were removed and rewetted as soon as evaporation showed a decline under steady state environmental conditions. The following measurements were made:

(a) *Total Energy and Light Energy Regime*

Two Philips HPL 400-W lamps were used for the light source, light intensity being regulated by adjusting the height of the lights above the leaf chamber. These lamps have good luminous-efficiency characteristics which are not dissimilar from sunlight, yielding $37.6 \text{ erg cm}^{-2} \text{ sec}^{-1}$ per foot candle (Gaastra 1959). Light intensity at the leaf surface was calibrated against height of the lamps with a flat-surface photometer (Giovanelli 1953) and a similar calibration of total incident energy was made with a Kipp solarimeter mounted in the same position as the leaf. In addition a calibration was obtained for net radiation above and below a leaf and above and below wet blotting paper with a miniature net radiometer (Funk 1962). This

instrument had a sensing head of approximately 1.0 cm diameter so that errors due to instrument shading should have been minimized. The calibrations are shown in Figure 1.

(b) *Transpiration and Evaporation*

These quantities were determined continuously by measuring the differences in water vapour content of the air stream before and after it had passed through the chamber. A differential thermocouple psychrometer was used for this purpose, providing absolute and differential measurements of the vapour pressure in each air

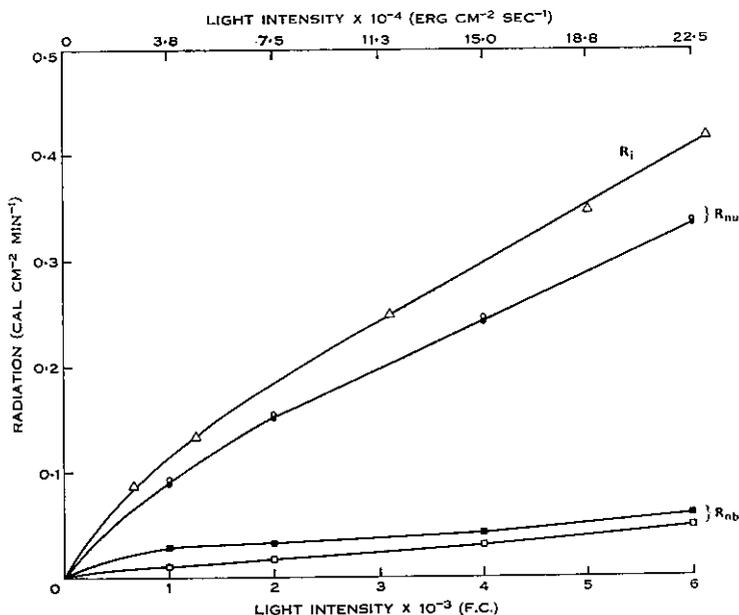


Fig. 1.—Relationship between light intensity at the leaf surface and total incident radiation at upper leaf surface (Δ), R_i , net radiation above the leaf (\bullet) or blotting paper (\circ), R_{nu} , and net radiation below the leaf (\blacksquare) or blotting paper (\square), R_{nb} . The net radiometer was not inverted for the R_{nb} measurements.

stream. Photosynthesis was measured simultaneously with an infrared gas analyser to detect differences in carbon dioxide concentration. Full details are given elsewhere (Bierhuizen and Slatyer 1964b).

(c) *Temperature and Vapour Pressure Difference from Leaf to Air*

In order to calculate the temperature ($t_l - t_a$) and vapour pressure ($e_l - e_a$) difference it was necessary to measure the surface temperature and the temperature and humidity of the bulk air.

Leaf (or blotting paper) surface temperature was measured with 44-gauge copper-constantan thermocouples which were cemented lightly over cross-threads

of the nylon mesh so that when the leaf chamber was closed they were pressed against the leaf surface. At one stage measurements were made at three points downwind across the leaf on the underside (about 5 mm from the upwind edge, 5 mm from the downwind edge, and centre) and at the one point on the upperside (centre). The difference in temperature, so measured, between the upper centre and lower centre thermocouples at no stage exceeded ± 0.5 degC. The difference between the upwind and downwind underside thermocouples did not exceed ± 1 degC and was usually less than ± 0.5 degC and the lower centre thermocouple provided an estimate within ± 0.2 degC of the arithmetic mean of these two values. In consequence the lower centre thermocouple reading was used as the standard measurement of leaf surface temperature for the experiments reported in this paper.

The vapour pressure at the evaporating surface was taken as the saturation vapour pressure at the leaf temperature. Since the plants were grown throughout under high water conditions and since they were rewatered prior to each set of measurements the effective relative vapour pressure at the evaporating surfaces should have been higher than 0.990 and probably higher than 0.995. In consequence the error introduced by this procedure was considered to be negligibly small. Air temperature was measured by thermocouples located approximately 5 mm below the leaf surface, and for a time 5 mm above the surface, and also as the temperature of the air entering and leaving the chamber. Because of the low windspeeds used it was possible that the effective boundary layer thickness exceeded 5 mm on some occasions (Raschke 1956) and consequently a more realistic estimate of bulk air temperature was considered to be the temperature of the incoming air.

Bulk vapour pressure above the leaf was determined from the wet bulb temperature of the outlet air stream. Since the vapour pressure increases as the air is enriched by transpiration in passing over the leaf, an average of inlet and outlet vapour pressure would provide an estimate of the value over the mid point of the leaf, assuming that the leaf extended across the full width of the chamber. However, the leaf only extended half way across the chamber, so that the outlet air stream itself provided an effective average value.

(d) Rates of Air Movement

The cross-sectional area of the chamber was 40 cm² and flow rates were calculated from the volumetric flow, measured through flowmeters in litres min⁻¹, divided by the cross-sectional area. Flow rates of 1.5, 3.5, 5.5, and 7.5 litres min⁻¹, therefore, were assumed to correspond to velocities of 0.6, 1.5, 2.3, and 3.1 cm sec⁻¹ and these low speeds were used throughout this series of experiments.

III. RESULTS

In order to distinguish between internal and external diffusion resistances in the transpiration pathway it was desirable to examine first external resistance alone, using the wet blotting paper segments (with internal resistance not evident), and then to examine the combination of external and internal resistances in actual leaves.

(a) *Evaporation from Wet Simulated Leaf Surfaces in Relation to Vapour Pressure Differences*

In Figure 2 the relationship between observed evaporation, E' (in $\text{g } 100 \text{ cm}^{-2} \text{ hr}^{-1}$) from blotting paper segments is plotted against the vapour pressure difference from surface to air, Δe , for four windspeeds. It can be seen that there is a progressive increase in the slope of the curves and hence in the amount of evaporation

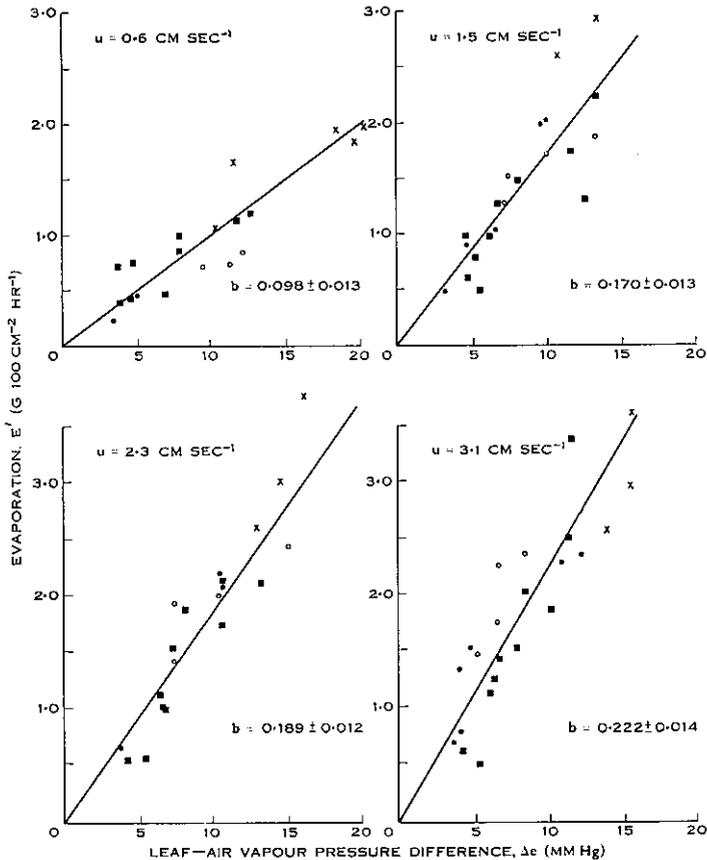


Fig. 2.—Relationship between evaporation, E' , from a wet surface and vapour pressure difference, Δe , for four windspeeds at air temperatures ($^{\circ}\text{C}$) of 27 (●), 30 (○), 35 (■), and 40 (×).

per unit vapour pressure difference ($E'/\Delta e$) as rate of air movement increases. The slopes and standard errors of the curves are 0.098 ± 0.013 , 0.170 ± 0.013 , 0.189 ± 0.012 , and 0.222 ± 0.014 , respectively, indicating a good fit of the data except that the slope of the 2.3 cm sec^{-1} windspeed group was lower than expected. There was no apparent reason for this anomaly which was found to be not significant when all the data were grouped for analysis. Using this procedure it was found that the complete set of data could be fitted by the relationship

$$E' = 0.128\Delta e.v^a,$$

where a is 0.47 ± 0.048 . This value of a was not significantly below 0.5, the value commonly assumed to apply under laminar air flow conditions.

The values for E' in Figure 2 can be converted from $g\ 100\ cm^{-2}\ hr^{-1}$ to values of E in absolute CGS units of $g\ cm^{-2}\ sec^{-1}$ by dividing by 3.6×10^5 and the values of Δe , in mm Hg, to $g\ cm^{-3}$ by multiplying by $0.623\rho/p$, where ρ has the value given previously and p is atmospheric pressure in mm Hg. It is then possible to calculate, from equation (5), external resistance, r_a , for each windspeed and this yields values of 3.5, 2.0, 1.8, and 1.6 $sec\ cm^{-1}$ at windspeeds of 0.6, 1.5, 2.3, and 3.1 $cm\ sec^{-1}$.

(b) *Transpiration from Leaves and the Estimation of Internal Resistances to Vapour Diffusion*

In Figure 3 the relationship between transpiration, T' (in $g\ 100\ cm^{-2}\ hr^{-1}$) and Δe is shown for leaves with stomata closed by the influence of darkness or metabolic

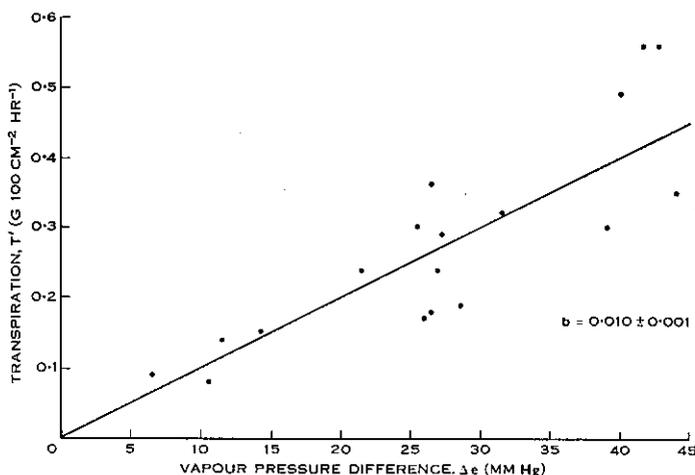


Fig. 3.—Relationship between cuticular transpiration, T' , from cotton leaves with closed stomata and vapour pressure difference, Δe , at a windspeed of 1.5 $cm\ sec^{-1}$.

inhibitors. The data are for a windspeed of 1.5 $cm\ sec^{-1}$. The slope of the line ($b = 0.010 \pm 0.001$) is much lower than for the data of Figure 2 and indicates the marked reduction in transpiration when the only pathway available for water vapour transfer is via the cuticle. The data provide an estimate of $(r_a + r_c)$ of 34.3 $sec\ cm^{-1}$ and, since the value of r_a for the appropriate windspeed was 2.0 $sec\ cm^{-1}$, these results yield an estimate for r_c of 32.3 $sec\ cm^{-1}$.

This result now permits r_s to be distinguished from r_t , although, because of the magnitude of r_c , the difference is seldom larger than 0.1 $sec\ cm^{-1}$.

The appropriate measurements were conducted with normal leaves in a 4 by 4 factorial experiment using the same four windspeeds as before and four light intensities (1000, 2000, 4000, and 6000 f.c., corresponding to 3.8, 7.5, 15.0, and 22.5×10^4 $erg\ cm^{-2}\ sec^{-1}$). Nine experiments were conducted at each light intensity and

windspeed. These comprised three air temperature levels (30, 35, 40°C) and three bulk relative vapour pressure levels ($\approx 0.4, 0.6, 0.8$). In processing the data, mean values of $\Delta c/T = (r_a + r_l)$ for the nine experiments at each light intensity and windspeed value were calculated in units of sec cm^{-1} , and values of r_l obtained using equation (6) and the r_a data of Figure 2. Values of r_s were then calculated from equation (4). The complete data for $(r_a + r_l)$, and r_s are given in Table 1. In Figures 4(a) and 4(b) mean values for each windspeed at all light intensities and for each light intensity at all windspeeds are presented, together with specific treatment values for $(r_a + r_l)$ and r_s . A logarithmic scale is used for convenience since the values plotted range from less than 1 to more than 30.

TABLE 1
SUMMARY OF RESISTANCES FOR ALL LIGHT INTENSITIES AND WINDSPEEDS
Each value is mean of nine determinations and is rounded off to nearest decimal point

Light Intensity.		Rate of Air Flow (cm sec^{-1})								Mean for Each Light Intensity	
		0.6		1.5		2.3		3.1			
		(f.c.)	($\text{erg cm}^{-2} \text{sec}^{-1}$)	($r_a + r_l$)	r_s	($r_a + r_l$)	r_s	($r_a + r_l$)	r_s		
1000	3.8×10^4	5.4	2.0	4.2	2.3	3.5	1.8	2.8	1.3	4.0	1.9
2000	7.5×10^4	4.5	1.0	3.5	1.6	3.1	1.4	2.7	1.1	3.5	1.3
4000	15×10^4	4.9	1.5	2.9	0.9	2.7	0.9	2.4	0.8	3.2	1.0
6000	22.6×10^4	4.6	1.1	2.9	0.9	2.7	0.9	2.9	1.3	3.3	1.1
Mean for each air flow		4.9	1.4	3.4	1.4	3.0	1.3	2.7	1.1		

The strong dependence of r_s on light intensity and the virtual absence of a windspeed effect are shown clearly in the diagram, as is the combined effect of light intensity and windspeed on $(r_a + r_l)$. For convenience, the value of r_s is diagrammatically depicted as decreasing from infinity in the dark exponentially to the values observed at the other light intensities. Although initial stomatal opening almost certainly commences at some finite light intensity, this presentation helps to indicate the major reduction in stomatal resistance as light intensity increases up to 3.8×10^4 $\text{erg cm}^{-2} \text{sec}^{-1}$. There is still a significant reduction beyond 7.5×10^4 $\text{erg cm}^{-2} \text{sec}^{-1}$ but no significant decrease is evident at light intensities exceeding 15.0×10^4 $\text{erg cm}^{-2} \text{sec}^{-1}$.

Although there is no evidence that cuticular resistance, r_c , is affected by environmental conditions, it was thought desirable to specifically examine the possible influence of temperature since this has been claimed to affect insect cuticle

permeability under some conditions (Beament 1958). Accordingly mean values of r_t were calculated for each windspeed and bulk air temperature and are presented

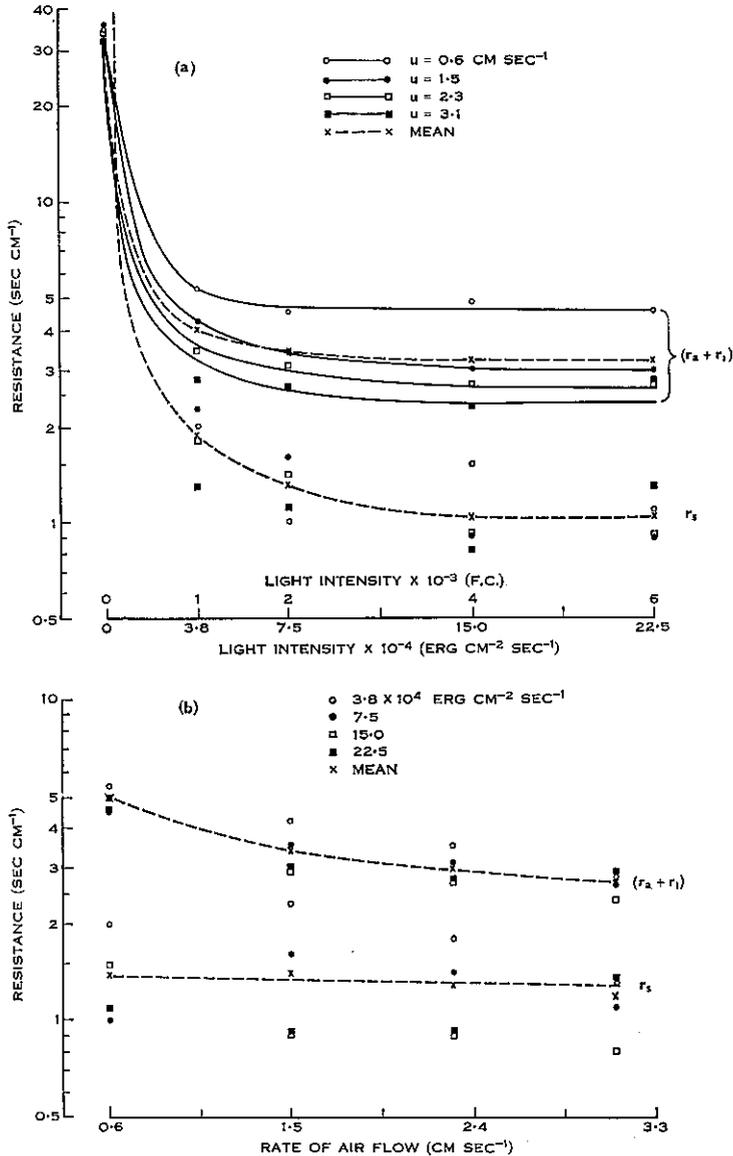


Fig. 4.—Effect of (a) light intensity and (b) windspeed on combined external and internal resistances ($r_a + r_i$) and stomatal resistance, r_s .

in Figure 5. Although some variation occurs there is no trend in the direction of either higher or lower temperatures and, since any significant change in r_e would directly influence r_b , it may be concluded that no temperature effect existed, at least with the range of temperatures used here.

(c) *Energy Balance of the Transpiring Leaf*

Although this investigation was primarily intended to evaluate the diffusive resistances to water vapour flow in the transpiration pathway it is of interest to examine the evidence available concerning heat transfer from leaf to air since similar values of r_a should apply in this transfer process [see eqn. (7)].

In the first place, the heat budget for a leaf can be descriptively written as

$$(R_{nu} - R_{nb}) = T + H + P, \tag{8}$$

where $(R_{nu} - R_{nb})$ is the difference between net radiation above and below the leaf, T is latent heat transfer as transpiration, H is sensible heat transfer, and P is net metabolic heat exchange (consisting mainly of energy consumed in photosynthesis) all expressed in the same units. Although a certain amount of heat is stored in the leaf it is always small and, in a situation where all other terms reach a steady state, it disappears.

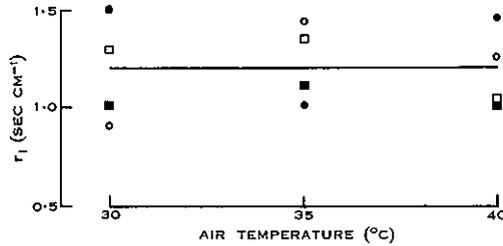


Fig. 5.—Effect of bulk air temperature on internal resistance, r_l , at windspeeds (cm sec⁻¹) of 0.6 (○), 1.5 (●), 2.3 (□), and 3.1 (■).

Since all terms except H were measured [the investigations on photosynthesis being the subject of separate publication (Bierhuizen and Slatyer 1964a)] it is possible to obtain an estimate of heat transfer and hence to compute heat transfer coefficients using the measured leaf temperature data (t_l) together with the estimated bulk air temperature (t_a) to obtain $\Delta t = (t_l - t_a)$.

These data are presented in Figures 6 and 7. In Figure 6 [$(R_{nu} - R_{nb}) - P$] is plotted against T for four light intensities in those cases where Δt was less than ± 0.5 degC and H could therefore be neglected. Each point represents the mean of seven observations. T and P have been converted into cal cm⁻² min⁻¹ assuming a conversion of 600 cal g⁻¹ water transpired and 3730 cal g⁻¹ carbohydrate photosynthesized. Although the contribution of P in terms of energy consumption is small ($\approx 4\%$ of T) the data are seen to give a surprisingly close fit which provides a good cross check on the accuracy of the data in Figures 3-5 and indicates that, in the absence of the heat flux term, H , all the incoming radiation can be effectively accounted for as transpiration and photosynthesis.

In Figure 7, estimates of H as $[(R_{nu} - R_{nb}) - T - P]$ are plotted against Δt using the leaf data of Figure 3 together with additional data from leaves with partially

closed stomata, and hence low transpiration. These were selected since the error in this relationship is reduced as the residual heat value used for H increases. Data for the normal leaves (Fig. 3) are included but were not used to calculate the regression coefficients since they were not considered to be as reliable, for the reason just mentioned. However, it can be seen that they fit well in the curves even though their scatter was greater. Data for the blotting paper experiments of Figure 2 are not included because H was always very small and usually negative. Even so, the slopes did not differ greatly from those given in Figure 7.

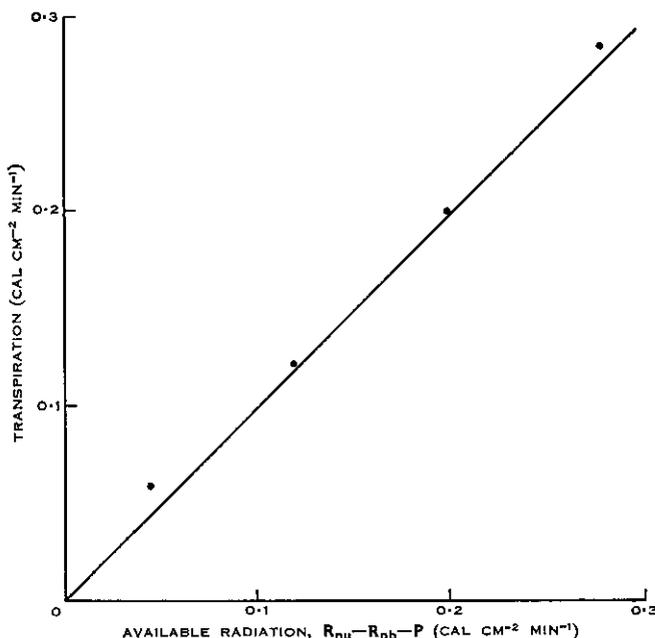


Fig. 6.—Relationship between transpiration and net radiation absorbed by the leaf, adjusted for the heat absorbed by apparent photosynthesis ($R_{na} - R_{ne} - P$). The 45° line demonstrates the expected slope of the relationship.

The mean regression coefficients ($\text{cal cm}^{-2} \text{min}^{-1} \text{degC}^{-1}$) were 0.0227 ± 0.0010 and 0.0263 ± 0.0011 for windspeeds of 1.5 and 3.1 cm sec^{-1} respectively. There is therefore a degree of dependence on windspeed but it is not as marked as was the case with the data of Figure 2. The values of r_a calculated from these data using equation (7) are 0.8 and 0.7 sec cm^{-1} . Both estimates are well below those calculated from Figure 2 and equation (3). This result together with the preceding observations, is considered in the discussion which follows.

IV. DISCUSSION

The values obtained for r_a from Figure 2, ranging from 1.6 to 3.5 sec cm^{-1} as windspeed declines from 3.1 to 0.6 cm sec^{-1} , agree well with those obtained by

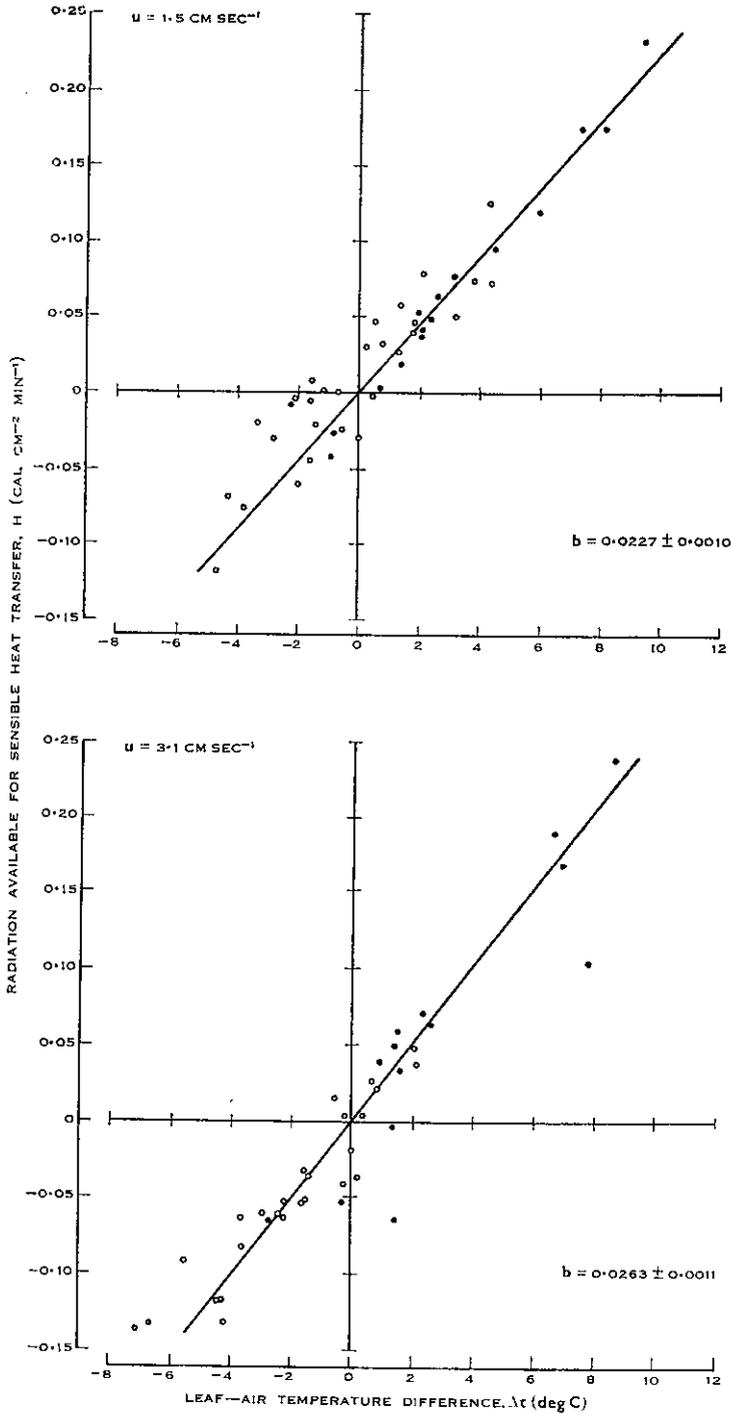


Fig. 7.—Relationship between sensible heat transfer, H , and the temperature difference, Δt , from surface to air at two windspeeds. ● Reduced transpiration. ○ Normal transpiration.

other investigators if their data are extrapolated to the appropriate range of windspeeds. Gaastra (1959) and Kuiper (1961), for example, obtained values for blotting paper segments of about 100 cm^2 which closely approximate those reported here and Raschke (1960) estimated r_a to be approximately 6.0 for a windspeed of 1 cm sec^{-1} across a leaf 10 cm wide.

Apart from the values themselves, it is also of interest to note that evaporation was proportional to $v^{0.5}$ at all windspeeds examined. This provides confirmation that the general considerations applying to the influence of windspeed on boundary layer thickness, and hence r_a , under laminar flow conditions (Martin 1943; Raschke 1956; Kuiper 1961) can be applied down to windspeeds as low as 0.6 cm sec^{-1} .

The data of Figure 7 indicated that sensible heat transfer was also influenced by windspeed, but to a power lower than 0.5. Moreover the actual values of r_a obtained from the heat transfer data, 0.8 and 0.7 sec cm^{-1} for windspeeds of 1.5 and 3.1 cm sec^{-1} respectively, were much lower (about 1.2.5) than those obtained from the vapour transfer data. They are also lower than values given by Raschke (1960) but resemble those of Takechi and Haseba (1962) who obtained values for $H/\Delta t$ of $0.03 \text{ cal cm}^{-2} \text{ min}^{-1} \text{ degC}^{-1}$ for a windspeed of 2.5 cm sec^{-1} .

Several factors may contribute to this discrepancy between the $E'/\Delta e$ and $H/\Delta t$ estimates. In the first place a preliminary analysis of transfer processes through a laminar boundary layer by C. W. Rose (unpublished data) shows that, in general, r_a is not the same for both sensible and latent heat, as was assumed in equation (7). Instead it appears that the ratio of r_a (sensible heat) to r_a (latent heat) may lie between 1.2 and 0, depending on the average relative vapour pressure in the boundary layer. With a relative vapour pressure of 0.6 (the mean used in these experiments) this ratio is probably about 0.7. Applying this correction therefore significantly improves the agreement but still leaves a factor of about two to be accounted for.

Other probable factors include the likelihood of the laminar boundary layer separating from the leaf over a fraction of its surface and errors in either leaf or air temperature measurement. Errors could also exist in the estimates of total heat transfer H , since these depend on the accuracy of measurements of net radiation received by the leaf and the energy consumed in transpiration and photosynthesis. In the case of heat transfer from blotting paper and actively transpiring leaves these estimates could possibly introduce significant errors since the residual term, H , was frequently less than 10% of the net radiation. However, in the case of the leaves with transpiration markedly reduced, which were used in Figure 7 to calculate $H/\Delta t$, H usually comprised more than 50% of the net radiation and the estimates should not have been in error by more than a small percentage. The net radiation measurements themselves were checked twice and very good agreement (less than 3% change) was found on each occasion. Furthermore, there is the evidence of Figure 6 where, in the absence of leaf-air temperature gradients, the energy utilized in transpiration and photosynthesis agrees very closely with the measured net radiation.

If the temperature measurements were subject to error, the effect on the calculated value of the vapour pressure difference Δe would be much less than on Δt . If Δt was underestimated, as is most probable, this would help to explain the

discrepancy between the two estimates of r_a and at the same time explain why valid estimates could still be made from the $E'/\Delta e$ relationship. Although leaf temperature is difficult to measure it is thought more probable that the measurements of bulk air temperature are more likely to be incorrect, particularly with the very slow windspeeds used and the probable complexity of the associated boundary layer.

Turning from these considerations to the estimates of internal resistances, only light intensity appears to influence r_s and that reductions in r_s continued to occur until light intensities of the order of 4000 f.c. (15.0×10^4 ergs $\text{cm}^{-2} \text{sec}^{-1}$) were reached. In a number of other species maximum stomatal opening appears to occur at much lower light intensities (Heath 1959) and the higher light intensity required for cotton is probably related to its natural climatic habitat. At the stage of minimum r_s the value for cotton was 1.1 sec cm^{-1} which is considerably lower than the figure of about 3 sec cm^{-1} obtained by either Gaastra (1959) for turnip, or 5 sec cm^{-1} by Kuiper (1961) for bean. This in turn suggests that, subject to adequate carbon dioxide and water supply, transpiration and photosynthesis in cotton are less likely to be affected by the limitations of the diffusion capacity of the stomata under high radiation conditions.

The value obtained for r_c , 32.3 sec cm^{-1} , is quite high for a mesophytic crop plant and indicates that stomatal closure in cotton can regulate transpiration very effectively. r_c was unaffected by any of the experimental treatments imposed, including air temperature. Although the range of air temperatures used in these experiments was only $30\text{--}40^\circ\text{C}$ there was no evidence of the type of effect reported by Beament (1958) for insect cuticle where he found sudden and pronounced increases in permeability of *Periplaneta americana* nymph cuticle as temperature increased above 30°C .

In summarizing the results it may be stated that, with the range of environmental conditions studied, transpiration per unit vapour pressure difference ($T'/\Delta e$) was influenced primarily by windspeed, and hence by external resistance r_a , at all except the lowest light intensity. Moreover, as windspeed decreased the relative influence of r_a on the combined resistance (r_a+r_i) increased rapidly. However, had light intensities below 1000 f.c. (3.8×10^4 erg $\text{cm}^{-2} \text{sec}^{-1}$) been utilized r_s would have dominated (r_a+r_i) and it was apparent that stomatal closure, and an increase in r_i to a value equal to r_c , dramatically altered the pattern of incident energy partition at the leaf surface. Under out-of-door conditions, with probable r_a values below 0.5 sec cm^{-1} , r_s would always dominate (r_a+r_i) and an increase in r_s from 1.0 to 2.0 sec cm^{-1} would be expected to reduce $T'/\Delta e$ by almost one-half.

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VI. REFERENCES

- BEAMENT, J. W. L. (1958).—The effect of temperature on the waterproofing mechanism of an insect. *J. Exp. Biol.* **35**: 494–519.
- BIERHUIZEN, J. F., and SLATYER, R. O. (1964a).—Photosynthesis of cotton leaves under a range of environmental conditions in relation to internal and external diffusive resistances. *Aust. J. Biol. Sci.* **17**: (in press).
- BIERHUIZEN, J. F., and SLATYER, R. O. (1964b).—An apparatus for the continuous and simultaneous measurement of photosynthesis and transpiration under controlled environmental conditions. CSIRO Aust. Div. Land Res. Reg. Surv. Tech. Pap. No. 24.
- BROWN, H. T., and ESCOMBE, F. (1900).—Static diffusion of gases and liquids in relation to the assimilation of carbon and translocation in plants. *Philos. Trans. B* **193**: 223–91.
- FUNK, J. P. (1962).—A net radiometer designed for optimum sensitivity and a ribbon thermopile used in a miniaturized version. *J. Geophys. Res.* **67**: 2753–60.
- GAASTRA, P. (1959).—Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature, and stomatal diffusion resistance. *Meded. LandbHoogesch., Wageningen* **59**: 1–68.
- GIOVANELLI, R. G. (1953).—An omnidirectional photometer of small dimensions. *J. Sci. Inst.* **30**: 326–8.
- HEATH, O. V. S. (1959).—The water relations of stomatal cells and the mechanisms of stomatal movement. In "Plant Physiology". (Ed. F. C. Steward.) Vol. 2. pp. 193–250. (Academic Press Inc.: New York.)
- KUIPER, P. J. C. (1961).—The effects of environmental factors on the transpiration of leaves, with special reference to stomatal light response. *Meded. LandbHoogesch., Wageningen* **61**: 1–49.
- MARTIN, E. (1943).—Studies on evaporation and transpiration under controlled conditions. Publ. Carneg. Instn. No. 550. pp. 1–48.
- MASKELL, E. J. (1928).—Experimental researches on vegetable assimilation and respiration. XVIII. The relation between stomatal opening and assimilation. A critical study of assimilation rates in the cherry laurel. *Proc. Roy. Soc. B* **102**: 488–533.
- PENMAN, H. L., and SCHOFIELD, R. K. (1951).—Some physical aspects of assimilation and transpiration. *Symp. Soc. Exp. Biol.* **5**: 115–29.
- RASCHKE, K. (1956).—Über die physikalischen Beziehungen zwischen Wärmeübergangszahl, Strahlungsaustausch, Temperatur und Transpiration eines Blattes. *Planta* **48**: 200–38.
- RASCHKE, K. (1960).—Heat transfer between the plant and the environment. *Annu. Rev. Pl. Physiol.* **11**: 111–26.
- SLATYER, R. O., and BIERHUIZEN, J. F. (1964).—The influence of several transpiration suppressants on transpiration, photosynthesis, and water-use efficiency of cotton leaves. *Aust. J. Biol. Sci.* **17**: 131–46.
- STALFELT, M. G. (1956).—Die stomatare transpiration und die Physiologie der Spaltöffnungen. In "Handbuch der Pflanzenphysiologie". (Ed. W. Ruhland.) Vol. 3. pp. 351–426. (Springer-Verlag: Berlin.)
- TAKECHI, O., and HASEBA, T. (1962).—Studies on the leaf temperature. (2) On the heat transfer from the leaf of citrus in laminar flow. *J. Agric. Meteorol., Tokyo* **18**: 92–7.