

# EFFECT OF LIGHT INTENSITY AND LEAF TEMPERATURE ON PHOTOSYNTHESIS AND TRANSPIRATION IN WHEAT AND SORGHUM

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## Summary

Wheat stomata offered less resistance to water and carbon dioxide diffusion than sorghum stomata at light intensities of 0.06 and 0.26 cal cm<sup>-2</sup> min<sup>-1</sup> (400–700 nm) but resistances were comparable at 0.46 cal cm<sup>-2</sup> min<sup>-1</sup>. Consequently, transpiration rates were higher in wheat than in sorghum, except at the high light levels, in leaf chamber experiments described here. Rates of photosynthesis were higher in sorghum than in wheat, with the greatest difference at high light levels. This resulted in a greater efficiency of dry matter production relative to water use in sorghum. Transpiration rate increased with increased temperature in both species. Photosynthesis was independent of temperature in wheat, and in sorghum under low light conditions, but otherwise photosynthesis increased with temperature in sorghum. In both species, efficiency of water use decreased as temperature increased at all light intensities. Water vapour concentration difference between the intercellular spaces and the air was comparable in wheat and sorghum and increased with temperature. The carbon dioxide concentration difference between air and intercellular spaces was substantially greater in sorghum than in wheat and increased with leaf temperature. Maximum values were obtained at the intermediate light level in sorghum.

## I. INTRODUCTION

Wheat plants were shown in earlier experiments to transpire at about 2.25 times the rate of sorghum plants per unit leaf area, under a range of temperatures (17–32°C) and low light intensities (1100–2800 f.c.) (Downes 1969). Calculations based on leaf temperature and transpiration rates suggested that, under these conditions, sorghum stomata offered greater resistance to gas exchange than did wheat stomata. Despite the higher resistance to CO<sub>2</sub> transfer, sorghum and other tropical grasses maintained higher net assimilation rates than temperate grasses.

Because of the ecological and agronomic significance of the photosynthesis to transpiration ratio, these parameters and their components were studied in further experiments reported here. Wheat and sorghum leaves were subjected to a range of temperature and light regimes in a leaf chamber, and net photosynthetic rate (*P*) and transpiration rate (*T*) were measured simultaneously.

## II. MATERIALS AND METHODS

### (a) Plants

Seedlings of wheat (*Triticum aestivum* L. cv. Gabo) and Sudan grass (*Sorghum sudanense* Stapf. cv. Greenleaf) were established in glasshouses at 24/19°C day/night temperatures (with the day temperature operating between 8.30 a.m. and 4.30 p.m.) and with a 16-hr photoperiod.

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When six to eight leaves had emerged, plants were moved in the late afternoon to a constant-temperature room (24°C). Next morning, portion of a young attached leaf 25–35 cm<sup>2</sup> in area were enclosed in the leaf chamber (the second youngest emerged wheat leaf and the third youngest emerged sorghum leaf were used). The rest of the plant was partly illuminated by the light source. Roots were maintained at 25°C in aerated Hoagland's solution.

(b) *Leaf Chamber*

The system for measuring  $P$  and  $T$  was similar to that described by Bierhuizen and Slatyer (1964). A leaf in a Perspex chamber was exposed to air exchanging at about 2.5 litres/min in open circuit (Gaastra 1959). Flow across the chamber was increased by recycling air by pump from the outlet to the inlet side of the chamber at 13 litres/min (Troughton 1969). Air alone or air enriched with CO<sub>2</sub> was supplied from polyvinyl chloride balloons (Troughton and Slatyer 1969) so that the air at the chamber outlet contained  $300 \pm 20$  p.p.m. CO<sub>2</sub>.

Light was provided by a 500 W quartz iodine (tungsten) lamp and passed through a 6-cm water filter. This gave intensities up to 0.5 cal cm<sup>-2</sup> min<sup>-1</sup> of photosynthetically active radiation (400–700 nm). Intensity was varied by altering the distance between the source and the leaf chamber. Radiation was monitored over the 400–700 nm range by silicon Solar cells (using BG38 and GG19 Schott & General filters) which had been calibrated with an RG8 filter against a Kipp solarimeter (McPherson 1969).

Leaf temperature was measured with two copper constantin thermocouples which touched the underside of the leaf. Air temperature in the chamber was varied by passing the tubes carrying the incoming and recycling air through water baths which were heated or cooled as necessary. This allowed leaf temperature to be maintained anywhere in the range 15–35°C. CO<sub>2</sub> content of the air before and after the leaf chamber was measured by an infrared gas analyser and water vapour content was determined, before and after the leaf chamber, by two differential psychrometers (Slatyer and Bierhuizen 1964).

(c) *Theoretical Considerations*

Gaastra (1959) proposed that the following equations be used in evaluating the various components of  $P$  and  $T$ :

$$P = (C_a - C_c)/(r_a + r_s + r_m)CO_2, \quad (1)$$

$$T = (W_i - W_a)/(r_a + r_s)_{\text{water}}, \quad (2)$$

where  $C_a$  and  $C_c$  represent the CO<sub>2</sub> concentrations in the external air and in the chloroplast respectively,  $W_i$  and  $W_a$  the water vapour concentrations in the intercellular spaces and air respectively, and  $r_a$ ,  $r_s$ , and  $r_m$  represent resistances provided by the boundary layer, stomata and intercellular spaces of the leaf, and mesophyll cells, respectively, to water vapour and CO<sub>2</sub>, as defined by the subscripts.

However, although these equations have been widely used, it has been suggested (Gaastra 1959; Whiteman and Koller 1967) that values of  $r_m$  should be calculated only under conditions of light saturation and limiting CO<sub>2</sub> concentrations in the external air. Thus, in the comparative study reported here, the use of  $r_m$  is not appropriate in wheat in low light or in a sorghum under any circumstances because of lack of light saturation. Both Whiteman and Koller (1967) and Moss and Rawlins (1963) used a general equation proposed by Gaastra (1959):

$$P = (C_a - C_i)/(r_a + r_s)CO_2, \quad (3)$$

where  $C_i$  represents the CO<sub>2</sub> concentration in the intercellular spaces.

Use of this equation, which does not include  $r_m$ , results in the effects which would otherwise be included in  $r_m$  being included in the numerator. These include the effect of photorespiration in releasing CO<sub>2</sub>, activity of carboxylation enzymes, feed-back inhibition of photosynthesis (which may occur if "sink source" hypotheses are correct), and translocation limitations to photosynthesis. This general equation has an advantage in that it is not necessary to make any assumptions as to the value of  $C_c$ , and in making  $P/T$  comparisons which are indicative of efficiency

of water use; resistance terms are eliminated so that efficiency is proportional to  $(C_a - C_i)/(W_i - W_a)$ . Bierhuizen and Slatyer (1965) have discussed the significance of the denominator in efficiency of water use but the importance of the numerator does not appear to have been investigated.

(d) Data

Equations 2 and 3 were used. The value of  $T$  was measured and the value of  $W_i - W_a$  was calculated from leaf temperature, psychrometer readings, and tables provided by Slatyer (personal communication) but similar in derivation to those of List (1963). Thus  $(r_a + r_s)_{\text{water}}$  could be calculated. The blotting-paper technique (Gaastra 1959) was used to estimate  $(r_a)_{\text{water}}$ . Because of doubts concerning the real value of  $(r_a)_{\text{CO}_2}$ , which can be expected to vary between  $1.0 (r_a)_{\text{water}}$  and  $1.7 (r_a)_{\text{water}}$  depending on the relative contributions of mass exchange and diffusion respectively (Gaastra 1959), the mean value of  $1.35 (r_a)_{\text{water}}$  was arbitrarily chosen and used in calculations. This value for  $(r_a)_{\text{CO}_2}$  corresponds with that of Gale and Poljakoff-Mayber (1968). Errors in the choice of  $(r_a)_{\text{CO}_2} = 1.35 (r_a)_{\text{water}}$  are not great because of the low value of  $(r_a)_{\text{water}}$  ( $0.55-0.60 \text{ sec cm}^{-1}$ ) obtained by blotting-paper techniques. The value of  $(r_s)_{\text{CO}_2}$  was assumed to be  $1.7 (r_s)_{\text{water}}$  (Gaastra 1959), a little higher than that suggested by Gale and Poljakoff-Mayber (1968). Thus, the values of  $(r_a + r_s)_{\text{CO}_2}$  were calculated and since  $P$  was known from gas analyser and flow readings, a value for  $C_a - C_i$  could be determined.

Light intensity was set at one of the three levels  $0.06$ ,  $0.26$ , and  $0.46 \text{ cal cm}^{-2} \text{ min}^{-1}$  of photosynthetically active radiation for experiments, and are referred to as light levels 1, 2, and 3 respectively. In a subsidiary study, two further levels,  $0.16$  and  $0.36 \text{ cal cm}^{-2} \text{ min}^{-1}$  were used. Leaf temperature was changed slowly along the range  $15-35^\circ\text{C}$  with leaves in the chamber for no more than 2-3 hr. Several leaves were exposed to the above conditions so that the tables include data from a number of leaves.

TABLE 1

TRANSPIRATION RATE AND WATER VAPOUR CONCENTRATION DIFFERENCE AND RESISTANCE IN WHEAT (W) AND SORGHUM (S) IN RESPONSE TO LEAF TEMPERATURE AND LIGHT INTENSITY

Light Intensity* ( $\text{cal cm}^{-2} \text{ min}^{-1}$ )	15°C		20°C		25°C		30°C		35°C	
	W	S	W	S	W	S	W	S	W	S
$10^6 \times$ Transpiration rate, $T$ ( $\text{g cm}^{-2} \text{ sec}^{-1}$ )										
0.06	10	3	12	4	13	5	14	7	16	8
0.26	—	—	12	—	15	5	17	8	19	10
0.46	—	—	12	—	15	14	17	17	22	22
$10^6 \times$ Water vapour concn. difference, $W_i - W_a$ ( $\text{g cm}^{-3}$ )										
0.06	6	8	10	12	15	17	22	24	29	30
0.26	—	—	9	—	13	12	18	17	24	24
0.46	—	—	9	—	13	13	19	17	27	24
Water vapour resistance, $r_a + r_s$ ( $\text{sec cm}^{-1}$ )										
0.06	0.6	2.1	0.8	2.6	1.1	3.1	1.5	3.3	1.9	3.6
0.26	—	—	0.8	—	0.9	2.4	1.2	2.2	1.3	2.4
0.46	—	—	0.8	—	0.9	0.9	1.1	1.0	1.2	1.1

\* Range 400-700 nm.

III. RESULTS

(a) Transpiration Rate

At each light intensity,  $T$  for wheat leaves increased with increases in temperature. This was due to an increase in  $W_i - W_a$ . At light level 1, stomatal resistance increased with increasing temperature and this tended to reduce  $T$ . This effect was less pronounced at higher levels of light intensity (Table 1).

$T$  values for sorghum leaves, as for wheat, did not increase markedly with light intensity, except that in sorghum a higher rate was evident at light level 3. Stomatal movement was apparently significant in modifying  $T$  in sorghum. At low light levels stomatal resistance increased with temperature as it did in wheat, but temperature had little effect on stomatal resistance at higher light levels. In wheat, stomatal resistance decreased as light intensity was raised. However, this effect was much more marked in sorghum (Table 1).

At low and medium light intensity levels  $T$  was much lower in sorghum than in wheat, due to the greater stomatal resistance to gas flow in sorghum. At light level 3, however, where stomatal resistances were comparable,  $T$  values were similar.

(b) *Net Photosynthetic Rate*

In wheat, the low values of  $P$  obtained at light level 1 remained approximately constant, irrespective of temperature, but increased at higher light levels, with a maximum between 25 and 30°C (Table 2). The value of  $C_a - C_i$  increased with

TABLE 2  
PHOTOSYNTHETIC RATE AND CO<sub>2</sub> CONCENTRATION DIFFERENCE AND RESISTANCE IN WHEAT (W) AND SORGHUM (S) IN RESPONSE TO LEAF TEMPERATURE AND LIGHT INTENSITY

Light Intensity* (cal cm <sup>-2</sup> min <sup>-1</sup> )	15°C		20°C		25°C		30°C		35°C	
	W	S	W	S	W	S	W	S	W	S
$10^8 \times$ Photosynthetic rate, $P$ (g cm <sup>-2</sup> sec <sup>-1</sup> )										
0.06	5	5	5	6	5	6	5	7	5	7
0.26	—	—	8	—	9	13	11	14	10	15
0.46	—	—	9	—	10	20	9	24	9	25
$10^8 \times$ CO <sub>2</sub> concn. difference, $C_a - C_i$ (g cm <sup>-3</sup> )†										
0.06	4	18	7	26	10	34	12	36	14	39
0.26	—	—	9	—	13	45	18	51	20	59
0.46	—	—	9	—	14	28	17	36	18	45
CO <sub>2</sub> resistance, $r_a + r_s$ (sec cm <sup>-1</sup> )										
0.06	0.9	3.3	1.2	4.2	1.7	5.1	2.5	5.5	3.1	5.9
0.26	—	—	1.1	—	1.4	4.0	1.8	3.5	2.0	3.9
0.46	—	—	1.1	—	1.4	1.4	1.8	1.5	1.9	1.7

\* Range 400–700 nm.

† When  $C_a = 300$  p.p.m. and  $C_i = 0$ ,  $C_a - C_i = 59 \times 10^{-8}$  g cm<sup>-3</sup>.

temperature under each light regime, values being a little higher at levels 2 and 3 than at level 1. Stomatal resistance to CO<sub>2</sub> movement was greater at the low light level and this was apparently a significant factor in the lower  $P$  values under these conditions.

In sorghum there was a marked increase in  $P$  with increase in light intensity. At light level 1, the rate was relatively constant over the temperature range but at higher light levels  $P$  increased with temperature until a plateau was reached about 30°C (Table 2). The value of  $C_a - C_i$  for sorghum increased rapidly with temperature and, although the response patterns followed the same trends at each light level,

values were appreciably higher at light level 2 than at light levels 1 and 3. A subsidiary experiment indicated that at light intensity levels of 0.16, 0.26, and 0.36 cal cm<sup>-2</sup> min<sup>-1</sup> the values of  $C_a - C_i$  were similar but lower values were observed at levels 1 and 3. The high resistance to CO<sub>2</sub> movement at low light intensity in sorghum was associated with the low value of  $P$  observed and resistance was also important at light level 2. In contrast, decreased values for  $C_a - C_i$  were observed at light level 3, even though very high rates of CO<sub>2</sub> fixation were realized (to  $25 \times 10^{-8}$  g cm<sup>-2</sup> sec<sup>-1</sup> or 90 mg dm<sup>-2</sup> hr<sup>-1</sup>).

In sorghum at light level 1,  $P$  was only a little higher than that of wheat because, though  $C_a - C_i$  was much higher in sorghum, so was  $(r_a + r_s)_{CO_2}$ . At light level 3, however,  $P$  in sorghum reached 2.5 times the maximum rate attained by wheat. Since the values for  $(r_a + r_s)_{CO_2}$  were comparable the greater values for  $C_a - C_i$  in sorghum were related in this difference in  $P$  between species.

### (c) $P/T$ Ratio

The lower value for  $T$  in sorghum at light levels 1 and 2 and the higher  $P$  values at light levels 2 and 3 are reflected in  $P/T$  ratios shown in Figures 1(a), 1(b), and 1(c).

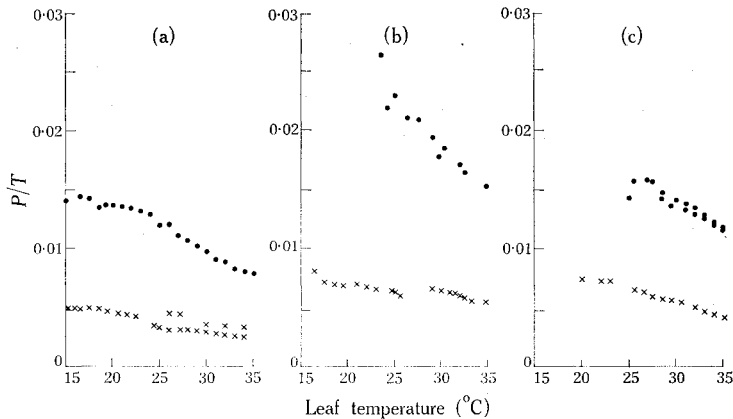


Fig. 1.—(a)–(c)  $P/T$  ratio of wheat (×) and sorghum (●) in response to temperature, at light levels 1–3 respectively.

Under all conditions, the sorghum  $P/T$  values were substantially higher than those of wheat. Both species were a little more efficient in their use of water at low rather than at high temperatures. Wheat efficiency was greater at light levels 2 and 3 than at 1. Sorghum was more efficient at light level 2 than at either extreme.

## IV. DISCUSSION

The results support earlier evidence (Downes 1969) that at low light levels sorghum stomata offer greater resistance to movement of water than do wheat stomata. This is responsible for the lower value for  $T$  in sorghum under these conditions. At high light levels, stomata of both species are open and  $T$  values are comparable.

On the other hand,  $P$  values increase markedly with light intensity in sorghum, and at high levels of radiation they also increase with temperature to 30°C. The stomatal resistance to CO<sub>2</sub> movement in sorghum appears to be related to low  $P$  values at light levels 1 and 2 but this is offset by high values of  $C_a - C_i$ . At light level 1, sorghum stomatal resistance increased with leaf temperature, whereas at higher light levels it was less sensitive to temperature. It may be significant that both  $C_a - C_i$  and  $(r_a + r_s)_{CO_2}$  increased with temperature at light level 1. Thus, a decrease in  $C_i$  was accompanied by an increase in resistance. This tendency was also evident in wheat under all light conditions and does not support the hypothesis that decreases in  $C_i$  induce stomatal opening (Ketellapper 1963). Further evidence against this hypothesis is suggested by  $C_i$  values for sorghum at 35°C where, at light level 2,  $C_i$  was approximately zero, yet the value for  $(r_a + r_s)_{CO_2}$  was 3.9 sec cm<sup>-1</sup>. An increase in light intensity caused  $C_i$  to increase and  $(r_a + r_s)_{CO_2}$  to decrease.

The value of  $C_a - C_i$  increased with temperature in both species but particularly in sorghum. This term appears to be related to the temperature sensitivity of  $P$  in sorghum, since  $(r_a + r_s)_{CO_2}$  has the opposite effect, increasing as it does with increasing temperature. Increase in the CO<sub>2</sub> concentration gradient with increased temperature may reflect the activity of the enzymes active in photosynthesis. A similar temperature response curve was reported for phosphoenol pyruvate carboxylase activity by Treharne and Cooper (1969). In wheat, on the other hand, photorespiration which results in CO<sub>2</sub> being released and recycled (Zelitch 1968) would tend to reduce the CO<sub>2</sub> concentration gradient. Data of Jolliffe and Tregunna (1968) suggest that photorespiration increases with temperature—as does the CO<sub>2</sub> compensation point (Eggle and Schenk 1953). This would mask the effect of increased carboxylase activity with increasing temperature in wheat, since wheat possesses photorespiration. This may explain why the CO<sub>2</sub> concentration gradient does not increase with increased temperature as much in wheat as in sorghum (Table 2).

At low temperatures, where the effect of photorespiration is negligible (Jolliffe and Tregunna 1968), the value of  $C_a - C_i$  is still much lower in wheat than in sorghum. At light level 1 and 15°C for example, the respective values are  $4 \times 10^{-8}$  and  $18 \times 10^{-8}$  g cm<sup>-3</sup>. This suggests that photorespiration is not the only factor in reducing the CO<sub>2</sub> concentration gradient in wheat below that of sorghum.

The effect of light intensity on  $P$  values in sorghum and other tropical grasses is well documented (see Cooper and Tainton 1968). The expected increase in  $P$  values with increased radiation was found in this study; however, two other factors also emerge. The marked increase in  $P$  values can be attributed mainly to a decrease in the value of  $(r_a + r_s)_{CO_2}$  with increased light intensity. In terms of the CO<sub>2</sub> concentration gradient, however, maximum values are obtained at light level 2 (or in the range 0.16–0.36 cal cm<sup>-2</sup> min<sup>-1</sup>). Increased light intensity above this level is accompanied by a decrease in the value of the  $C_a - C_i$  term. This may be explained by some reduction in translocation of the products of photosynthesis associated with the two interdependent types of chloroplasts involved in photosynthesis in tropical grasses (Slack, Hatch, and Goodchild 1969).

With the dissection of the components of  $P$  in the manner used here, it is clear that under high light intensity and high temperature conditions sorghum is operating near its physical limit but wheat is only utilizing about one-third of the

CO<sub>2</sub> concentration gradient possible with  $C_i$  values about 200 p.p.m. Thus, it appears that wheat may have the potential to increase  $P$  in response to demands which might arise after defoliation or on grain filling (see King, Wardlaw, and Evans 1967), in contrast to sorghum which does not appear to have this flexibility.

Using the parameter  $P/T$  as a measure of water use efficiency, sorghum is clearly superior to wheat. The components of  $P$  and  $T$  used here indicate that efficiency is proportional to  $[(C_a - C_i)/(W_i - W_a)]$ . The tables indicate that the values for  $W_i - W_a$  do not vary appreciably with species in any environment used but the  $C_a - C_i$  term is the component which gives sorghum its efficiency. This is more pronounced at the intermediate rather than under the extreme light conditions. The greater efficiency of both species at low temperatures in this study is a function of the different slopes of the two terms when plotted against temperature.

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#### VI. REFERENCES

- BIERHUIZEN, J. F., and SLATYER, R. O. (1964).—An apparatus for the continuous and simultaneous measurement of photosynthesis and transpiration under controlled environmental conditions. Tech. Pap. Div. Land Res. CSIRO Aust. No. 24.
- BIERHUIZEN, J. F., and SLATYER, R. O. (1965).—Effect of atmospheric concentration of water vapour and CO<sub>2</sub> in determining transpiration-photosynthesis relationships of cotton leaves. *Agric. Meteorol.* **2**, 259-70.
- COOPER, J. P., and TAINTON, N. M. (1968).—Light and temperature requirements for the growth of tropical and temperate grasses. *Herb. Abstr.* **38**, 167-76.
- DOWNES, R. W. (1969).—Difference in transpiration rates between tropical and temperate grasses under controlled conditions. *Planta* **88**, 261-73.
- EGLE, K., and SCHENK, W. (1953).—Der Einfluss der Temperatur auf die Lage des CO<sub>2</sub>-Kompensationspunktes. *Planta* **43**, 83-97.
- GAASTRA, P. (1959).—Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature, and stomatal diffusion resistance. *Meded. LandbHoogeschool, Wageningen* **59**, 1-68.
- GALE, J., and POLJAKOFF-MAYBER, A. (1968).—Resistance to the diffusion of gas and vapor in leaves. *Physiologia Pl.* **21**, 1170-6.
- JOLLIFFE, P. A., and TREGUNNA, E. B. (1968).—Effect of temperature, CO<sub>2</sub> concentration, and light intensity on oxygen inhibition of photosynthesis in wheat leaves. *Pl. Physiol., Lancaster* **43**, 902-6.
- KETELLAPPER, H. J. (1963).—Stomatal physiology. *A. Rev. Pl. Physiol.* **14**, 249-70.
- KING, R. W., WARDLAW, I. F., and EVANS, L. T. (1967).—Effect of assimilate utilization on photosynthetic rate in wheat. *Planta* **77**, 261-76.
- LIST, R. J. (1963).—“Smithsonian Meteorological Tables.” (Smithsonian Institution: Washington, D.C.)
- MCPHERSON, H. G. (1969).—Photocell-filter combinations for measuring photosynthetically active radiation. *Agric. Meteorol* **6**, 347-56.

- MOSS, D. N., and RAWLINS, S. L. (1963).—Concentration of carbon dioxide inside leaves. *Nature, Lond.* **197**, 1320–1.
- SLACK, C. R., HATCH, M. D., and GOODCHILD, D. J. (1969).—Distribution of enzymes in mesophyll and parenchyma sheath chloroplasts of maize leaves in relation to the C<sub>4</sub>-dicarboxylic acid pathway of photosynthesis. *Biochem. J.* **114**, 489–98.
- SLATYER, R. O., and BIERHUIZEN, J. F. (1964).—A differential psychrometer for continuous measurements of transpiration. *Pl. Physiol., Lancaster* **39**, 1051–6.
- TREHARNE, K. J., and COOPER, J. P. (1969).—Effect of temperature on the activity of carboxylases in tropical and temperate Gramineae. *J. exp. Bot.* **20**, 170–5.
- TROUGHTON, J. H. (1969).—Plant water status and carbon dioxide exchange of cotton leaves. *Aust. J. biol. Sci.* **22**, 289–302.
- TROUGHTON, J. H., and SLATYER, R. O. (1969).—Plant water status, leaf temperature, and the calculated mesophyll resistance to carbon dioxide of cotton leaves. *Aust. J. biol. Sci.* **22**, 815–27.
- WHITEMAN, P. C., and KOLLER, D. (1967).—Interactions of carbon dioxide concentration, light intensity and temperature on plant resistances to water vapour and carbon dioxide diffusion. *New Phytol.* **66**, 463–73.
- ZELITCH, I. (1968).—Investigations on photorespiration with a sensitive <sup>14</sup>C-assay. *Pl. Physiol., Lancaster* **43**, 1829–37.