

MECHANISMS REGULATING PHOTOSYNTHESIS IN *PENNISETUM TYPHOIDES*

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Abstract

Leaf chamber studies were conducted on single attached leaves of *Pennisetum typhoides* (Burm.) S. & H. (bulrush millet) to identify and describe the processes regulating photosynthesis.

Stomatal resistance to CO₂ diffusion was the most variable of the resistances regulating net photosynthetic rates at optimum temperatures (35°C). It varied widely with radiation and constituted at normal CO₂ concentrations 35–85% of the total resistance. The variation with external CO₂ concentration was essentially linear in the range 200–500 ng cm⁻³. The residual resistance was relatively small. At high radiation levels, values ranged from 0.2–1.0 s cm⁻¹ constituting from 10 to 40% of the total resistance to photosynthesis.

Net photosynthetic rates varied considerably with leaf maturity, particularly with respect to the stage of individual leaf development, but also with order of leaf emergence. This variation was due largely to changes in stomatal resistance with maturity, although less significant changes in residual resistance also occurred. High net photosynthetic rates, of up to 277 ng CO₂ cm⁻² s⁻¹, were recorded.

I. INTRODUCTION

It is well established that photosynthesis in plant leaves is dependent on a series of interacting physical and biochemical processes each of which affect the rate of the overall process. The potential rates of the individual processes vary widely and so does their importance in the regulation of photosynthesis. The identification and description of the slower processes which have the greatest influence on photosynthesis is seen as an important step in providing a more efficient basis for planning crop management, plant breeding, and further experimentation.

Rate-regulating processes may operate by restricting the transport of CO₂ from the outside air to the site of photosynthesis in the chloroplasts, by influencing the rate of its photochemical incorporation, or by controlling its subsequent biochemical utilization. Gas-exchange analysis under controlled conditions can be used to determine the relative importance of such groups of processes. Considerable evidence has accumulated demonstrating that for a large number of species, the resistances to CO₂ transport play an important role in regulating photosynthesis. Stomatal resistance is

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particularly important in this respect because of its magnitude and variability (Bierhuizen and Slatyer 1964; Lake 1967; Meidner 1969; Troughton 1969; Troughton and Slatyer 1969; Gifford and Musgrave 1970; Wilson and Ludlow 1970). For these reasons, experiments with *Pennisetum typhoides* (Burm.) S. & H. were designed to obtain the information necessary for estimating the relative magnitude of the resistances to CO₂ transport, and for interpretation of their role in regulating photosynthesis.

II. THEORY

The relationships between the rate of net photosynthesis and the processes directly affecting it are conveniently described using an analogue of Ohm's law based on Fick's law of diffusion. The form of the equations used by various workers has varied considerably, as has interpretation of the results produced. Difficulty has often arisen when interpretation of the analogue has been more literal than is justified, and when similar notation and terminology have been used to convey different ideas.

For the present paper the net flux of CO₂ into the leaf, F , is given by:

$$F = \frac{c_t - \Gamma}{r'_a + r'_s + r'_r} = \frac{c_t - c_w}{r'_a + r'_s} = \frac{c_w - \Gamma}{r'_r} \quad (1)$$

where c_t and c_w are the CO₂ concentration in the ambient air and at the surface of the mesophyll cells respectively. Γ is the CO₂ compensation point which is assumed to be the CO₂ concentration at the effective carboxylation/decarboxylation surface inside the cell, under conditions where CO₂ supply is limiting F . The symbols r'_a and r'_s refer to the "resistances" to CO₂ transport in the boundary layer, and between the boundary layer and the mesophyll cell walls respectively.

F , c_t , Γ , r'_a , and r'_s can be measured (see, for example, Slatyer 1970), and r'_r is obtained algebraically from equation (1).

The term r'_r has been referred to as the residual resistance (Gifford 1970) and contains those components of the total resistance to photosynthesis, $\Sigma r'$, not represented by $(r'_a + r'_s)$. On the part of the CO₂ response (F/c_w) curve, where CO₂ is limiting F , r'_r is identical with the intracellular resistance (see Slatyer 1970). At higher values of c_w , non-linearity develops as other factors begin to exert control over F . Under these conditions, the CO₂ concentration at the carboxylation/decarboxylation surface exceeds Γ . By using equation (1) this effect causes an apparent increase in r'_r . In the present experiments, for reasons given below, there was some doubt as to where the F/c_w curve deviated from linearity. Consequently it was regarded more appropriate to use the residual resistance, r'_r , than to use the intracellular resistance.

The stomatal (r'_s) and boundary layer (r'_a) resistances were estimated in the usual manner from water vapour fluxes and concentration differentials. Conversion of the stomatal resistances determined for water vapour transport, to those applicable to CO₂, was made by multiplying the former values by the ratio of the diffusivities for water vapour, D_w , and CO₂ D_c , in air. The value used was based on the values supplied by the International Critical Tables (1929) and from other work in the field of diffusion (Montgomery 1947; Lee and Wilke 1954; Fuller *et al.* 1966), which yield $D_w = 0.220 \text{ cm}^2 \text{ s}^{-1}$, $D_c = 0.138 \text{ cm}^2 \text{ s}^{-1}$, both at 0°C. Hence $D_w/D_c = 1.594$,

and is independent of temperature. It has been questioned whether the diffusion coefficients determined in free air apply to diffusion through small apertures. However, Milthorpe and Penman (1967) found that any such error is negligible in the computation of R .

In converting r_a to r'_a , R was raised to the two-thirds power (giving $R = 1.37$) to account for the non-diffusive portion of the boundary layer transfer (Cowan 1968; Gale and Poljakoff-Mayber 1968).

III. METHODS

A leaf chamber was used to provide accurate environmental control over single attached leaves. A metered air flow ($\pm 2\%$ accuracy) was sampled before and after passage through the leaf chamber, and measurements were made of water vapour concentration by using differential psychrometers (Slatyer and Bierhuizen 1964). Comparative calibration checks indicated errors in water vapour concentration differentials across the leaf chamber of $\pm 2\%$ at transpiration rates 50% of the maximum. The CO_2 concentration was measured using a URAS2 infrared gas analyser calibrated with Wösthoff gas-mixing pumps and the calibration varied by no more than $\pm 1.5\%$ at ambient concentrations. Comparative calibration checks indicated errors in CO_2 concentration differentials across the leaf chamber of not greater than $\pm 2\%$ at CO_2 exchange rates 50% of the maximum. Leaf and air temperatures were measured with 42 s.w.g. copper-constantan thermocouples ($\pm 0.3^\circ\text{C}$ accuracy). Those measuring leaf temperature were held by tension of the wire against the underside of the leaf. The leaf temperature value used was the mean of measurements at two or three positions on the leaf. For a detailed consideration of the effects of measurement errors on the calculated resistances to CO_2 and water vapour exchange see Slatyer (1971).

The light source used was an AC xenon arc (Wotan XBF 2500) fitted with a reflector which gave even light distribution over the leaf ($\pm 2.5\%$ over most of the leaf, $\pm 5.0\%$ maximum in the leaf chamber). Small silicon photovoltaic cells (active area 0.3 by 0.4 cm) fitted with glass filters (Schott and General, BG38 and GG19) were used to determine the flux of photosynthetically active radiation (PAR) incident on the leaf (McPherson 1969). These instruments were calibrated against a filtered thermopile solarimeter ($\pm 2.5\%$ accuracy) in terms of photon flux density (400–700 nm waveband) expressed as E (einsteins) $\text{cm}^{-2} \text{s}^{-1}$. The conversion from energy to photon units was made using the lamp manufacturer's spectral emittance curves. The photon unit is more appropriate than energy units as photosynthesis is essentially a quantum-dependent reaction. For the xenon lamp used, conversion to energy units (in W m^{-2}) can be made from $\text{nE cm}^{-2} \text{s}^{-1} \div 0.46$ (400–700 nm waveband). Full sunlight $\simeq 200 \text{ nE cm}^{-2} \text{s}^{-1}$.

The Perspex leaf chamber was of similar construction to that described by Jarvis and Slatyer (1966) but rectangular in shape, and with one chamber enclosing a leaf area of approximately 100 cm^2 . The actual enclosed leaf area was measured by planimeter from the leaf silhouette obtained on a sheet of self-developing photographic paper (Kodak, Studio Proof F) placed under the leaf and exposed. All flux measurements related to leaf area are based on this projected area. Relatively even airflow over the leaf surface was provided by two inlet and two outlet manifolds running parallel to the main axis of the leaf. The velocity due to the normal throughflow was supplemented by pumping air through an external recycling loop. It was necessary to take the relative magnitude of these flows into account in calculating the actual concentration of CO_2 and water vapour entering the leaf chamber. Ambient concentrations were then taken as the average for the air streams actually entering and leaving the leaf chamber.

Pennisetum typhoides (Burm.) S. & H. cv. Katherine Pearl plants (C.P.I. No. 11378; cf. Australian Herbage Plant Register, Division of Plant Industry, CSIRO, 1967), were grown in aerated modified Hoaglands solution in a glasshouse with air temperatures approximately 30°C (day) and 15°C (night). The photoperiod was maintained at over $12\frac{1}{2}$ hr to ensure that floral initiation did not occur. A review of some aspects of the morphological development, physiology, and agronomy of this species is given by Norman and Begg (1968).

IV. RESULTS

(a) Leaf Temperature

A broad temperature optimum was established for single leaf photosynthesis in the range 35–40°C. Pooled data from several leaves are shown in Figure 1. Measure-

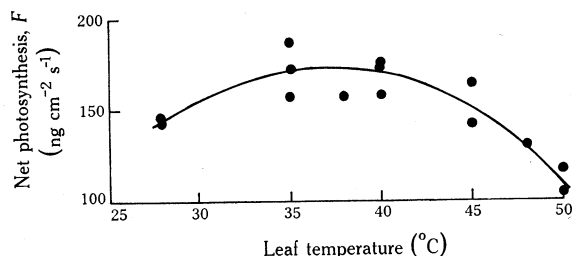


Fig. 1.—Response of net photosynthesis, F , to leaf temperature ($c_i \approx 500 \text{ ng cm}^{-3}$, $\text{PAR} \approx 130 \text{ nE cm}^{-2} \text{ s}^{-1}$).

ments obtained after the leaves had been taken to temperatures markedly different from the optimum are excluded as significant pretreatment effects were evident (cf. Downton and Slatyer 1972).

All subsequent experiments were conducted with leaf temperatures maintained at $35 \pm 2^\circ\text{C}$.

(b) CO_2 Concentration

Net photosynthesis showed an essentially linear response to external CO_2 concentrations in the range 200–500 ng cm^{-3} [Fig. 2(a)]. However, the slope of the curves was influenced by the incident flux density of PAR, indicating that some

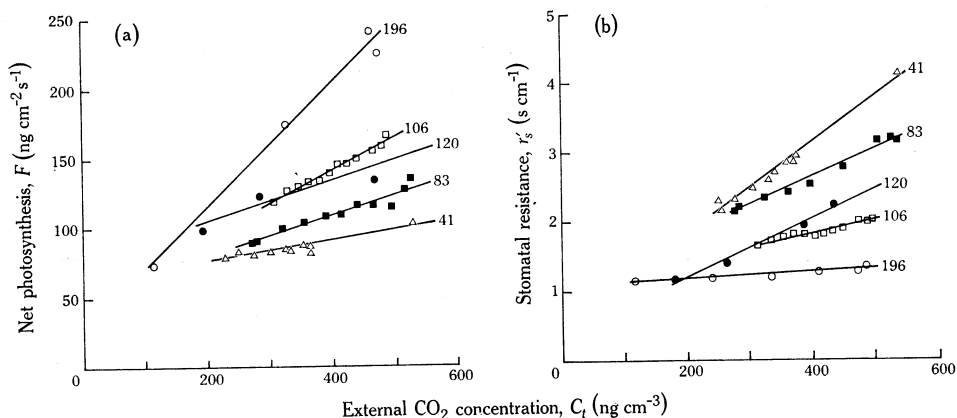


Fig. 2.—(a) Response of net photosynthesis, F , to external CO_2 concentration, c_i , at various levels of PAR. (b) Response of stomatal resistance, r_s , to CO_2 concentration, expressed as a function of the external CO_2 concentration, c_i , at various levels of PAR. The actual PAR values are indicated on each curve in units of $\text{nE cm}^{-2} \text{ s}^{-1}$.

radiation-dependent factor was mediating in the effect of c_i on F . Stomatal resistance estimates were obtained from water vapour measurements made simultaneously with the CO_2 exchange measurements and the response pattern with variation of c_i and PAR was seen to be similar, but inversely proportional to that of F [Fig. 2(b)].

The obvious implication that stomatal resistance played an important role in regulating net photosynthesis was investigated by comparing the change in the total resistance to net photosynthesis with the change of stomatal resistance for the range of external CO_2 concentration and PAR considered (Fig. 3). The boundary layer resistance was held at a low and constant value throughout ($r'_a = 0.5 \text{ s cm}^{-1}$) as indicated by the horizontal broken line. The diagonal line has unit slope and indicates the contribution of the boundary layer and stomatal resistances (calculated from water vapour measurements) to the total resistance to net photosynthesis [calculated from CO_2 measurements by rearranging the left-hand side of equation (1)]. The vertical distance between this line and the data points represents the residual resistance.

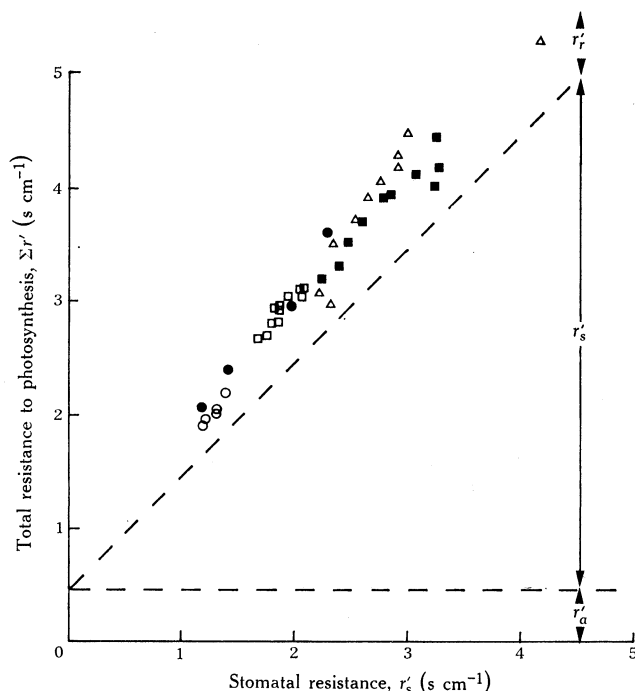


Fig. 3.—Contribution of stomatal resistance, r'_s , to the total resistance to net photosynthesis, $\Sigma r'$, in leaves of similar maturity but under different flux densities of PAR (data for each shown with a different symbol), and for a range of external CO_2 concentrations (PAR = $41\text{--}196 \text{ nE cm}^{-2} \text{ s}^{-1}$, $c_t = 100\text{--}550 \text{ ng cm}^{-3}$).

It can be seen that the residual resistance made a relatively small and constant contribution to $\Sigma r'$ (r'_r ranging from $0.2\text{--}0.9 \text{ s cm}^{-1}$, with an average value of 0.5 s cm^{-1}). In contrast, however, stomatal resistance values were larger, and varied over a wider range ($1.2\text{--}4.0 \text{ s cm}^{-1}$). Stomatal resistance, then, exerted the greatest single influence on the rate of net photosynthesis, accounting for 60–80% of $\Sigma r'$.

Considerable difficulty was experienced in achieving reliable results for external CO_2 concentrations below 200 ng cm^{-3} because of an unusual physiological response that occurred in this range. The symptoms involved visible tissue damage and irregular CO_2 exchange rates with a net release of CO_2 by the illuminated leaf often in excess of normal uptake rates. The use of extremely high humidity air eliminated the effect but under these conditions accurate estimates of stomatal resistance using water vapour measurements could not be made. It was possible, however, to establish that the “ CO_2 compensation point”, Γ , was zero, under the conditions used in these experiments, and this value was used in equation (1) to calculate values of $\Sigma r'$.

(c) Photosynthetically Active Radiation and Maturity

The response of F to PAR was determined for leaves of varying maturity. These experiments were conducted with leaf temperatures regulated to approximately 35°C , near normal ambient CO_2 concentrations ($c_i \approx 500 \text{ ng cm}^{-3}$), and a range of PAR flux densities incident on the leaf from zero to twice full sunlight.

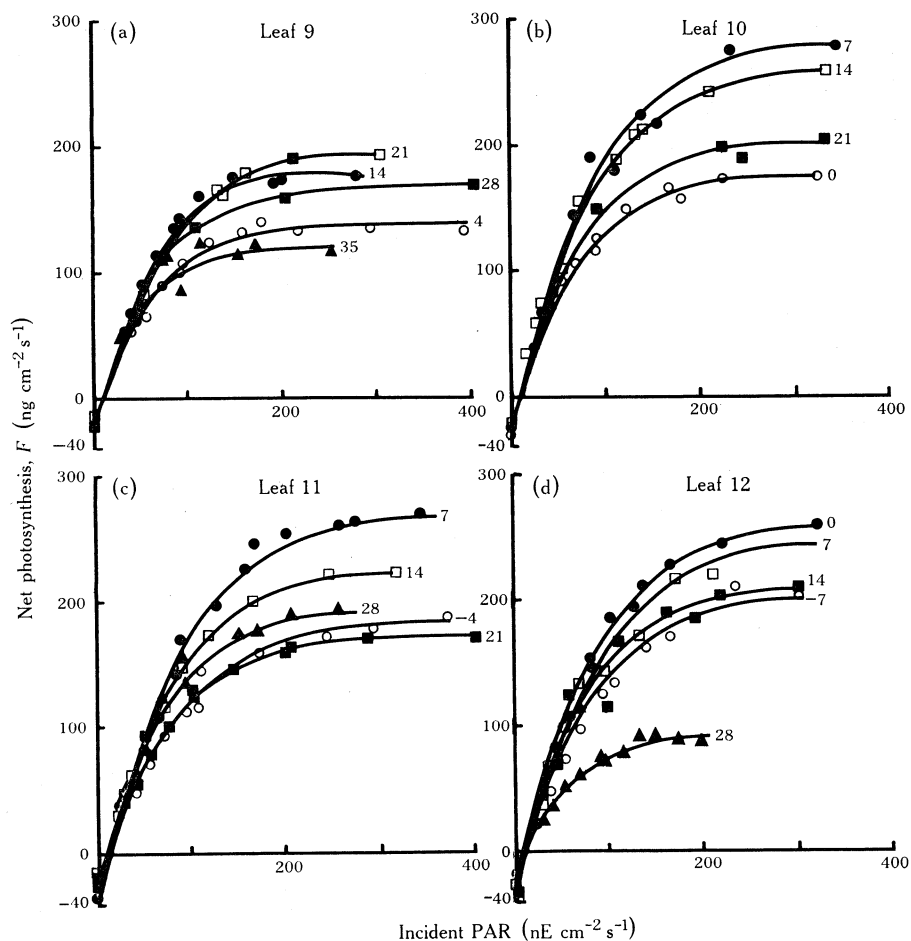


Fig. 4.—Response of net photosynthesis, F , to incident PAR for four leaves, (a)–(d), two from each of two plants. The leaf number indicates the order of emergence. Each leaf was sampled at approximately weekly intervals to determine changes with individual leaf maturity. The numbers on each curve refer to the number of days after full emergence ($c_i \approx 500 \text{ ng cm}^{-3}$).

Two aspects of maturity have been shown to affect photosynthesis: the order of emergence of leaves and the stage of individual leaves in their own maturity cycle (Thorne 1963; Jewiss and Woledge 1967). Both aspects have been considered here. The maturity class for any given leaf at a given time was specified in two ways: one value giving emergence order and numbered in sequence up the stem from the first

true leaf to develop; the other specifying the stage of any individual leaf in its maturity cycle as indicated by the time, in days, from full emergence. Appearance of the ligule was taken as indicating full emergence of a leaf and it was confirmed during the course of the experiments that lamina elongation had ceased at that stage.

The light response curves for two leaves from each of two plants are presented in Figures 4(a)–4(d), each graph showing the response for an individual leaf sampled at approximately weekly intervals. “Light saturation” at normal external CO_2 concentrations occurred at high incident PAR flux densities, equivalent to approximately full sunlight. Net photosynthesis under these conditions reached values of up to $277 \text{ ng cm}^{-2} \text{ s}^{-1}$. Respiration rates measured in the dark averaged $-22 \text{ ng cm}^{-2} \text{ s}^{-1}$ which represents approximately 8% of maximum net photosynthesis rates.

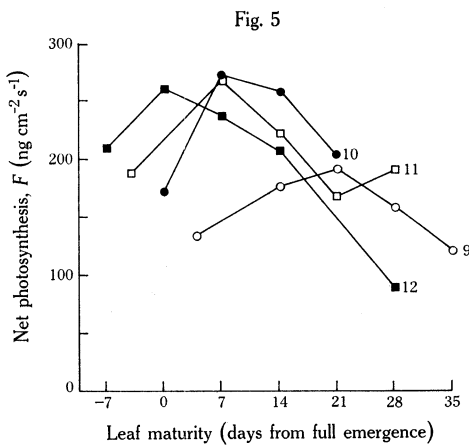


Fig. 5

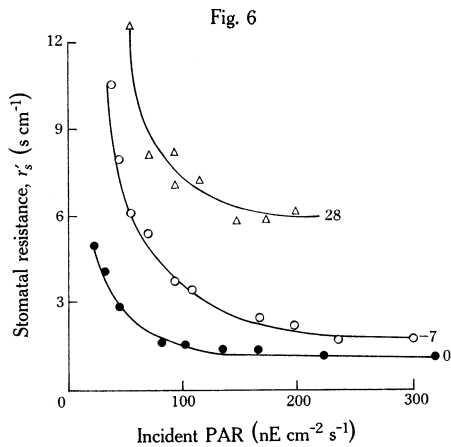


Fig. 6

Fig. 5.—Change, with leaf maturity, of rates of “light-saturated” net photosynthesis, F . The order of leaf emergence is indicated by the numbers on each curve.

Fig. 6.—Stomatal resistance, r_s' , as a function of PAR showing changes with maturity in the 12th leaf to emerge [cf. Fig. 4(d)]. The numbers on each curve refer to the number of days, after full emergence, of the test leaf.

Large effects of individual leaf maturity were evident. As the percentage differences in F were similar at all levels of PAR the change of net photosynthesis with maturity could be conveniently represented by the change in “light saturated” rates, $F_{\max}$ (Fig. 5). All four leaves studied showed an increase of $F_{\max}$ to a maximum, then a subsequent decline towards leaf senescence. No significant trend of respiration rates measured in the dark could be detected.

Figure 5 also reveals that the order of leaf emergence affected the value of $F_{\max}$, and the stage in the leaf maturity cycle that the maximum $F_{\max}$ was reached.

In considering the cause of the changes in the rate of net photosynthesis with both PAR and maturity it was first of all evident that the family of light response curves for any one leaf [Figs. 4(a)–4(d)] deviated near the origin and remained curvilinear down to low PAR levels. This suggested that the rate-restricting process, causing differences among the “light saturated” rates of net photosynthesis for different maturity classes, had a significant effect over a wide range of PAR. It also

showed that even at low flux densities, equivalent to 10% of full sunlight, factors other than the supply of radiant energy played an important role in regulating the rate of net photosynthesis.

The behaviour of stomatal resistance estimated during these experiments indicated that it might again account for many of the observed changes in net photosynthesis. A curvilinear decrease in stomatal resistance accompanied increasing PAR up to approximately full sunlight and the rate and extent of change varied with leaf maturity. Representative results are shown in Figure 6 for the 12th leaf to emerge [cf. Fig. 4(d)].

The relative importance of stomatal resistance and the other two resistances regulating photosynthesis was assessed, as before, by comparing their relative magnitude and variability. Figure 7 shows the results for leaves 9–12 at different maturity stages and over a range in PAR from 10–200% of full sunlight ($20\text{--}400\text{ nE cm}^{-2}\text{ s}^{-1}$).

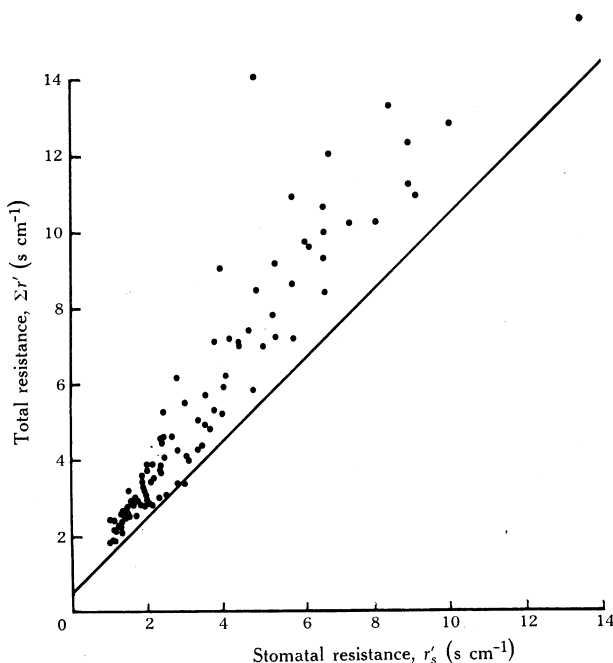


Fig. 7.—Contribution of stomatal resistance, r'_s , to the total resistance to net photosynthesis, $\Sigma r'$, for four leaves at different stages in their maturity cycle and for a range of PAR $20\text{--}400\text{ nE cm}^{-2}\text{ s}^{-1}$ ($c_i \simeq 500\text{ ng cm}^{-3}$).

Stomatal resistance exerted the greatest influence on the rate of net photosynthesis, contributing from 35–85% of $\Sigma r'$. The residual resistance made a smaller contribution which, as would be expected, increased with decreasing PAR. It is evident that, as in the first series of experiments, the minimum values of r'_s are unusually small indicating high efficiency in the system r'_s describes.

V. DISCUSSION

The results presented here provide strong confirmation of the extremely high photosynthetic capacity of *Pennisetum typhoides*, a feature already documented under

field conditions (Begg 1965). The highest rates observed were $277 \text{ ng cm}^{-2} \text{ s}^{-1}$, and light saturation occurred at PAR flux densities approximating to full sunlight, as has been observed for other tropical crops (Moss 1963; Hesketh and Baker 1967; Cooper and Tainton 1968; Bull 1969; Gifford 1970; Ludlow and Wilson 1971). The ratio of dark respiration to maximum net photosynthesis, of approximately 8%, is similar to that found for *P. purpureum* and other tropical grasses by Ludlow and Wilson (1971). The temperature response of photosynthesis, and the high temperature optimum, shown here for *P. typhoides*, is also similar to those reported for other tropical grasses (Miller 1960; El-Sharkawy and Hesketh 1964; Murata *et al.* 1965; Gifford 1970; Ludlow and Wilson 1971). These features, together with the low residual resistance values, and a CO_2 compensation point close to zero are consistent with the possession by *P. typhoides* of the C_4 -dicarboxylic pathway for photosynthesis.

The low values for r'_r indicate an unusually high efficiency for the processes involved in the transport of CO_2 through the mesophyll tissue and in its photochemical incorporation and subsequent utilization. The initial slope of the F/c_w curve indicates a residual resistance in the order of $0.1\text{--}0.2 \text{ s cm}^{-1}$. Unfortunately the leaf damage associated with low CO_2 concentrations prevented the initial slope from being clearly established. These values are so low [values for C_4 plants are seldom much lower than 1.0 s cm^{-1} (see, for example, Slatyer 1970)] that it seems possible that they are underestimated to some degree. Although great care was taken with the measurements, Slatyer (1971) has shown that quite small errors affect r'_r , particularly where r'_s represents a large proportion of $\Sigma r'$.

The findings presented in this paper re-emphasize the importance, in whole-leaf studies of photosynthesis, of evaluating the various resistances to CO_2 transport and particularly identifying stomatal and non-stomatal components. This applies whether the studies are intended to establish levels of photosynthetic capability or to elucidate the fundamental processes themselves. It is possible, for example, that some of the genotypic differences in photosynthetic rates that have been described (Hesketh 1963; Izhar and Wallace 1967; Björkman 1968; Wareing *et al.* 1968) may have been caused by differences in stomatal resistances to CO_2 transport rather than by the mechanisms proposed.

Probably the most noteworthy feature of the results is the strong evidence that stomatal resistance to CO_2 transport is the primary factor regulating photosynthesis under the conditions used in these experiments. Of particular interest is the evidence that stomatal resistance was the main variable factor associated with the different light response curves which were obtained from leaves of different maturity classes. In many respects this reflects the high biochemical efficiency of the leaf material, so that CO_2 supply, rather than photosynthetic capacity, appeared to be limiting the maximum rates of photosynthesis which were observed.

VI. ACKNOWLEDGMENT

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