PHOTOSYNTHESIS OF TROPICAL PASTURE PLANTS

I. ILLUMINANCE, CARBON DIOXIDE CONCENTRATION, LEAF TEMPERATURE, AND LEAF–AIR VAPOUR PRESSURE DIFFERENCE

By M. M. Ludlow* and G. L. Wilson†

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Abstract

Carbon dioxide and water vapour exchange of attached, young, fully expanded leaves of tropical pasture species were measured in an open gas analysis system. The influence of illuminance, carbon dioxide concentration, leaf temperature, and leaf–air vapour pressure difference on net photosynthetic rate and carbon dioxide transfer resistances was studied.

Net photosynthesis of grass leaves only approached light saturation at 10,000 f.c., whereas the light saturation point for legumes was 4000–5000 f.c. At high illuminance, the mean leaf net photosynthetic rate of grasses (60 mg CO_2 dm^{-2} hr^{-1}) was twice that of legumes (28 mg CO_2 dm^{-2} hr^{-1}), and associated with lower mesophyll resistances. Mean quantum efficiencies were 0·10 and 0·06 moles CO_2 per Einstein for grasses and legumes, respectively. Stomatal resistance varied with illuminance, but mesophyll resistance was unaffected above 3000–4000 f.c. Calculated mesophyll resistances increased below this intensity, but their significance is not clear. The unsaturated light response curve of grass leaves resulted from a continual decrease of stomatal resistance with increasing illuminance.

The net photosynthetic rate of grass stems was greater than that for legumes, and was affected by illuminance. Errors involved in neglecting stem surface area in growth analysis studies are discussed.

The net photosynthetic rate of legume leaves was much higher when the upper surface rather than the lower was illuminated, but there was little difference with grass leaves.

The net photosynthesis–illuminance curves of grass and legume leaves were markedly affected by carbon dioxide concentration. At high illuminance and carbon dioxide concentrations less than 400 $\mu l\ l^{-1}$, the net photosynthetic rate of grass leaves responded more to changes in carbon dioxide concentration than did that of legume leaves. However, net photosynthesis of grass leaves was saturated with carbon dioxide at lower concentrations compared with legume leaves, because of a higher stomatal resistance.

Grass leaves released no carbon dioxide into carbon dioxide-free air except at low illuminance, whereas carbon dioxide efflux from legume leaves occurred at all illuminances. At high illuminance the maximum efflux was about 1·5 times the dark respiration rate, and a minimum efflux occurred at 45 f.c. The response of carbon dioxide efflux to illuminance is discussed in relation to the balance between photorespiration and dark respiration.

The reduction of net photosynthesis of grass and legume leaves measured in bright light at leaf–air vapour pressure differences greater than 12 mmHg was accompanied by an increase in stomatal resistance.

* Botany Department, University of Queensland; present address: Division of Tropical Pastures, CSIRO, St. Lucia, Qld. 4067.

† Agriculture Department, University of Queensland, St. Lucia, Qld. 4067.

Although the minimum temperatures for net photosynthesis (measured in bright light) were similar, the optimum and maximum temperatures were higher for grasses than for legumes. The leaf net photosynthetic rate of grasses was greater than that of legumes at all temperatures. The Q_{10} of dark respiration rate was 2. There was a marked interaction between the effects of leaf temperature and illuminance on net photosynthesis.

Factors affecting the relationship between leaf temperature and net photosynthesis are discussed.

I. Introduction

Ludlow and Wilson (1968, 1970) showed that the higher relative growth rate of tropical pasture grasses compared with legumes was the result of a higher net assimilation rate which resulted from a higher photosynthetic rate. Carbon dioxide exchange studies were then undertaken to examine in detail the net photosynthetic behaviour of components of pasture canopies. This work compared species and leaves of varying age or position on the one plant; it examined the effects of a number of environmental factors, including the residual effects of previous environmental history; and some physiological analyses of behaviour were made. This paper reports the effects of illuminance, carbon dioxide concentration, leaf temperature, and leaf–air vapour pressure difference on net photosynthesis and resistances to carbon dioxide transfer.

II. Materials and Methods

(a) *Materials*

Only species with leaves morphologically suitable for leaf-chamber studies were used; these are listed in the following tabulation:

	Grasses
Buffel grass	*Cenchrus ciliaris* L. cv. Biloela
Coloratum	*Panicum coloratum* L. cv. Kabulabula CPI16796
Elephant grass	*Pennisetum purpureum* Schum. Q5088
Green panic	*Panicum maximum* Jacq. var. trichoglume Eyles cv. Petrie
Guinea grass	*Panicum maximum* Jacq.
Hamil grass	*Panicum maximum* Jacq. cv. Hamil
Molasses grass	*Melinis minutiflora* Beauv.
Rhodes grass	*Chloris gayana* Kunth cv. Samford
Ruzi grass	*Brachiaria ruziziensis* Germain & Evrard cv. Kennedy
Setaria	*Setaria sphacelata* (Schum.) Stapf. ex Massey cv. Nandi
S. almum	*Sorghum almum* Parodi cv. Crooble
	Legumes
Calopo	*Calopogonium mucunoides* Desv.
Centro	*Centrosema pubescens* Benth.
Dolichos	*Dolichos uniflorus* Lam. cv. Leichhardt
Glycine	*Glycine wightii* (R.Grah. ex Wight & Arn) Verdcourt cv. Cooper
Greenleaf desmodium	*Desmodium intortum* (Mill.) Urb. cv. Greenleaf
Puero	*Pueraria phaseoloides* (Roxb.) Benth.
Silverleaf desmodium	*Desmodium uncinatum* (Jacq.) D.C. cv. Silverleaf
Siratro	*Phaseolus atropurpureus* D.C. cv. Siratro
Vigna	*Vigna luteola* (Jacq.) Benth. cv. Dalrymple

Plants were grown from seed in 20-cm pots containing about 2·7 kg of alluvial clay-loam fertilized with 12 g of an NPK fertilizer (5:15:5), in growth cabinets at 30°C, 70% relative humidity, and

182–193 W m^{-2} (fluorescent lamps), in 14-hr days. Pots were watered twice daily and fertilized with a complete mineral nutrient solution (Aquasol, 2·1 g per litre) and 20 ml of a urea solution (20 g per litre) every 10 days.

(*b*) *Apparatus*

A detailed description of the design, construction, calibration, and operation of the gas-exchange apparatus is given by Ludlow (1969*a*). It consisted of an open system (Gaastra 1959; Björkman and Holmgren 1963; Parkinson 1968) in which CO_2 concentration, water vapour pressure, leaf temperature, and illuminance were measured and controlled. Simultaneous measurement of CO_2 and water vapour exchange, leaf temperature, and air temperature were made on leaves in Perspex chambers. The CO_2 concentration of the air before and after the leaf chamber was measured with an infrared gas analyser operated differentially (25–50 μl CO_2 per litre air f.s.d.). A differential psychrometer (Slatyer and Bierhuizen 1964) was used to measure the change in water vapour pressure of the air as it passed over the leaf. Leaf temperatures were measured with fine gauge (42 S.W.G.) thermocouples carefully positioned to make contact with the abaxial surface. The light source was a 1500 W quartz–iodine lamp with filters (8 cm of water, Schott KG 1 filter, and diffusing glass) to reduce the non-visible component. Illuminance at the leaf surface was measured with a selenium cell calibrated in foot candles. The relationship between illuminance and visible radiation (0·4–0·7 μm, measured with a pyranometer and a Wratten RG8 gelatine filter) was approximately linear, and 10,000 f.c. was equivalent to 475 W m^{-2}.

(*c*) *Calculation of Carbon Dioxide and Water Vapour Transfer Resistances*

The method of calculating resistances to water vapour transfer has been described previously (Holmgren, Jarvis, and Jarvis 1965; Begg and Jarvis 1968). The boundary layer resistance was obtained using wet blotting paper of similar shape to leaves. The mean CO_2 concentration and water vapour pressure was taken to be the same as that leaving the chamber because the air was mixed thoroughly by a fan (Holmgren, Jarvis, and Jarvis 1965). Stomatal (r_s) and boundary layer (r_a) resistances to CO_2 transfer were calculated from the corresponding resistances to water vapour transfer and the ratio of the diffusion coefficient for CO_2 and water in air which was taken as 1·71 (Gaastra 1959).

The resistance remaining when r_a and r_s were subtracted from the total resistance to CO_2 transfer was called mesophyll resistance by Gaastra (1959). It is now recognized that this comprises more than physical diffusive resistance. Monteith (1963) defined two additional resistances, those of excitation and carboxylation. No purpose is served in the present work by considering the components, and the term mesophyll resistance is used in the comprehensive sense. However, to avoid confusion, the symbol r_M is used rather than r_m, which tends now to be reserved for the physical component. It was calculated from the equation

$$r_M = [(C_{\text{amb.}} - \Gamma)/P_N] - (r_a + r_s), \tag{1}$$

where P_N is the net photosynthetic rate, $C_{\text{amb.}}$ is the ambient CO_2 concentration, and Γ is the CO_2 compensation concentration (Whiteman and Koller 1968). A particular problem arises from the need for a value for Γ corresponding to each value of P_N, when it is impractical to estimate Γ experimentally on each occasion. Because Whiteman and Koller (1967*a*) reported Γ to be constant down to 1000 f.c., r_M was calculated throughout the light range, using values of Γ determined at high light. However, doubt must attach to the significance of mesophyll resistances shown for low illuminance. In other cases, unless otherwise stated, it was assumed that Γ was constant.

When the term leaf resistance to CO_2 transfer (r_l) is used, it is equivalent to the sum of r_s and r_M.

(*d*) *Technique*

Gas exchange measurements were made on the youngest fully expanded leaf of a legume runner or grass tiller at a leaf temperature of $30 \pm 0·1$°C and a water vapour pressure deficit of 17 ± 3 mmHg unless otherwise stated. When measurements were completed, the leaf (or stem) was detached from the plant and its area and dry weight were determined. Several replicate measurements were made on each species.

(i) *Illuminance*

The relationship between P_N and illuminance, hereafter called the light response curve, was determined in the following manner which gave the most consistent results. The leaf was allowed to equilibrate at 3000–4000 f.c. for at least 30 min and P_N measured at stepwise increments of illuminances up to 10,000 f.c. and then down to 0 f.c. Only steady-state values were used in calculations. When the light was turned off, CO_2 evolution increased at first and then decreased as stomata closed (Ludlow and Jarvis 1971). Therefore, dark respiration rates (R_D) were measured 30 min after extinguishing the light when steady rates of CO_2 release occurred.

Before measurements were made on stems, laminae (and petioles of legumes leaves) were cut from runners and tillers. For grasses, "stems" comprised actual stem tissue and leaf sheaths, and for legumes, unfolded leaves were included with stems.

As the leaf chambers could not be illuminated from below, the leaf was inverted when the influence of illuminating the lower surface was studied.

(ii) *Carbon Dioxide Concentration*

Light response curves were established at different CO_2 concentrations in the following sequence: 300, 200, 450, 900, 1350, and 0 μl per litre. The concentrations were not always exactly these because the mean concentration in the chamber depended upon leaf size and activity. The air flow rate was adjusted so that the concentration in the air leaving the chamber was close to the required value.

(iii) *Leaf–Air Vapour Pressure Difference*

Leaf–air vapour pressure differences between 3 and 25 mmHg were obtained by varying the vapour pressure of the incoming air. Transpiration could not be measured at leaf–air vapour pressure differences less than 6 mmHg because condensation of water vapour occurred in the outlet of the leaf chamber, but net photosynthetic rate was measured down to values of 3 mmHg. Only steady-state values were recorded and illuminance was 9400 f.c.

(iv) *Leaf Temperature*

Leaf temperatures between 10 and 60°C were obtained by varying the temperature of the incoming air and of water in jackets above and below the leaf. As it was not possible to maintain a constant water vapour pressure at all temperatures in this range, the air was saturated at each temperature and therefore no transpiration measurements or resistance calculations could be made. The leaf–air vapour pressure difference was less than 2 mmHg.

The effect of previous temperature conditions on subsequent values for P_N was minimized by conducting experiments in two parts. P_N was measured as leaf temperature was reduced stepwise from 40°C for grasses and 35°C for legumes to 10°C, and R_D was recorded as temperature was increased over the same range. The leaf was left overnight in the chamber through which air at 30°C passed at 2·7 litres min^{-1}. The next day P_N was measured as temperature was progressively increased from 35°C for grasses and 30°C for legumes to 60°C, and R_D measured as temperature was decreased over this range. Only steady-state values were recorded at each temperature. The same procedure was used to investigate the influence of temperature upon the light response curves. These were obtained at optimum and suboptimum temperatures, the leaf allowed to recover overnight from the effects of the cold temperatures, and light response curves obtained at supra-optimal temperatures during the following day. To reduce the "time effect" on P_N, only five illuminances were used at supra-optimal temperatures. In addition, to decrease the possibility of stomatal closure, leaves were not exposed to illuminances less than the light compensation point.

III. Results

(a) *Illuminance*

The light response curves of grasses and legumes are presented in Figure 1. The P_N of grass leaves only approached light saturation at 10,000 f.c., whereas the light saturation point for legume leaves was 4000–5000 f.c. At 10,000 f.c., P_N varied

within both grasses and legumes (Table 1) but the mean value for grasses was about twice that for legumes. The P_N of setaria, molasses grass, ruzi grass, and dolichos may not be typical for these species because the plants did not look as healthy as field-grown plants.

There was a small systematic error in the calculated values of r_s (and hence of r_M) estimated in connection with the data of Figure 1, and it is preferred to present only their sum (r_l) in Table 1. However, the estimated r_s and r_M values were not so erroneous as to prevent their use for comparative purposes. The mean r_l for legumes was more than twice that for grasses, and this appeared to result from higher r_M values. Within grass and legume groups, differences in r_l could not be attributed solely to differences in r_s or r_M.

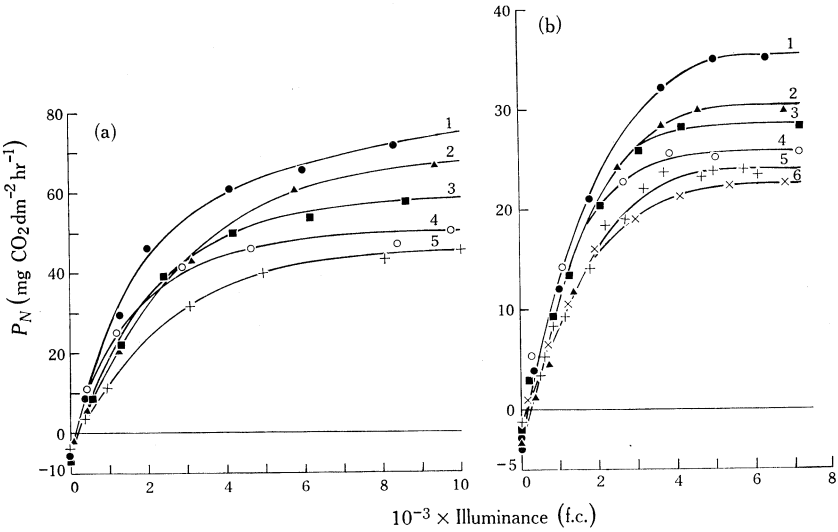


Fig. 1.—Relationship between illuminance and net photosynthetic rate (P_N) of (*a*) 11 grasses [*1*, *S. almum*, elephant grass, green panic; *2*, Hamil grass, buffel grass; *3*, coloratum, guinea grass; *4*, molasses grass, setaria, Rhodes grass; *5*, ruzi grass] and (*b*) 9 legumes [*1*, vigna, centro, puero; *2*, Siratro; *3*, calopo; *4*, greenleaf desmodium; *5*, silverleaf desmodium, dolichos; *6*, glycine]. Measured at CO_2 concentration of 290 ± 10 $\mu l\, l^{-1}$. Note that the scales of the ordinate are different in (*a*) and (*b*).

The mean dark respiration rate for grasses was about twice the corresponding value for legumes, but there was variation within both groups (Table 1). As photorespiration cannot be measured accurately (Ludlow and Jarvis 1971), R_D is compared with net rather than total photosynthesis. R_D was a similar proportion of P_N for both grasses and legumes, and differences in R_D between species were not associated with differences in r_s. R_D was not influenced by the illuminance of the preceding light period, but it was lower at the end of the night than at the beginning.

A rectangular hyperbola (Hesketh and Moss 1963) fitted the light response curves:

$$(I-I_0)/P_N = [(I-I_0)/P_N(\text{max.})+1/KP_N(\text{max.})], \qquad (2)$$

where P_N(max.) and K are constants, I is illuminance, and I_0 is the light compensation point. The linear regression of $(I-I_0/P_N)$ upon $I-I_0$ (J. L. Monteith, personal communication) was highly significant ($P < 0{\cdot}001$) for all grasses and for legumes at illuminances below the light saturation point.

The initial slope of the light response curve (Table 1) was determined from equation (2) (Hesketh 1963). Similar results were obtained when it was calculated from the linear portion of the light response curve at low illuminances or with

TABLE 1

NET PHOTOSYNTHETIC RATE (P_N), BOUNDARY LAYER (r_a) AND LEAF (r_l) RESISTANCE TO CO_2 TRANSFER, DARK RESPIRATION RATE (R_D), LIGHT COMPENSATION POINT (I_0), INITIAL SLOPE OF LIGHT RESPONSE CURVE, AND MAXIMUM EFFICIENCY OF NET PHOTOSYNTHESIS ($E = P_N/I$) OF TROPICAL GRASS AND LEGUME LEAVES

P_N, r_a, and r_l were measured at 10,000 f.c. and 280 ± 5 μl l^{-1} CO_2 concentration. Values are means for two leaves

Species	P_N (mg CO_2 dm^{-2} hr^{-1})	r_a (sec cm^{-1})	r_l (sec cm^{-1})	R_D (mg CO_2 dm^{-2} hr^{-1})	R_D/P_N (%)	I_0 (f.c.)	$10^2\times$ Initial Slope (mg CO_2 dm^{-2} hr^{-1} f.c.$^{-1}$)	E
Grasses								
S. almum	73	0·9	1·4	4·2	6	100	3·6	2·4
Elephant grass	73	1·1	1·4	6·2	8	200	3·6	1·9
Green panic	70	0·9	1·7	5·9	8	150	3·0	2·0
Buffel grass	66	0·9	2·0	3·8	4	125	2·5	1·8
Hamil grass	66	0·5	2·1	3·9	6	175	2·5	1·8
Coloratum	59	0·9	2·1	5·8	10	200	3·0	1·8
Guinea grass	56	0·9	2·5	5·0	9	200	3·1	1·9
Rhodes grass	53	1·1	2·2	3·5	6	100	3·4	2·3
Setaria	51	0·9	2·6	4·9	10	150	2·8	2·0
Molasses grass	50	1·0	2·7	6·5	13	225	3·4	2·2
Ruzi grass	46	0·9	3·3	4·3	9	180	2·5	1·1
Mean	60	0·9	2·1	4·9	8	164	2·9	2·0
S.E.							±0·1	±0·1
Legumes								
Centro	37	0·4	4·3	2·4	6	115	2·1	1·4
Vigna	36	0·7	3·8	3·3	9	125	1·6	1·3
Puero	33	0·4	4·9	2·5	7	115	2·1	1·7
Siratro	30	0·4	3·8	3·7	12	250	1·2	1·1
Calopo	26	0·7	5·7	2·8	11	100	1·5	1·5
Greenleaf desmodium	26	0·7	5·6	3·0	12	150	2·3	1·3
Silverleaf desmodium	25	0·7	5·8	1·5	6	150	1·1	0·8
Dolichos	22	0·7	6·7	—	—	—	1·9	—
Glycine	20	0·7	7·6	2·8	14	150	2·4	1·1
Mean	28	0·6	5·3	2·8	10	145	1·8	1·4
S.E.							±0·2	±0·1

Monteith's (1965) method which uses another form of equation (2). The mean value for legumes was only about 60% of that for grasses. On the other hand, the mean light compensation points were similar (Table 1).

Changes in P_N with illuminance can be explained partly in terms of leaf resistance (Fig. 2). Boundary layer resistance was approximately constant, the rise at lower light intensities resulting from the low air flow rates used in measuring low

photosynthetic rates. Stomatal resistance increased slowly with decreasing illuminance to about 2000 f.c. or less, then rapidly. Values were not greatly different between

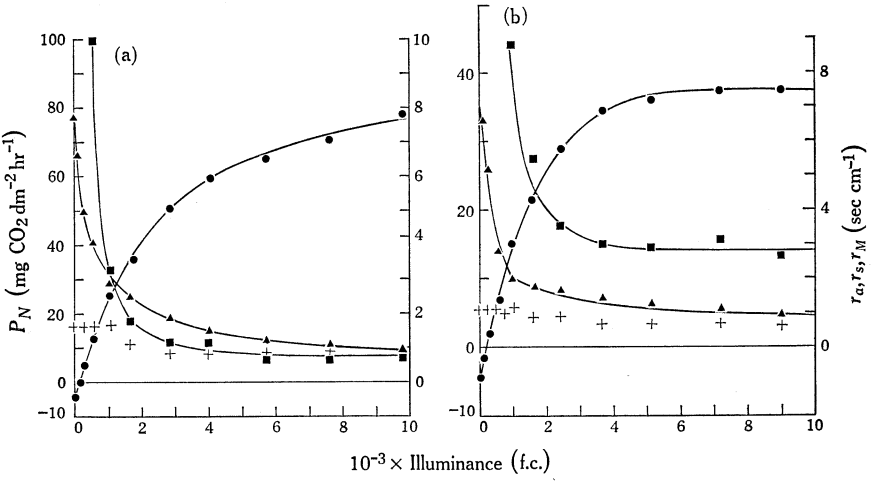


Fig. 2.—Relationship between illuminance, net photosynthetic rate (P_N, ●), and boundary layer (r_a, +), stomatal (r_s, ▲), and mesophyll (r_M, ■) resistances to CO_2 transfer of (*a*) elephant grass and (*b*) calopo leaves. Measured at a CO_2 concentration of 300 ± 10 μl l^{-1}. Note that the scales of the ordinate are different in (*a*) and (*b*).

the two groups at higher light. However, r_M was constant in both cases down to 3000–4000 f.c., although much higher for the legume. If the assumption that Γ is

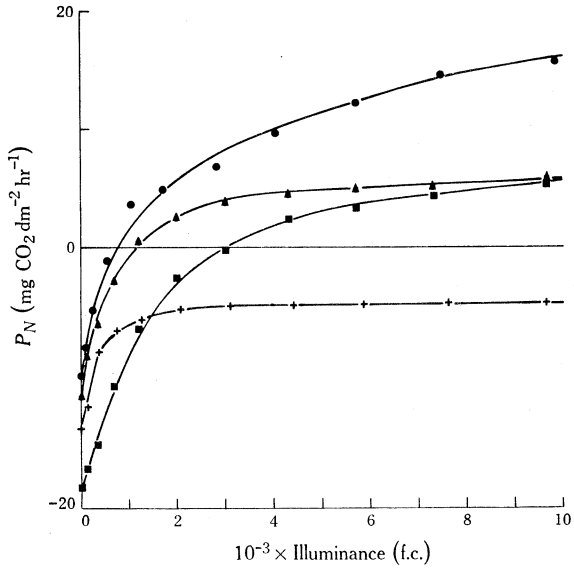


Fig. 3.—Relationship between illuminance and net photosynthetic rate (P_N) of stems of molasses grass (●), Siratro (▲), ruzi grass (■), and calopo (+). Measured at a CO_2 concentration of 320 ± 10 μl l^{-1}.

constant down to 1000 f.c. is correct, then r_M rose quickly as 1000 f.c. was approached, particularly in the case of the legume.

The shape of light response curves of stems (Fig. 3) was approximately similar to those for leaves, and only extreme types of curves are shown. Grass stems were not light saturated at 10,000 f.c. whereas the mean light saturation point for stems of four legumes (Siratro, vigna, calopo, and glycine) was about 5000 f.c. All grass stems, but onlysome legume stems, had positive P_N values, and grass stems had lower stomatal resistances (Table 2). However, there was little difference in mean R_D between grasses and legumes when it was expressed on a projected area (Table 2) or dry

TABLE 2

NET PHOTOSYNTHETIC RATE (P_N), DARK RESPIRATION RATE (R_D), BOUNDARY LAYER (r_a) AND STOMATAL (r_s) RESISTANCES TO CO_2 TRANSFER, AND LIGHT COMPENSATION POINT (I_0) OF GRASS AND LEGUME STEMS

P_N and r_s were measured at 10,000 f.c. and at 322 ± 5 (and 300 ± 5) $\mu l\, l^{-1}$ CO_2 concentration for grass and legume stems, respectively. R_D was measured at $335 \pm 5\, \mu l\, l^{-1}$ CO_2 concentration. Data are means for two stems

Species	P_N (mg CO_2 dm^{-2} hr^{-1})	r_a (sec cm^{-1})	r_s (sec cm^{-1})	R_D (mg CO_2 dm^{-2} hr^{-1})	R_D/P_N (%)	I_0 (f.c.)
Grasses						
Buffel grass	15·5	1·4	3·9	16·8	109	3050
Molasses grass	12·8	1·5	4·2	10·0	79	750
Ruzi grass	6·7	1·7	1·7	19·4	288	2500
Hamil grass	5·8	1·7	2·8	8·3	143	1200
Mean	10·2	1·6	3·2	13·6	133	1880
Legumes						
Siratro	4·3	1·1	5·4	13·8	322	1500
Vigna	3·6	1·1	6·0	13·5	375	2750
Calopo	−3·6	1·1	4·3	12·8	—	—
Glycine	−9·4	0·9	7·0	17·7	—	—
Mean	−1·3	1·0	5·7	14·5	348	2125

weight basis. As seen for leaves, differences in R_D within grass and legume groups were not associated with differences in r_s. The higher R_D and lower P_N resulted in a higher R_D/P_N ratio when comparing stems with leaves, and when comparing legume and grass stems.

The mean light compensation points were similar for grass and legume stems (Table 2), and higher than the corresponding values for leaves (Table 1). The r_s of stems, like that of leaves, varied with illuminance, being little affected by illuminances above 1000 f.c. but increasing markedly below it.

The effect on P_N and resistances of illuminating both leaf surfaces independdently is shown in Figure 4. The light response curves and resistances of grass leaves were unaffected by direction of illumination. Similar results were obtained with *S. almum* and Hamil grass leaves. P_N of calopo was always less when illuminated on the lower surface. The lower P_N was accompanied by a higher r_s and r_M. The higher r_s which occurred when the lower surface was illuminated was not due to a transitory handling effect or to previous low illuminance, because similar light

response curves were obtained when P_N was measured immediately after inverting the leaf, and again after the inverted leaf had been in the chamber overnight.

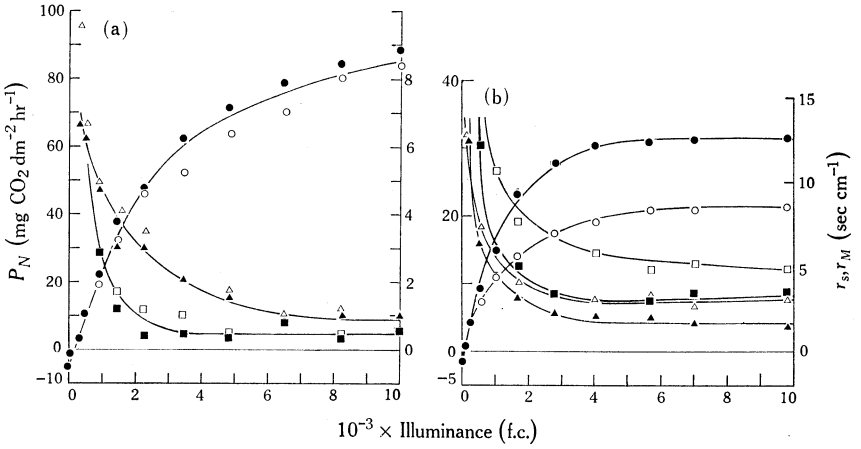


Fig. 4.—Effect of illuminating the upper (solid symbols) or lower (open symbols) surfaces of (*a*) elephant grass and (*b*) calopo leaves on net photosynthetic rate (P_N) and CO_2 transfer resistances (r_s and r_M). A description of symbols is given in Figure 2. Measured at a CO_2 concentration of 300 ± 10 μl l^{-1} and r_a of 0·75 sec cm^{-1}. Note that the scales of the ordinate are different in (*a*) and (*b*).

(*b*) *Carbon Dioxide Concentration*

Because of similarity between the grass species, and between the legumes, data for only one of each are shown (Fig. 5). Vigna leaves were light saturated at low CO_2 concentrations but became progressively less so as the concentration increased.

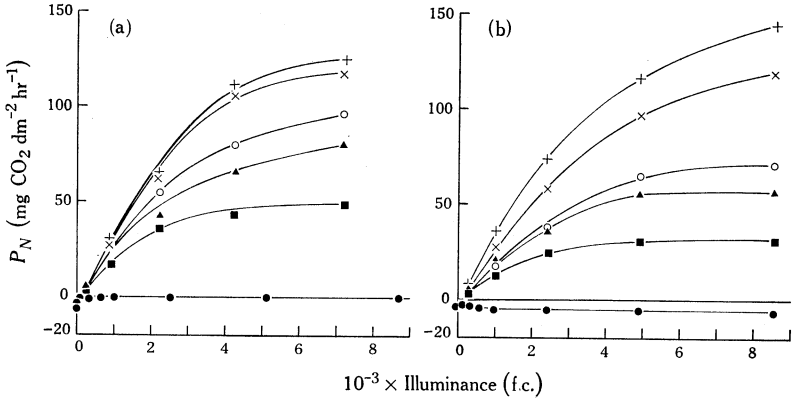


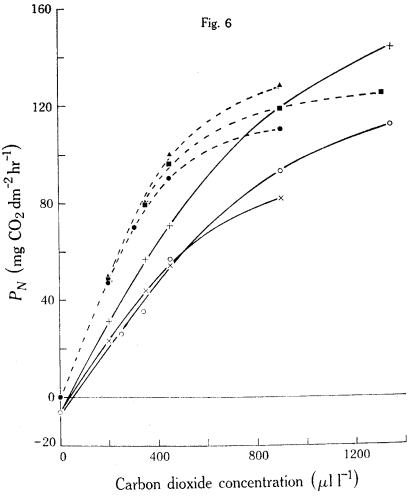
Fig. 5.—Effect of CO_2 concentration on the relationship between illuminance and net photosynthetic rate (P_N) of (*a*) elephant grass and (*b*) vigna leaves. + = 1350; × = 900; ○ = 450; ▲ = 350; ■ = 200; ● = 0 μl l^{-1} CO_2 concentration.

P_N responded to increased concentration at all illuminances, and most at high illuminance. Elephant grass leaves behaved in a similar way. Although light saturation

was not quite attained at any experimental CO_2 level above zero, at 200 μl l^{-1} the shape of the curve approached that of a normal light saturated legume response curve at 350 μl l^{-1}. Again, the response to CO_2 was greatest at highest illuminances.

Carbon dioxide evolution into CO_2-free air is described later.

Carbon dioxide response curves of the three grasses and three legumes at a high illuminance are given in Figure 6. Those for the three grasses were comparable but there were differences within the legumes. Grasses had zero CO_2 compensation point compared with approximately 40 μl l^{-1} for legumes, and a greater efficiency of CO_2 utilization (steeper slope of the P_N–CO_2 concentration curve) at low CO_2 levels. Despite this higher efficiency, the P_N of legumes reached that of the grasses at high concentrations because grass leaves were CO_2 saturated at lower concentrations.



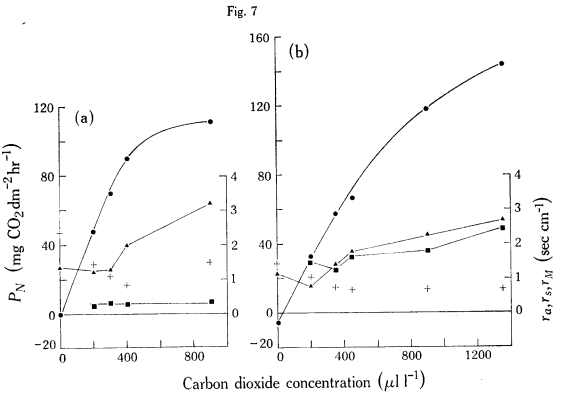


Fig. 6.—Relationship between CO_2 concentration and leaf net photosynthetic rate (P_N) of three grasses (broken lines: ▲ Hamil grass; ■ elephant grass; ● *S. almum*) and three legumes (solid line: + vigna; ○ calopo; × Siratro). Measured at 8500 f.c.

Fig. 7.—Relationship between CO_2 concentration, net photosynthetic rate (P_N, ●), and boundary layer (r_a, +), stomatal (r_s, ▲), and mesophyll (r_M, ■) resistances to CO_2 transfer of (*a*) *S. almum* and (*b*) vigna leaves. Measured at 8500 f.c.

Resistances in relation to CO_2 concentration are shown in Figure 7 for one grass and one legume. In all cases r_M, while much lower for grasses, was little affected by CO_2 supply up to 900 μl l^{-1} but increases at 1350 μl l^{-1} were sometimes recorded. On the other hand, r_s increased with CO_2 from 200–300 μl l^{-1} up to the higher concentrations, particularly for the grasses. At zero CO_2, r_s also increased slightly for both groups.

Further experiments were conducted to define more exactly the effect of illuminance on CO_2 efflux because of its importance in the study of photorespiration. As interest centred on efflux at very low illuminances, a large number of measurements were made below 1000 f.c. Figures 8(*a*) and 8(*b*) show typical CO_2 efflux and r_s responses for grasses and legumes. All grasses behaved similarly to elephant grass, showing no CO_2 efflux above 1000 f.c., while below this level there was an increase to

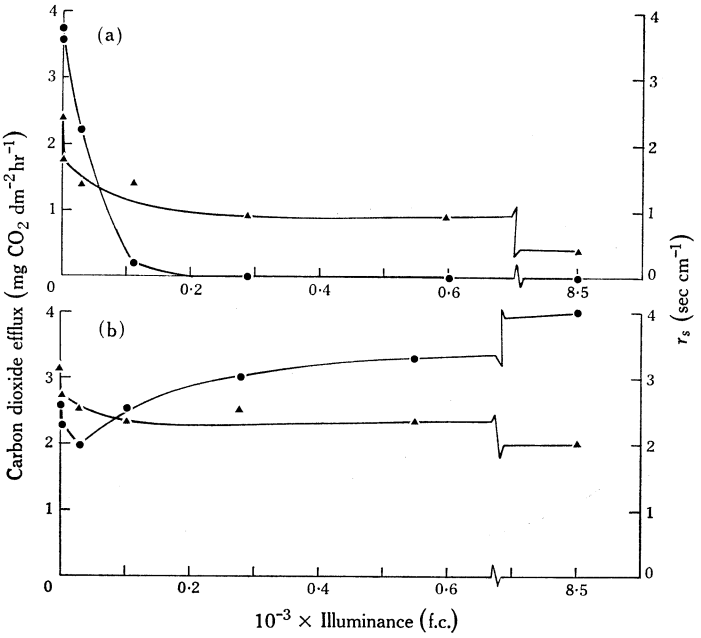


Fig. 8.—Relationships between illuminance, CO_2 efflux (●), and stomatal resistance to CO_2 transfer (r_s, ▲) of (*a*) elephant grass and (*b*) glycine leaves at low CO_2 concentrations (less than 8 μl l^{-1}). (*a*) $r_a = 2{\cdot}4$ sec cm^{-1}; (*b*) $r_a = 1{\cdot}4$ sec cm^{-1}.

TABLE 3

EFFECT OF LIGHT AND DARK ON CO_2 EFFLUX AT LOW AMBIENT CO_2 CONCENTRATIONS (0–10 μl l^{-1})

Data are means for at least two leaves

Species	(A) R_D (mg CO_2 dm^{-2} hr^{-1})	(B) Efflux at 8500 f.c.	B/A	Illuminance at Minimum Efflux (f.c.)	Minimum Efflux (mg CO_2 dm^{-2} hr^{-1})
Grasses					
Hamil grass	3·50	0	0	—	—
S. almum	2·88	0	0	—	—
Elephant grass	2·84	0	0	—	—
Ruzi grass	2·62	0	0	—	—
Mean	2·96	0	0	—	—
Legumes					
Siratro	3·22	4·66	1·45	43·7	2·20
Vigna	2·95	4·53	1·54	47·5	1·86
Glycine	2·75	4·40	1·60	35·0	2·19
Calopo	2·57	4·50	1·75	55·0	1·64
Mean	2·87	4·52	1·58	45·3	1·97

R_D levels. In the legumes, efflux was highest at high illuminance and decreased only slightly until low illuminance when it fell quickly to a minimum, thereafter increasing to R_D levels. Stomatal resistances, while higher for legumes, were in both cases little influenced by increasing illuminance after an initial fall. A summary of the CO_2 efflux experiments is given in Table 3. Because grass leaves had no CO_2 efflux above 1000 f.c., the ratio of maximum efflux at 8500 f.c. to R_D was zero. The efflux from legume leaves at 8500 f.c. was, however, about 1·6 times R_D. The minimum efflux occurred at about 45 f.c., and its magnitude was about 70% of R_D and 44% of the efflux at 8500 f.c.

(c) *Leaf–Air Vapour Pressure Difference*

The relationships between P_N, leaf resistances, and leaf–air vapour pressure difference for elephant grass and vigna are shown in Figure 9. The response of both species was similar, P_N being unaffected by leaf–air vapour pressure difference between

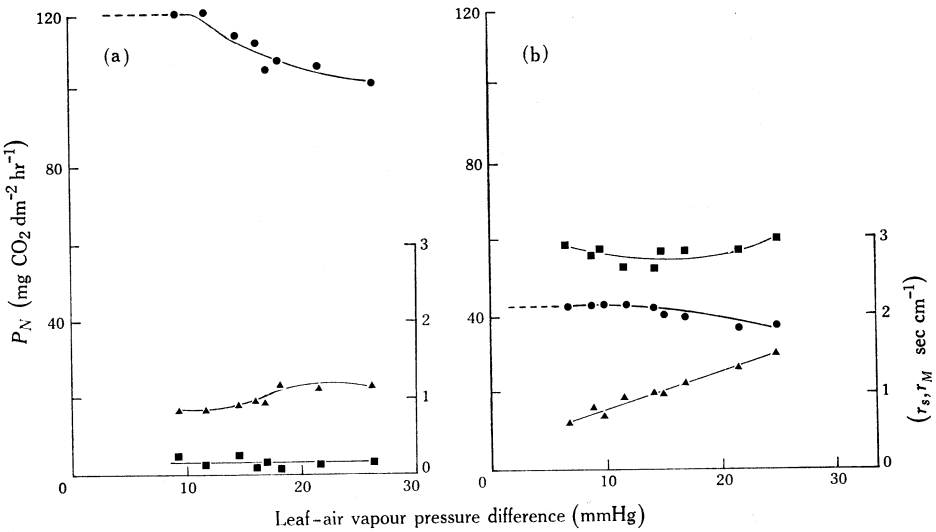


Fig. 9.—Effect of leaf–air vapour pressure difference on net photosynthetic rate (P_N, ●) and stomatal (r_s, ▲) and mesophyll (r_M, ■) resistances to CO_2 transfer of (*a*) elephant grass and (*b*) vigna leaves. Measured at 9400 f.c., 30°C, 300±5 μl l^{-1} CO_2 concentration. The broken line represents P_N measured after condensation had occurred (see text). r_a = 0·7 sec cm^{-1}.

0 and 12 mmHg but declining by 20% between 12 and 25 mmHg. The decline of P_N was accompanied by an increase in stomatal resistance, whereas mesophyll resistance appeared to be unaffected.

(d) *Leaf Temperature*

Typical relationships between temperature and P_N and R_D for a grass and a legume are shown in Figure 10. R_D increased logarithmically with temperature so that the Q_{10} for all leaves was 2 between 10 and 50°C. P_N and R_D of grasses were higher than the corresponding values for legumes at all temperatures. The shape of the curve relating P_N to temperature was similar within grass and within legume

groups. One such relationship for each group is given in Figure 11. P_N declined at a greater rate at temperatures above compared with below the optimum. Temperature

Fig. 10

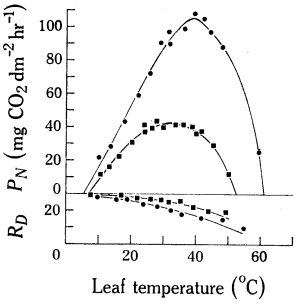


Fig. 11

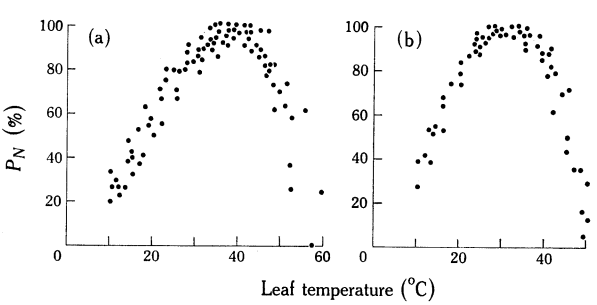


Fig. 10.—Effect of leaf temperature on net photosynthetic rate (P_N) and dark respiration rate (R_D) of buffel grass (●) and calopo (■) leaves. Measured at 9500 f.c., 300 ± 5 μl l^{-1} CO_2 concentration, less than 2 mmHg leaf–air vapour pressure difference. Units for R_D as for P_N.

Fig. 11.—Effect of leaf temperature on net photosynthetic rate (P_N, expressed as a percentage of the maximum value for each species) of leaves of (*a*) six grasses (buffel grass, elephant grass, Hamil grass, molasses grass, ruzi grass, and *S. almum*) and (*b*) four legumes (calopo, glycine, Siratro, and vigna). Only one set of data are presented for each species. Measured at 9500 f.c., 300 ± 5 μl l^{-1} CO_2 concentration, and less than 2 mmHg leaf–air vapour pressure difference.

TABLE 4

OPTIMUM, MAXIMUM, AND MINIMUM LEAF TEMPERATURES FOR NET PHOTOSYNTHETIC RATE (P_N)

P_N measured at 9500 f.c. and 300 ± 5 μl l^{-1} CO_2 concentrations. Values are the mean of data for either two or three leaves

Species	Leaf Temperature (°C)		
	Minimum	Optimum	Maximum
Grasses			
Buffel grass	6·0	39·0	61·0
Elephant grass	6·7	36·7	58·5
Hamil grass	9·7	37·5	58·3
Molasses grass	6·2	39·2	58·0
Ruzi grass	8·5	37·8	55·8
S. almum	5·0	39·5	52·0
Mean	7·0	38·3	57·3
Legumes			
Calopo	6·7	33·7	50·7
Glycine	5·0	30·8	50·5
Siratro	6·2	30·2	50·2
Vigna	7·5	31·2	49·0
Mean	6·3	31·5	50·1

had a greater effect on P_N of buffel grass in the range 39 ± 10°C than upon vigna within the range 32 ± 10°C (Fig. 10). Cardinal temperatures (minimum, optimum,

and maximum) were determined by expressing P_N as a percentage of the maximum value for each experiment. The mean minimum temperatures were comparable for grasses and legumes, but the optimum and maximum values were higher for grasses (Table 4). There was only small variation in these parameters within both groups of plants.

The response of net photosynthesis to illuminance or temperature depended upon the level of the other factor [Figs. 12(*a*)–12(*d*)]. The light saturation point of

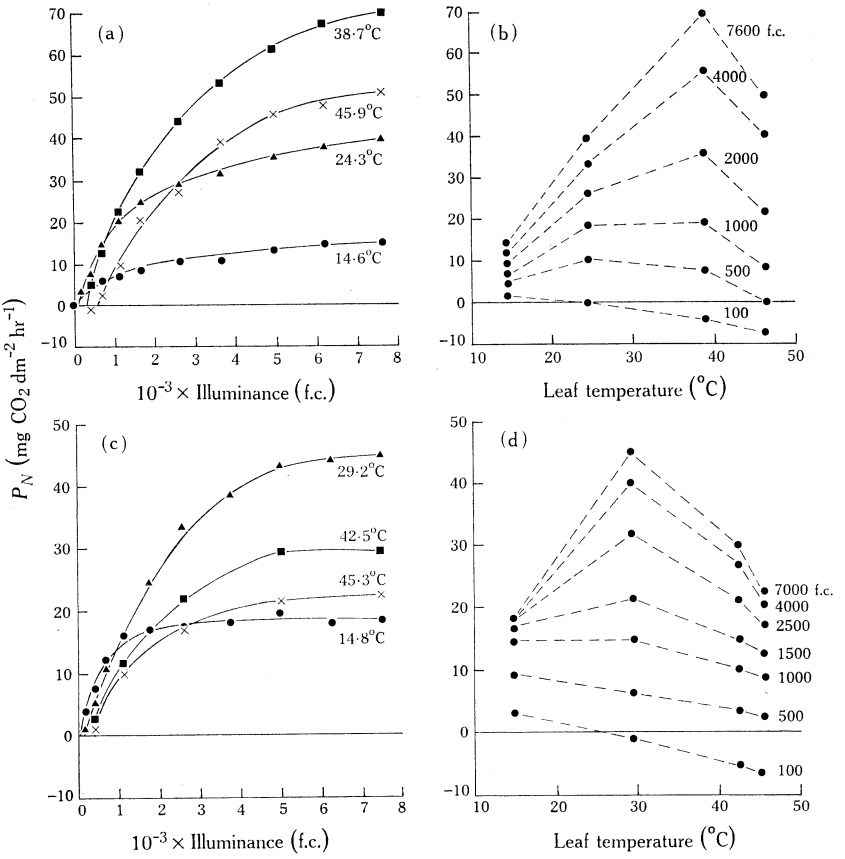


Fig. 12.—Interrelationship between net photosynthetic rate (P_N) and illuminance (*a*, *c*, measured at the temperatures shown) and between P_N and leaf temperature (*b*, *d*, measured at the illuminances shown) for leaves of elephant grass (*a*, *b*) and vigna (*c*, *d*). Measured at 300 ± 5 μl l^{-1} CO_2, less than 2 mmHg leaf–air vapour pressure difference.

vigna declined at temperatures greater and less than 29°C and P_N of elephant grass was light saturated at 15°C. The light compensation point and dark respiration rate (determined by extrapolation) of vigna and elephant grass increased with temperature. The optimum temperature declined with illuminance until, at 100 f.c., P_N decreased almost linearly as temperature increased.

IV. Discussion

These tropical pasture grasses which are members of the tribes Chlorideae and Paniceae of the Gramineae have leaf net photosynthetic rates which are high at normal ambient CO_2 concentrations and near-optimum temperatures and approach light saturation only at illuminances of 10,000 f.c. They have zero CO_2 compensation concentration, no apparent photorespiration, and large parenchyma sheaths surrounding leaf vascular bundles (bundle sheaths). Therefore, these grasses can be included in the group which contains some tropical grasses, some species of Cyperaceae, and some dicotyledons in the families Amaranthaceae, Chenopodiaceae, and Portulaceae, and which also have these characteristics as well as the C_4 dicarboxylic acid pathway of CO_2 fixation (Hesketh and Baker 1967; Downton and Tregunna 1968; Laetsch 1968; Hatch and Slack 1970).

Tropical pasture legumes, on the other hand, appear to belong to a group which includes temperate grasses and most dicotyledons (Hesketh and Baker 1967), because P_N was light saturated at 4000–5000 f.c. (Fig. 1) and the mean P_N at 10,000 f.c., normal ambient CO_2 concentration, and near-optimum temperature was 26 mg CO_2 dm^{-2} hr^{-1} (Table 1). These data are consistent with those for another tropical legume, Townsville stylo (Begg and Jarvis 1968), and a number of temperate legumes (Hesketh and Moss 1963; Murata and Iyama 1963; Brown, Blaser, and Dunton 1966). Tropical legumes have no prominent bundle sheaths and have the Calvin pathway of CO_2 fixation, apparent photorespiration, and a CO_2 compensation concentration of 40 $\mu l\ l^{-1}$.

At high illuminance, normal ambient CO_2 concentrations, and near-optimum temperatures the difference in P_N between grasses and legumes was accompanied by a difference in r_M rather than r_s as previously demonstrated by Hesketh and Baker (1967) for the two photosynthetic groups. A more detailed analysis of the differences in P_N will be presented in a later paper.

(*a*) *Illuminance*

Dark respiration rates were 8–10% of P_N (Table 1), falling within the range of 5–10% given in a review by Gaastra (1963). The higher R_D of grass leaves is compatible with the higher respiration rate of grass plants compared with legumes (Ludlow and Wilson 1970). In contrast to some published data (Holmgren and Jarvis 1967; Begg and Jarvis 1968), there was no relationship between R_D and r_s.

Hesketh (1963) and Monteith (1965) reported little variation in the initial slope of light response curves for a wide range of species. However, differences have been shown between species (Loach 1967), and ecotypes of the same species (Björkman and Holmgren 1963). Differences in initial slope between grasses and legumes reported here (Table 1) were verified in other experiments. For example, the initial slope for green panic was significantly ($P \ll 0{\cdot}01$) greater than that for Siratro (Wilson and Ludlow 1970). Because photorespiration rate could not be measured accurately, quantum efficiencies were calculated from net photosynthetic rates. Therefore, the values given underestimate the real quantum efficiencies. Using a value of $1{\cdot}8 \times 10^{-11}$ Einsteins sec^{-1} cm^{-2} $f.c.^{-1}$ for absorption by an "average" leaf (Gaastra 1959),

mean quantum efficiencies for grasses and legumes were, respectively, 0·10 and 0·06 moles CO_2 per Einstein. The value for grasses is one of the highest values reported for leaves (Gaastra 1959), and the mean value for legumes is comparable with data for Townsville stylo (0·05, Begg and Jarvis 1968) and for *Plantago lanceolata* and *Solidago virgaurea* (0·066 and 0·063 respectively, Björkman 1966).

The efficiency of light utilization ($E = P_N/I$) is of interest in crop production studies because it is a measure of the ability to fix CO_2 per unit of incident (or preferably, absorbed) radiation. It allows a comparison of CO_2 fixing capacities by different species over a range of illuminances (Fig. 13). Grass leaves were more

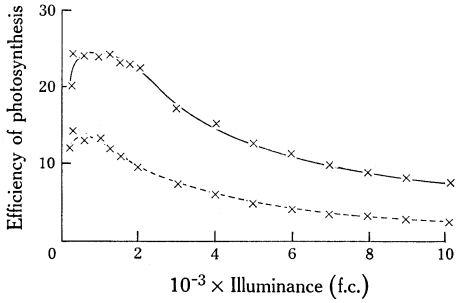


Fig. 13.—Relationship between illuminance and efficiency of net photosynthesis (expressed as mg CO_2 dm^{-2} hr^{-1} per 1000 f.c.) of leaves of *S. almum* (———) and greenleaf desmodium (– – – –). Measured at 290±10 $\mu l\ l^{-1}$ CO_2 concentration.

efficient than those of legumes at all illuminances, the relative efficiency increasing with illuminance. The maximum efficiency of the legume was only two-thirds of that of the grass. It is also interesting in the concept of ideal canopy structure, where, other things being equal, maximum photosynthetic output depends upon leaf orientation such that the illuminance is $I_{max.}$, $I_{max.}$ being the illuminance at which E is a maximum (Warren Wilson 1960; Ludlow 1969*b*). $I_{max.}$ can be determined graphically from the E–I relationship (Fig. 13) or from a formula derived from equation (2):

$$I_{max.} = I_0 + (I_0/K)^{\frac{1}{2}} \qquad (3)$$

The value of $I_{max.}$ for grasses and legumes was about 900 f.c.; this is comparable with values of 800 f.c. given by Warren Wilson (1960) and 1000 f.c. calculated from data of Hesketh (1963) and Hesketh and Moss (1963).

The response of r_s to illuminance is consistent with published data (Gaastra 1959; Ehrler and van Bavel 1968). Mesophyll resistance remained constant between 10,000 and 3000 f.c. whereas Bierhuizen and Slatyer (1964) and Whiteman and Koller (1967*a*) found that it increased below 6000 f.c. The increase in calculated r_M at lower intensities is perhaps partly the result of an increase in Γ as pointed out earlier, but probably also includes real mesophyll resistance components among which increases in excitation and carboxylation resistances (Monteith 1963; Chartier 1966) rather than changes in resistance to CO_2 transfer across the mesophyll are important.

The difference between grasses and legumes in the shape of the light response curve at illuminances above 5000 f.c. appears to result solely from a difference in response of r_s rather than a difference in the photosynthetic process because r_M is constant (Figs. 2 and 4). Furthermore, as R. M. Gifford (personal communication)

has shown for maize, if the light response curves of grass and legume leaves are re-adjusted to a constant minimum r_s, both are light saturated at about 2000 f.c. Subsequent work (D. Pasternak, unpublished data) has shown the great importance of r_s in leaves of *Sorghum vulgare*, another tropical grass, in bright light.

The responses of P_N and r_s of stems to illuminance was qualitatively similar to that for leaves, and the relative differences between grasses and legumes were similar to those for leaves. The low P_N, high light compensation point, and high R_D/P_N ratio of stems compared with leaves resulted from both a higher respiratory activity and a lower photosynthetic capacity. The higher R_D of stems may arise simply from the much greater thickness of tissue per unit of projected area, on which the rate is based. At high illuminance the mean P_N of grass stems was larger than the corresponding value for legumes. The legumes studied could be divided into two groups: those with green stems which had a positive P_N in bright light, and those with reddish brown stems which had negative P_N values. The amount of chlorophyll, which rarely limits P_N of leaves (Gaastra 1963), may be an important determinant of stem net photosynthesis.

The low P_N in conjunction with the low proportion of stem in some of these species (Ludlow and Wilson 1970) means that stem surface may be neglected in growth analysis studies. However, Thorne (1959) and Begg and Jarvis (1968) have shown relatively high net photosynthetic activity in stems, and in some species the stem is a conspicuous fraction of total photosynthetic surface.

The differing responses of grass and legume leaves to direction of illumination agrees with observations made by Moss (1964, 1965) for grasses and dicotyledons. Differences in reflectivity may explain differences in initial slope (Moss 1964) and part of the differences in r_M (Fig. 4), but it is not the only factor involved because differences in P_N still exist when reflection is taken into account (Starzecki 1962). Stomatal resistance of legume leaves was also higher when the lower surface was illuminated. Moss (1964) found that stomata on the lower surface closed when illuminated, but could be reopened by increasing the relative humidity. By decreasing stomatal resistance of the lower surface, he was able to increase P_N but not to the level attained when the upper surface was illuminated. It is thus apparent that differences in r_M are involved. Legume leaves therefore are adapted to be illuminated on the upper surface. In the field this mode of illumination is ensured by the heliotropic behaviour of the leaves (Begg and Jarvis 1968; unpublished observations on species used in these experiments).

(*b*) *Carbon Dioxide Concentration*

The P_N–CO_2–illuminance responses were of a Harder rather than a Blackman type (Rabinowitch 1951; Thomas 1965), divergence of the curves (Fig. 5) above the light compensation point indicating that P_N was limited by both the photochemical and diffusion processes until light saturation. It is not possible to determine under all conditions how much of the response to illuminance is due to the effect on the photochemical process or to the effect on r_s and the diffusion process (Figs. 2 and 4). The differences in light saturation (Fig. 5) and the greater response to CO_2 at high illuminance (Fig. 6) depend on the extent to which the diffusion process was limiting.

Mean CO_2 compensation points for grasses and legumes agree with published data (Downton and Tregunna 1968), while the differing efficiencies of CO_2 utilization compare with the findings of Holmgren (1968). The differences in initial slopes of the CO_2 response curves indicate differences in the rate of renewal of the CO_2 receptor, or the diffusion of CO_2 to the site of synthesis (Hesketh 1963). Such differences are expressed in terms of r_M and r_s in this analysis.

Responses of P_N at high illuminance (Fig. 6) are similar to those described by Hesketh (1963). The linear response to CO_2 concentration between 0 and 400 μl l^{-1} CO_2, incidentally, enables the methods of both Holmgren, Jarvis, and Jarvis (1965) and Whiteman and Koller (1968) to be used to calculate mesophyll resistances at 300 μl l^{-1}. The CO_2 saturation point of grasses appeared to be lower than that of legumes. Grasses seemed to be saturated at about 1000 μl l^{-1} but values as low as 700–800 μl l^{-1} were obtained for leaves whose r_s was more affected by CO_2 concentration. These values are lower, whereas those for legumes (although never reached in these experiments) were probably higher than a mean value of 1500 μl l^{-1} for most higher plants (Rabinowitch 1951; Gaastra 1959). In contrast, Begg and Jarvis (1968) report a value of 400 μl l^{-1} for Townsville stylo.

For technical reasons, r_a values differed with CO_2 concentration, thus complicating the analysis of P_N variations in terms of r_s and r_M. Nevertheless, the insensitivity of r_M to CO_2 at concentrations above 200–300 μl l^{-1} (cf. also Bierhuizen and Slatyer 1964; Whiteman and Koller 1967*a*) means that P_N variation is to be understood largely in terms of differences in CO_2 concentrations and r_s variation. Up to 450 μl l^{-1}, the higher P_N of grasses (Fig. 6) arose from much lower values of r_M (Fig. 7). At higher concentrations this advantage was offset by greater increases of r_s in grasses than in legumes. At 900 μl l^{-1}, the mean r_s for all grasses was 3·4 sec cm^{-1} compared with 2·4 for legumes, and the legume which was least responsive in stomatal closure attained the highest value of P_N (Fig. 6). The greater stomatal sensitivity of the grasses resulted in greater limitation by the diffusion process at high levels of CO_2 and hence to saturation of P_N at lower CO_2 levels compared with legumes. Some biochemical limitations may be a contributory factor to CO_2 saturation of grasses because the measurements were made at 30°C, and subsequent work reported here showed that 38°C is the optimum for net photosynthesis.

The increases of r_s with both increasing and decreasing ambient CO_2 concentration beyond the 200–400 μl l^{-1} range agree with observations for many species (Heath 1959; Whiteman and Koller 1967*a*; Parkinson 1968), although other reports are in disagreement (Gaastra 1959; Bierhuizen and Slatyer 1964).

Zero carbon dioxide efflux from grasses except at very low illuminance (Figs. 5 and 8) is similar to that recorded by El-Sharkawy, Loomis, and Williams (1967, 1968) for *Amaranthus edulis*. There are two possible explanations for this behaviour. Firstly, assuming that photorespiration is absent, it is conceivable that when the incident illuminance is 100 f.c., the illuminance in some cells is close to zero and dark respiration is "switched on". The number of such cells and hence CO_2 efflux would increase as incident illuminance decreases. If, alternatively, CO_2 is evolved in the light, whether from dark or photorespiration, the proportion of it reassimilated increases until at 100 f.c. the efflux is zero.

The efflux of CO_2 by legumes at low ambient concentration and a wide range of illuminances, with a minimum value at low illuminance, is similar to the behaviour reported for a number of other plants (Holmgren and Jarvis 1967; Poskuta, Nelson, and Krotkov 1967; Zelawski 1967; Brix 1968). The minimum point might be understood as that illuminance at which the balance between photorespiration in the better illuminated cells, the dark respiration in those cells in which this process is "switched on", and the reassimilation of respired CO_2 results in a minimum CO_2 release. This is supported by the fact that if the efflux curves are extrapolated below the minimum, they pass close to the origin. The CO_2 efflux curves of vigna and a number of other species (El-Sharkawy, Loomis, and Williams 1967; Holmgren and Jarvis 1967; Brix 1968) are light saturated at low illuminances, whereas those of other legumes (present data) and some other species (Poskuta, Nelson, Krotkov 1967; Zelawski 1967) are not.

The evidence from both grasses and legumes supports the view that there are different respiratory processes in the light than in the dark (Jackson and Volk 1970). The mean efflux at 8500 f.c. is zero for grasses and $4 \cdot 52$ mg CO_2 dm^{-2} hr^{-1} for legumes, which is $1 \cdot 6$ times R_D. The implications of the results from the CO_2 efflux experiments in relation to photorespiration will be discussed more fully in a subsequent paper.

(*c*) *Leaf–Air Vapour Pressure Difference*

The P_N of tropical pasture grasses and legumes responds differently to changes in leaf–air vapour pressure difference compared with other plants for which information is available. Bierhuizen and Slatyer (1964) found that P_N of cotton leaves was unaffected by leaf–air vapour pressure differences between 10 and 25 mmHg but it decreased 14% between 25 and 40 mmHg. Whiteman and Koller (1964, 1967*b*) reported that P_N of *Pinus halepensis* declined linearly by 37% between 4 and 20 mmHg whereas for desert plants and *Helianthus annuus* it sometimes decreased but was mostly unaffected.

The reduction of P_N at leaf–air vapour pressure differences greater than 12 mmHg was due mainly to an increase of stomatal resistance. Whiteman and Koller (1964, 1967*a*) and Gale, Kohl, and Hagan (1966) also showed that stomatal resistance increased with leaf–air vapour pressure difference and, in some cases, that mesophyll resistance was also affected. The increase in calculated stomatal resistance at large vapour pressure differences may, in part at least, be due to invalidity of the assumption that the vapour pressure at the cell wall was the saturated vapour pressure at the leaf temperature (Jarvis and Slatyer 1970).

The effects described here are only upon instantaneous photosynthetic rates of leaves attached to well-watered plants growing under conditions of low evaporative demand. Longer periods of exposure of whole plants may have more severe effects.

(*d*) *Leaf Temperature*

The cardinal temperatures of net photosynthesis for these grasses (7, 38, and 57°C) are comparable with those for other tropical grasses (Miller 1960; El-Sharkawy and Hesketh 1964; Murata, Iyama, and Honma 1965). Legumes (6, 31, and 50°C)

behave as warm climate dicotyledons (El-Sharkawy and Hesketh 1964; Begg and Jarvis 1968), with a similar minimum but lower optimum and maximum temperatures compared with grasses. Cardinal temperatures of tropical grasses and legumes are higher than the corresponding values for temperate species (Miller 1960; Murata, Iyama, and Honma 1965). The optimum temperatures for P_N of tropical grasses and legumes are similar to the optimum temperatures for growth (Anon. 1966; Cooper and Tainton 1968; Whiteman 1968) and, approximately, for the activity of the primary carboxylating enzymes (Treharne and Cooper 1969).

The response of buffel grass to temperature and the P_N at the optimum temperature were greater than those of vigna, because other processes of photosynthesis (e.g. the diffusion process) are less limiting. Similarly, if photorespiration is inhibited by reducing oxygen concentration, the optimum temperature increases as well as P_N (Jolliffe and Tregunna 1968; Hofstra and Hesketh 1969). Therefore Gaastra's (1959, 1963) conclusion that temperature has little influence on P_N at normal carbon dioxide concentrations and in bright light should not be applied to tropical grasses or other plants with high photosynthetic rates. The only model of canopy photosynthesis to incorporate the temperature–P_N response is that of Idso and Baker (1967).

The higher values of P_N at 30°C presented here compared with those of illuminance and CO_2 experiments may, in part, be the result of the lower leaf–air vapour pressure differences used in these experiments. Data in Figure 9 indicate that the leaf–air vapour pressure differences used previously (17 ± 3 mmHg) could depress P_N by up to 10%.

The Q_{10} of P_N was greatest at temperatures just above the minimum (Langridge and McWilliam 1967), and values of 1·6 and 1·3 respectively for grasses and legumes between 20 and 30°C are comparable with reported values (Thomas 1965). Chmora and Oya (1967) consider that under conditions of normal carbon dioxide concentration and saturating illuminance, Q_{10} reflects the diffusion coefficient of carbon dioxide in the aqueous phase of the cell, which is 1·2–1·3. On the other hand, the Q_{10} of R_D was 2.

The lower P_N at sub- and supra-optimal temperatures appears to result from increases in either one or both of r_s and r_M (Whiteman and Koller 1964, 1967*a*; Kuiper 1965), and at supra-optimal temperatures for legumes an increased photorespiration rate is probably also involved (Jackson and Volk 1970). Tropical pasture grasses do not appear to possess photorespiration (Wilson and Ludlow 1970) although at temperatures approaching the maximum, respiratory carbon dioxide production sometimes occurs (Hofstra and Hesketh 1969).

The light response curves varied with temperature (Fig. 12). Light saturation of grass leaves and the decreasing light saturation point of legume leaves at sub- and supra-optimal temperatures probably resulted from an increased limitation of photosynthesis by the biochemical or diffusion process, whereas the increase in dark respiration rate and light compensation point with temperature reflects an effect on respiration.

The relationship between P_N and leaf temperature is influenced by illuminance (Hiroi and Monsi 1966; Chmora and Oya 1967; Fig. 12), vapour pressure of the air (Kriedemann 1968*a*), temperature (Mooney and Shropshire 1967), and light intensity history (Kriedemann 1968*b*). Therefore all these factors must be taken into consideration when determining the optimum temperature for net photosynthesis; for ex-

ample, the lower optimum temperature of 25°C for cotton reported by Ludwig, Saeki, and Evans (1965) compared with 33°C (El-Sharkawy and Hesketh 1964) probably reflects the different illuminance at which P_N was measured (1700 f.c.; cf. 10,000 f.c.). Furthermore, data presented here which were obtained at saturated vapour pressures may not apply to air of lower vapour pressure.

In conclusion, tropical grass leaves have superior photosynthetic characteristics compared with tropical legume leaves, resulting in higher net photosynthetic rates and efficiency of light utilization at all illuminances. There is little light saturation at intensities approaching full daylight, and photosynthetic rates are independent of which side the leaf is illuminated. The higher photosynthetic capacity of grass leaves is likely to be a major determinant of the higher photosynthetic rate and net assimilation rate of whole plants. Furthermore, because of lower resistances to CO_2 transfer (mainly mesophyll resistance) the response of P_N to changes in illuminance, CO_2 concentration, leaf temperature, and leaf–air vapour pressure difference was greater for grasses than for legumes. Possession of these characteristics gives grasses a considerable ecological advantage over legumes.

V. Acknowledgments

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VI. References

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