PHOTOSYNTHESIS OF TROPICAL PASTURE PLANTS

II.* TEMPERATURE AND ILLUMINANCE HISTORY

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Abstract

Grasses and legumes were grown at two temperatures in controlled-environment rooms and at three illuminances (obtained by shading) in a glasshouse. Carbon dioxide and water vapour exchange of leaves were measured in an open gas analysis system.

Net photosynthetic rates of grasses and legumes grown at 20°C and measured at 30°C were lower (and transfer resistances were concomitantly higher) than values for plants grown at 30°C, but almost complete acclimatization to the higher temperature occurred within 15 hr. Dark respiration rates varied with species and with illuminance prior to measurement, but were unaffected by growth temperature.

Shading markedly affected the anatomy and the photosynthetic characteristics of both grass and legume leaves. Shaded leaves were thinner and contained fewer, smaller, and less densely packed cells than unshaded leaves. Light saturation point, light compensation point, and dark respiration rate declined as the level of shading increased, but the initial slope of the light response curve was unaffected. The lower net photosynthetic rate of shaded leaves was associated with increased stomatal and mesophyll resistances, and it is argued that the latter arose from higher carboxylation resistances. Net photosynthetic rate was positively related to leaf thickness, specific leaf weight, and the reciprocal of mesophyll resistance. These relationships and the relationship between net photosynthesis and chlorophyll content are discussed.

I. Introduction

The photosynthetic capacity of leaves is determined not only by the prevailing environmental conditions but also by those experienced in the past. We have described the effects of some current environmental factors on leaf net photosynthetic rate and carbon dioxide transfer resistances of tropical pasture grass and legume plants which had a common environmental history (Ludlow and Wilson 1971). In this paper, we show how the temperature and illuminance at which leaves develop, and to which they are exposed prior to measurement, influence photosynthetic characteristics measured under standard conditions. Grasses used in these experiments have the C_4 dicarboxylic acid pathway of carbon dioxide fixation whereas legumes have the Calvin cycle.

II. Materials and Methods

The apparatus, measurement procedures, and methods of calculating results were described previously (Ludlow and Wilson 1971). Plants were adequately supplied with water and mineral nutrients, and measurements were made on the youngest fully expanded leaves. Net photo-

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synthetic rate (P_N), dark respiration rate (R_D), and stomatal (r_s) and mesophyll resistance (r_M) to carbon dioxide transfer were calculated from the rates of carbon dioxide and water vapour exchange. Mesophyll resistance is taken to be the sum of the biophysical and biochemical resistances between the mesophyll cell wall and the site of the carboxylation where the carbon dioxide concentration is zero. Carbon dioxide compensation concentrations (Γ) were taken as 0 and 40 μl l^{-1} for grasses and legumes, respectively, regardless of treatment. The consequence of this assumption in the calculation of mesophyll resistance will be discussed later.

(*a*) *Temperature History*

Plants of the following species were grown in two growth cabinets, one at 20°C and the other at 30°C constant temperature:

	Grasses
Buffel grass	*Cenchrus ciliaris* L. cv. Biloela
Coloratum	*Panicum coloratum* L. cv. Kabulabula CPI16796
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.
Ruzi grass	*Brachiaria ruziziensis* Germain & Evrard cv. Kennedy
Setaria	*Setaria sphacelata* (Schum.) Stapf. & Hubbard ex Massey cv. Nandi
	Legumes
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
Silverleaf desmodium	*Desmodium uncinatum* (Jacq.) D.C. cv. Silverleaf
Vigna	*Vigna luteola* (Jacq.) Benth. cv. Dalrymple

Illuminance (1300–1900 f.c. $\equiv$ 182–193 W m^{-2} short-wave irradiance) and relative humidity ($70\pm10\%$) were similar in each cabinet. Cultural techniques have been described by Ludlow and Wilson (1968). Two other grasses and five other legumes either grew poorly at 20°C or produced leaves which were unsuitable for leaf-chamber studies. Gas-exchange measurements were not made on these species except *Chloris gayana* Kunth cv. Samford, for which dark respiration rates are given. Growth of all species at both temperatures is described elsewhere (Ludlow and Wilson 1970).

After an equilibration period of 1 hr at 30°C in the leaf chamber, light response curves (the relationship between leaf net photosynthetic rate, P_N, and illuminance) were determined. Values of P_N for grass leaves were lower on plants grown at 20°C than at 30°C. To determine whether leaf net photosynthesis of plants grown at 20°C could acclimatize to 30°C, leaves were allowed to remain overnight (15 hr of darkness) in the chamber after light response curves had been obtained. The following day, leaf dark respiration rates (R_D) were measured before the light was turned on, and then a light response curve established. In summary, the following measurement sequence was used: a light response curve terminating with an R_D measurement which defined the rate for the beginning of the overnight acclimatization period, an R_D measurement at the end of the overnight period, and a light response curve which terminated with an R_D measurement.

(*b*) *Illuminance History*

Seeds of Siratro (*Phaseolus atropurpureus* D.C. cv. Siratro) and green panic were sown in boxes of sand and watered with a mineral nutrient (half-strength Aquasol) and fungicide (Captan) solution. The boxes were watered daily with tap water and placed in an evaporatively cooled glasshouse in which temperature fluctuated diurnally between 18 and 30°C and relative humidity between 99 and 55%. Two weeks after sowing, the seedlings were transplanted into half-strength Hoagland's solution. The mean short-wave radiation in the glasshouse during this period was 435 cal cm^{-2} day^{-1}.

Pots which contained either four legume or two grass plants were assigned to the three illuminance treatments, and thereafter the nutrient solution was renewed every 2 weeks and 3–5 ml of iron citrate solution (a quarter of the strength used in normal Hoagland's solution) was added every 2 or 3 days. Deionized water was supplied as required.

The three treatments were full illuminance inside the glasshouse (I_1, 100%), and shaded with one (I_2, 33%) and two (I_3, 11%) layers of Sarlon cloth. Relative values for short-wave radiation were similar to those of illuminance and the mean daily short-wave radiation for the three treatments were 369, 133, and 48 cal cm^{-2}.

Gas-exchange measurements were made on leaves of 50-day-old plants, 36 days after the illuminance treatments had been imposed. To reduce the effect of diurnal and day-to-day fluctuations in environmental conditions, light response curves were determined in a randomized block design experiment. Leaves, one from each treatment, were measured daily in a random order, and measurements were made on consecutive days to give four replicates.

Because of large visual differences in chlorophyll content, an estimate of chlorophyll concentration was made on leaves similar to those used for gas-exchange experiments. Leaves were stored in a darkened refrigerator after collection, and chlorophyll determinations were completed within 5 hr. Thirty 1·1 cm diameter disks for each illuminance treatment were cut from laminae, 15 were used for chlorophyll extraction, and the remainder for dry weight determination. Chlorophyll was extracted by boiling the disks in 80% ethanol, and optical density of the solution measured with a Beckman model DU spectrophotometer at 660 nm using a tungsten source. Optical density was used as an index of chlorophyll concentration (Shimshi 1967). Specific leaf area (leaf area per unit dry weight) was calculated from the dry weight of leaf disks.

Transverse sections were cut from the centre of the lamina preserved in formalin–acetic acid–alcohol, taken through a t-butanol series, and embedded in paraffin. Microtome sections (10 μm thick) were stained with safranin and fast green, and mounted permanently.

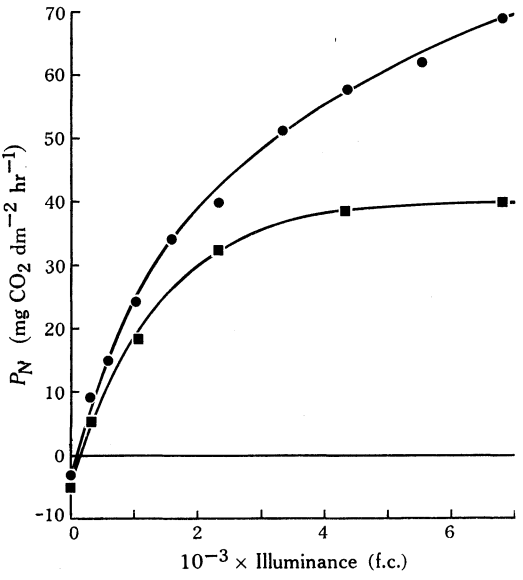

Fig. 1.—Light response curves of a *Panicum coloratum* leaf from a plant grown at 20°C measured before (■) and after (●) overnight acclimatization at 30°C. Conditions: 305±5 μl l^{-1} CO_2, 30±1°C leaf temperature, 17±3 mmHg leaf–air vapour pressure difference.

III. Results and Discussion

(a) *Temperature History*

Light response curves of grasses and legumes grown at 30°C have been published (Ludlow and Wilson 1971). Because the shape of the response curves of leaves from legumes grown at 20°C were similar to those from plants grown at 30°C, they are not

presented. On the other hand, both growth temperature and acclimatization influenced the shape of the light response curves of grasses (Fig. 1). The initial slope was unaffected but net photosynthesis of unacclimatized leaves approached light saturation. Acclimatized leaves had response curves which were similar to those which developed at 30°C.

Dark respiration rates differed between grasses and legumes and with conditions of illumination preceeding measurement (Table 1). In view of the variability within

TABLE 1

LEAF DARK RESPIRATION RATES (R_D) OF PLANTS GROWN AT 20°C CONSTANT TEMPERATURE AND MEASURED AT THE BEGINNING OF (A), THE END OF (B), AND IN THE DAY FOLLOWING (C) OVERNIGHT ACCLIMATIZATION, COMPARED WITH THOSE FROM PLANTS GROWN AT 30°C AND MEASURED AT THE BEGINNING OF OVERNIGHT ACCLIMATIZATION

Conditions: 325 ± 5 μl l^{-1} CO_2, $30 \pm 0 \cdot 1$°C leaf temperature

Species	R_D (mg CO_2 dm^{-2} hr^{-1}): Growth Temp. 20°C			Growth Temp. 30°C
	A	B	C	
Grasses				
B. ruziziensis	2·9	0·8	2·8	4·3
C. ciliaris	4·4	0·9	4·1	3·8
C. gayana	4·4	2·3	—	3·5
P. coloratum	4·9	2·4	3·4	5·8
P. maximum (green panic)	5·1	0·8	3·0	5·9
P. maximum (guinea)	3·2	1·2	3·1	5·0
Mean	4·1	1·4	3·3	4·7
Legumes				
D. intortum	1·8	0·9	—	3·0
D. uncinatum	6·1	1·9	2·0	1·5
D. uniflorus	2·5	2·1	3·1	—
G. wightii	1·7	1·1	2·3	2·8
V. luteola	3·7	1·6	5·8	3·3
Mean	3·2	1·5	3·3	2·6

grass and legume groups, differences in R_D between plants grown at 20 and 30°C cannot be considered significant, but rates were higher for grasses than legumes at both growth temperatures except after acclimatization. As McCree and Troughton (1966) showed for *Trifolium*, R_D of both grasses and legumes decreased during the dark acclimatization period and increased after exposure to light on the following day. These changes as well as the difference between grasses and legumes, can probably be explained by differences in the size of the respiratory substrate pool, because they cannot be explained by differences in stomatal resistance.

Mean values of P_N (measured at 10,000 f.c.) of both grasses and legumes grown at 20°C were, prior to acclimatization, less than those of plants grown at 30°C, the difference being greatest in grasses (Table 2). Similar responses have been reported for some warm-climate dicotyledons (Hesketh 1968) and for some tropical grasses (Murata, Iyama, and Honma 1965; Carlson and Pearce 1967; Alberda 1969). However, the inhibition of P_N of plants grown at 20°C was almost completely removed during a 15-hr dark period at 30°C. The fact that leaves of plants grown at 30°C did not respond to acclimatization demonstrates that the inhibited rate of the leaves from plants grown at 20°C was not an artifact of the measurement procedure.

TABLE 2

LEAF NET PHOTOSYNTHETIC RATES (P_N) AND STOMATAL (r_s) AND MESOPHYLL (r_M) RESISTANCES TO CO_2 TRANSFER FROM PLANTS GROWN AT 20°C CONSTANT TEMPERATURE AND MEASURED BEFORE AND AFTER OVERNIGHT ACCLIMATIZATION TO 30°C, COMPARED WITH THOSE GROWN AT 30°C AND MEASURED BEFORE OVERNIGHT ACCLIMATIZATION

Conditions: 305 ± 5 $\mu l\, l^{-1}$ CO_2, 10,000 f.c., $30 \pm 0{\cdot}1$°C leaf temperature, 17 ± 3 mmHg leaf–air vapour pressure difference, $r_a = 0{\cdot}4$–$0{\cdot}5$ sec cm^{-1}. Units for r_s and r_M as for r_a; units for P_N: mg CO_2 dm^{-2} hr^{-1}

Species	Growth Temperature 20°C: Before Acclimatization			After Acclimatization			Growth Temp. 30°C: Before Acclimatization		
	P_N	r_s	r_M	P_N	r_s	r_M	P_N	r_s	r_M
Grasses									
B. ruziziensis	33	—	—	40	—	—	46	1·2	2·4
C. ciliaris	56	1·6	1·3	68	1·8	0·4	66	1·6	0·9
M. minutiflora	36	1·5	3·4	51	1·3	1·9	50	1·5	1·6
P. coloratum	40	2·4	2·1	69	2·3	0·1	59	2·2	0·5
P. maximum (green panic)	71	—	—	72	—	—	70	1·3	0·8
P. maximum (guinea)	44	1·9	2·0	62	2·1	0·5	56	1·9	1·0
P. maximum (Hamil)	43	2·3	1·6	66	2·4	0·2	66	1·4	0·7
S. sphacelata	41	2·9	1·2	42	2·1	1·9	51	2·1	1·0
Mean	45	2·1	1·9	59	2·0	0·8	58	1·6	1·1
Legumes									
D. intortum	20	2·8	5·3	—	—	—	26	1·0	4·5
D. uncinatum	19	2·0	6·4	21	1·9	5·8	25	1·2	5·0
D. uniflorus	16	2·7	8·5	26	2·1	4·0	22	2·0	4·9
G. wightii	19	2·3	6·4	19	1·9	6·6	20	1·3	6·5
V. luteola	18	2·6	6·6	21	1·5	6·1	—	—	—
Mean	18	2·5	6·6	22	1·8	5·6	23	1·4	5·2

The lower P_N of leaves from plants grown at 20°C was associated with higher values of r_s and r_M, which declined to values comparable with those from plants grown at 30°C after acclimatization (Table 2). Effects of growth temperature on r_s (Hofstra and Hesketh 1969; Treharne and Eagles 1970) and on r_M (Björkman and

Gauhl 1969*a*) and a reduction of r_s (Hofstra and Hesketh 1969) and r_M (Mooney and Harrison 1970) during acclimatization to 30°C have been reported. Whereas r_s and r_M were equally important in determining the lower P_N of leaves from plants grown at 20°C and the recovery of legume leaves during acclimatization, the increase in P_N of grass leaves during acclimatization was due solely to an increase in r_M. However, the importance of r_M of legume leaves may have been underestimated because it was assumed that Γ was independent of growth temperature, and there is some evidence that photorespiration rate (and hence Γ, Ludlow and Jarvis 1971) is higher for plants grown at 20°C and measured at 30°C than in plants grown at 30°C (Björkman, Nobs, and Hiesey 1970; Mooney and Harrison 1970).

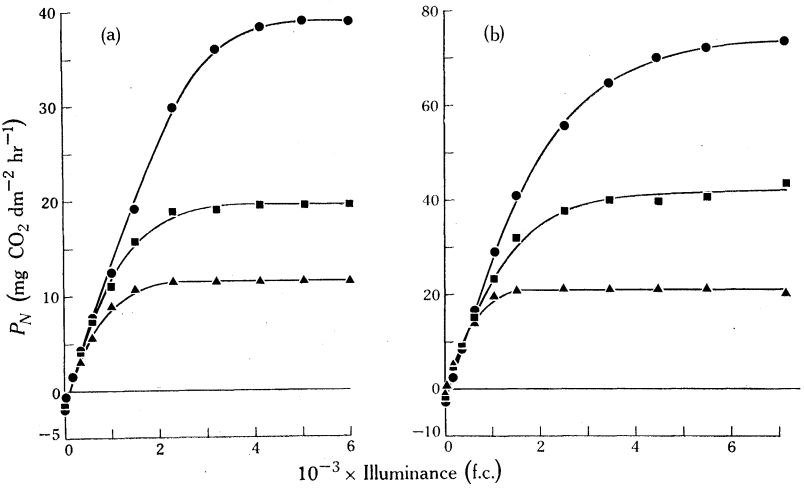

Fig. 2.—Light response curves of (*a*) Siratro and (*b*) green panic leaves which developed under three illuminance regimes (● = 100, ■ = 33, and ▲ = 11% daylight). Conditions: 300 ± 5 $\mu l\, l^{-1}$ CO_2, 30 ± 1°C leaf temperature, 17 ± 3 mmHg leaf–air vapour pressure difference.

Although the physical component of mesophyll resistance dependent upon cell size is influenced by growth temperature (Wilson 1970), it seems more likely that the higher r_M of plants grown at 20°C resulted from a higher value of the chemical component because r_M decreased during 15 hr of acclimatization. The fact that growth temperature had little effect on the initial slope of the light response curve (Fig. 1) and hence the photochemical component of r_M (excitation resistance, Monteith 1963) but has a marked effect on photosynthetic enzyme activity (Treharne and Eagles 1970) suggests that the biochemical component is involved. This could have arisen from a deficiency of photosynthetic enzymes or from an accumulation of photosynthate associated with the slow growth at 20°C (Woledge and Jewiss 1969; Ludlow and Wilson 1970), and the decrease in r_M during acclimatization could have resulted from respiration of the accumulated photosynthate or an increase in enzyme activity. There are data showing rapid changes in enzyme activity in response to illuminance (Hatch, Slack, and Bull 1969) but none for temperature.

In addition to the response of leaves to overnight acclimatization, other short-term changes in temperature affect net photosynthesis. Exposure of grass plants

to low night temperature (10°C for 5 hr) depressed net photosynthesis for several days (Ludlow and Wilson, unpublished data). Similar effects have been reported for other plants (Moss 1965; Izhar and Wallace 1967). The influence of short-term changes in temperature are important during treatment of plants prior to laboratory measurements of photosynthesis, and when interpreting the photosynthetic performance of plants in the field in relation to prevailing environmental conditions. Furthermore, when the response of net photosynthesis to temperature is being studied, exposure to extremes of temperature can affect subsequent performance. The procedure described

TABLE 3

DARK RESPIRATION RATES (R_D), EXPRESSED ON BOTH AREA AND DRY WEIGHT BASES, AND THE RATIO OF DARK RESPIRATION RATE TO NET PHOTOSYNTHETIC RATE (P_N) OF PLANTS GROWN AT THREE ILLUMINANCES (I_1, I_2, I_3)

Values are means of four replicates. Conditions: 325 ± 5 μl l^{-1} CO_2, $30 \pm 0{\cdot}1$°C leaf temperature, $I_1 = 100$, $I_2 = 33$, $I_3 = 11\%$ daylight

Species	Illuminance	R_D (mg CO_2 dm^{-2} hr^{-1})	R_D (mg CO_2 g^{-1} hr^{-1})	R_D/P_N (%)
Panicum maximum (green panic)	I_1	2·8	4·4	3·7
	I_2	1·7	5·4	4·0
	I_3	0·5	4·6	2·7
L.S.D. at 5% level		1·2	n.s.	—
Phaseolus atropurpureus (Siratro)	I_1	2·1	10	5·0
	I_2	1·7	20	7·7
	I_3	1·2	14	8·0
L.S.D. at 5% level		0·3	n.s.	—

by Ludlow and Wilson (1971), in which, the effects of sub-optimum temperatures are removed by overnight acclimatization, proved satisfactory for tropical grasses and legumes and for *Picea sitchensis* (Ludlow and Jarvis, unpublished data) as long as minimum temperatures for photosynthesis were not approached.

(*b*) *Illuminance History*

Light response curves of leaves from plants grown at three illuminances are presented in Figure 2. The light saturation point of leaves of both species decreased as the level of shading increased and resulted from a decreasing light saturation point for r_s and an increasing total resistance to carbon dioxide transfer. Also, as the degree of shading increased light compensation points of both grass (108, 48, and 32 f.c.) and legume (112, 76, and 56 f.c.) leaves decreased. In contrast to much published information (Wassink, Richardson, and Pieters 1956; Burnside and Böhning 1957; Loach 1967—cf. Björkman and Holmgren 1963; Hiesey, Björkman, and Nobs 1967), the initial slope of the light response curve was unaffected by shading. However, as has been reported previously (Ludlow and Wilson 1971) the initial slope of this curve for green panic leaves ($0{\cdot}026$ mg CO_2 dm^{-2} hr^{-1} f.c.$^{-1}$) was significantly ($P < 0{\cdot}01$) greater than that for Siratro ($0{\cdot}016$ mg CO_2 dm^{-2} hr^{-1} f.c.$^{-1}$) and quantum efficiencies based on incident irradiance and net photosynthesis were, respectively, $0{\cdot}10$ and $0{\cdot}06$ moles CO_2 Einstein^{-1}.

Dark respiration rate of leaves (on an area basis) decreased with the illuminance at which they developed (Table 3). This decline was not accompanied by significant increases in r_s measured in the dark, but appeared to be associated with a smaller amount of respiratory tissue because differences in R_D disappeared when it was expressed on a dry weight basis. Because the initial slope of the light response curve was unaltered by shading, changes in R_D and the light compensation point were correlated.

The ratio of R_D to P_N for green panic decreased as shading increased, whereas for Siratro, ratios were larger and increased (Table 3). Whole plants behave similarly, which explains, in part at least, the comparatively better growth of grasses at low illuminances (Ludlow and Wilson, unpublished data; Heslehurst and Wilson, unpublished data). This could give grasses a competitive advantage over legumes.

TABLE 4

LEAF NET PHOTOSYNTHETIC RATE (P_N) AND CARBON DIOXIDE TRANSFER RESISTANCES OF PLANTS GROWN AT THREE ILLUMINANCES (I_1, I_2, I_3)

Conditions: 300 ± 5 μl l^{-1} CO_2, 7000 f.c., $30 \pm 0{\cdot}1$°C leaf temperature, 17 ± 3 mmHg leaf–air vapour pressure difference, $I_1 = 100$, $I_2 = 33$, $I_3 = 11$% daylight

Species	Illuminance	P_N† (mg CO_2 dm^{-2} hr^{-1})	CO_2 Transfer Resistances (sec cm^{-1})		
			r_a	r_s†	r_M†
Panicum maximum (green panic)	I_1	72	0·8	1·0	0·8
	I_2	40	0·9	1·9	2·3
	I_3	22	1·6	4·0	4·9
L.S.D. at 1% level		10	—	2·0	0·8
Phaseolus atropurpureus (Siratro)	I_1	36	0·7	1·1	2·9
	I_2	20	0·7	1·5	6·3
	I_3	13	1·1	2·2	10·6
L.S.D. at 1% level		6	—	n.s.	2·4

† Significance of difference in P_N, r_s, and r_M values between green panic and Siratro at each illuminance is as follows (** $P < 0{\cdot}01$, * $P < 0{\cdot}05$):

Illuminance	P_N	r_s	r_M
I_1	**	n.s.	*
I_2	**	n.s.	**
I_3	n.s.	n.s.	**

In accordance with data for many herbaceous species (Burnside and Böhning 1957; Björkman and Holmgren 1963; Björkman 1968*a*), P_N (measured at 7000 f.c.) declined linearly as the level of shading increased, and except at the lowest illuminance the rate for green panic was significantly higher than that for Siratro (Table 4). The decline in P_N was accompanied by an increase in both r_s and r_M for green panic but mainly in r_M for Siratro (see also Holmgren 1968). Mesophyll resistance of Siratro was significantly higher than that of green panic in all cases, but stomatal resistances

were similar. The assumption in the calculation of r_M that Γ was the same for all treatments seems justified because photorespiration rate (Björkman 1968*b*) and Γ of ecotypes of *Solidago* (Holmgren 1968) are unaffected by the illuminance at which leaves develop. Therefore the increase in r_M with shading must have resulted from increases in one or more of its three components (transfer, excitation, and carboxylation resistances). Very little is known about the first two components, but there is a good correlation between P_N, r_M, and carboxydismutase activity of Calvin cycle plants (Björkman 1968*a*, 1968*b*; Holmgren 1968; Eagles and Treharne 1969) and between P_N and photosynthetic enzyme activity of C_4-dicarboxylic acid pathway plants (Hatch, Slack, and Bull 1969) grown at different illuminances, suggesting that the higher r_M of Siratro and green panic may have been due to higher carboxylation resistances.

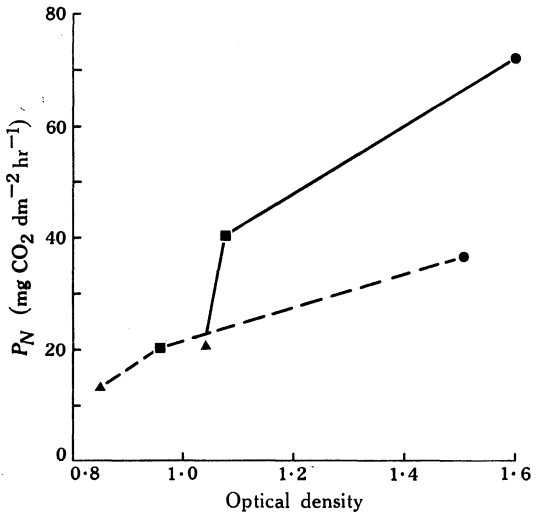

Fig. 3.—Relationship between net photosynthetic rate (P_N) and chlorophyll content (expressed as optical density) of Siratro (broken line) and green panic (solid line) which developed under three illuminance regimes (● = 100, ■ = 33, and ▲ = 11% daylight). Conditions: 300 ± 5 $\mu l\, l^{-1}$ CO_2, 7000 f.c., $30 \pm 0{\cdot}1$°C leaf temperature, 17 ± 3 mmHg leaf–air vapour pressure difference.

Two of the most outstanding characteristics of shaded leaves of herbaceous species is the lower chlorophyll concentration (Friend 1960; Björkman and Holmgren 1963; Navasero and Tanaka 1966) and altered structural characteristics such as leaf thickness and leaf dry weight per unit area (Holmgren 1968; Pearce and Lee 1969). In view of this, it is interesting to examine how these characteristics could influence P_N in the present experiment. Chlorophyll concentration (as shown by optical density) declined in both species as the level of shading increased, and was generally higher in green panic than in Siratro (Fig. 3). If chlorophyll concentration has a direct effect on P_N it should have the greatest effect on light-limited photosynthesis. The initial slope, however, was unaffected by shading. This suggests that the decrease in chlorophyll concentration is an effect of shading rather than a cause of the lower P_N (Table 4), which results from some other factor such as a lower photosynthetic enzyme activity. Support for this proposal are the lack of a relationship between P_N and chlorophyll concentration when differences in specific leaf area

(leaf area per unit dry weight) are taken into account, and the lack of a general relationship between P_N measured in bright light and chlorophyll concentration of leaves from different illuminance regimes (Wassink, Richardson, and Pieters 1956; Bordeaux and Laverick 1958; Loach 1967).

The effect of shading on leaf structure is shown in Figure 4. Shaded leaves were thinner, contained fewer, smaller, and less densely packed cells, and had smaller specific leaf weights (leaf dry weight per unit area) than unshaded leaves (green panic 0·30, 0·20, and 0·12 g dm^{-2} and Siratro 0·36, 0·14, 0·10 g dm^{-2} for 100, 33, and 11% relative illuminance, respectively). There are positive approximately linear relationships between P_N (measured at 7000 f.c., Table 4) and, the reciprocal of mesophyll resistance (Table 4), leaf thickness (Fig. 4), and specific leaf weight.

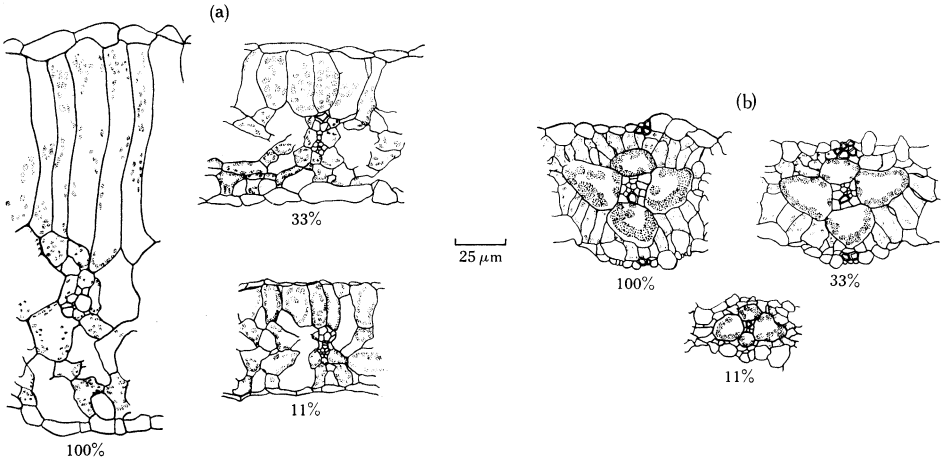

Fig. 4.—Transverse sections of (*a*) Siratro and (*b*) green panic leaves which developed under three illuminance regimes (100, 33, and 11% daylight).

These structural changes may influence P_N through the physical component of r_M, or, alternatively, they may simply parallel changes in some other factor such as photosynthetic enzyme activity which determines r_M and P_N. The latter seems more likely because when Siratro and green panic grown at the highest illuminance are compared and in other instances (Pearce, Brown, and Blaser 1968; Cunningham, and Strain 1969), there is a negative correlation between leaf thickness, specific leaf weight, and P_N.

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