PHOTOSYNTHESIS OF TROPICAL PASTURE PLANTS

IV.* BASIS AND CONSEQUENCES OF DIFFERENCES BETWEEN GRASSES AND LEGUMES

By M. M. Ludlow† and G. L. Wilson‡

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Abstract

Differences in leaf net photosynthetic rate were associated with differences in intracellular resistance. The larger intracellular resistance of legume leaves appeared to result from larger resistances to the movement of CO_2 from the mesophyll cell wall to the photosynthetic sites rather than from high resistances associated with its fixation at the sites.

Photorespiration could not be detected in grasses but their dark respiration rates at normal ambient CO_2 concentrations were higher than the values for legumes. Although legumes had an appreciable photorespiration rate, this alone could not account for their lower photosynthetic rates. The higher intracellular resistance appeared to be an equally important factor.

The photosynthetic advantage of individual grass leaves compared with legumes was reflected in higher productivity of whole plants and, to a lesser extent, of grass swards. Furthermore, it is an important determinant of the lower transpiration ratios of grasses at leaf, plant, and sward levels.

I. Introduction

Previous papers (Ludlow and Wilson 1971*a*, 1971*b*, 1971*c*) showed that the tropical pasture grasses which have the C_4-dicarboxylic acid pathway of CO_2 fixation (Hatch and Slack 1970) have higher rates of fixation than the tropical legumes which have the Calvin (or C_3) pathway. The present paper is the last to discuss the data of that experimental work. Initially it examines the causes of the differences, and then goes on to consider some implications for pasture production.

The earlier papers reported that the higher rates of net photosynthesis in grasses at normal CO_2 concentrations appear to be associated with lower intracellular resistances to CO_2 uptake. Now we attempt to obtain more accurate estimates of stomatal and intracellular resistances, and further, by using Chartier's (1970*a*) technique, to separate the latter into transport and carboxylation components.

In addition to those factors, the magnitude of respiration has a large effect on net photosynthesis, and values are presented. This requires estimates of photorespiration, in respect of which there are well-known differences between C_4 and C_3 plants.

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† Division of Tropical Pastures, CSIRO, St. Lucia, Qld. 4067.

‡ Agricultural Department, University of Queensland, St. Lucia, Qld. 4067.

Agronomically, efficiency of energy utilization in the fixation of CO_2 may be expressed in rates of dry matter accumulation, and in transpiration ratios (water use efficiencies). Growth rates were not measured in these experiments, but there are data in the literature on the performance of the same or similar species, and it is possible to consider them in the light of the observations made here. Transpiration rates of leaves were measured in the course of determining transfer resistances and the transpiration ratios derived from them are now presented and discussed.

II. Materials and Methods

Conditions of plant growth, the apparatus, and techniques have been described (Ludlow and Wilson 1971*a*). The species used in these experiments are indicated in Tables 1 and 2. Unless otherwise stated, all measurements were made on the youngest fully expanded leaf of a grass tiller or legume runner.

A. Basis of differences in leaf net photosynthetic rate

Differences in leaf net photosynthetic rate were analysed in two ways. Firstly, more accurate estimates of stomatal and intracellular resistance were obtained at low CO_2 concentrations where the relationship between net photosynthesis and CO_2 concentration is linear and where resistances are constant and minimal (Holmgren, Jarvis, and Jarvis 1965; Jarvis 1971). Chartier's (1970*a*) method was then used to separate the transport and carboxylation components of intracellular resistance. Secondly, rates of respiration in the light and dark were determined and compared with the rates of net photosynthesis.

(*a*) *Minimum Resistances to CO_2 Uptake*

(i) *Definitions*

Definitions of the resistances to CO_2 uptake given previously by Ludlow and Wilson (1971*a*) are applied here, with one exception. Mesophyll resistance (r_M) was defined as the resistance to CO_2 transfer between the mesophyll cell wall and the site of carboxylation where the CO_2 concentration is zero. Defined in this way, mesophyll resistance is composed not only of resistances to the movement of CO_2 from the cell wall to the sites of carboxylation, but also of the photochemical and biochemical resistances which control the rate of CO_2 fixation at the sites (Moss 1968; Jarvis 1971). Gaastra (1959) originally used the term mesophyll resistance to refer to the resistances to CO_2 movement from the mesophyll cell wall to the sites of carboxylation. Therefore, to avoid confusion and to conform to the convention used in a recent symposium on photosynthesis (Hatch, Osmond, and Slatyer 1971), we use the term intracellular resistance (r_i) instead of r_M (defined above) and use the term mesophyll resistance (r_m) in accordance with Gaastra's definition. However, mesophyll resistance may not be purely diffusional as Gaastra originally proposed, but probably also includes mass transfer (e.g. cytoplasmic streaming) and enzyme-mediated transport processes [e.g. carbonic anhydrase (E.C. 4.2.1.1)]. Monteith (1963) defined photochemical and biochemical resistances associated with the fixation process, but in this paper they will be considered collectively as carboxylation resistance (r_x). Thus,

$$r_i = r_m + r_x. \tag{1}$$

(ii) *Technique*

The relationship between CO_2 concentration and net CO_2 exchange at high illuminance (8000 f.c.) and near-optimum leaf temperature of 30°C was determined by supplying leaves sequentially with gases from cylinders whose CO_2 concentrations ranged from 62 to 205 μl l^{-1}, and with CO_2-free air. The same gases were used to calibrate the infrared gas analyser over a range of approximately 50 μl l^{-1} at each background CO_2 concentration. Dark respiration rate in CO_2-free air was determined at the end of each experiment.

Boundary layer resistance was held constant, and the average CO_2 concentration in the intercellular spaces (C_i) was calculated from the following equation:

$$C_i = C_a - P_N(r_a + r_s),$$

where C_a is the ambient CO_2 concentration, P_N is the rate of net photosynthesis, and r_a and r_s are boundary layer and stomatal resistances to CO_2 uptake calculated from the corresponding resistances to water vapour movement, using 1·37 and 1·606 as the ratios of the diffusion coefficients (Jarvis 1971). Intracellular resistance was calculated from the slope of the regression between P_N and C_i. The CO_2 compensation concentration (Γ) and the CO_2 efflux into CO_2-free air were obtained, respectively, by interpolation (CO_2 concentration at which $P_N = 0$) and extrapolation (rate of CO_2 evolution at $C_i = 0$).

Mesophyll and carboxylation components of intracellular resistance (equation 1) were calculated from published (Ludlow and Wilson 1971*a*, 1971*b*, 1971*c*) rates of net photosynthesis and resistances (measured at illuminances between 4000 and 11,000 f.c., 300±5 μl l^{-1} CO_2, and 30±0·1°C leaf temperature) using the method of Chartier (1970*a*). It was assumed that the rate of photorespiration was equal to the stimulation of net photosynthesis when the ambient oxygen concentration is reduced from 21 to 0·2% (oxygen effect), and that all the respiratory flux enters the intercellular spaces. The oxygen effect probably overestimates the respiratory flux but it has been shown that the size of the respiratory flux and its pathway have only a small effect on the values of r_x and r_m (Chartier, Chartier, and Čatský 1970; Ludlow 1971).

Values of r_m and r_x were obtained by solving equations using a least squares method (Chartier 1970*b*) instead of the graphical method described by Chartier (1970*a*). Both methods give similar results but the least squares approach is quicker and more accurate.

(*b*) *Respiration*

It is now well recognized that different respiratory processes operate in the light and darkness (Jackson and Volk 1970). The glycollic acid pathway operates in the light (Hatch, Osmond, and Slatyer 1971) but whether the tricarboxylic acid cycle normally associated with dark respiration operates in the light has been the subject of much controversy. Recent evidence indicates that after an initial inhibition on transfer to the light the tricarboxylic acid cycle appears to return to a rate approaching that in darkness (CSIRO Aust. Div. Food Res. Report of Research 1970–71, p. 12; Chapman and Osmond, personal communication). For simplicity, we will assume that the tricarboxylic acid cycle operates at the same rate in both light and dark. Therefore,

we define photorespiration as the process of CO_2 release in the light and calculate its rate by adding the estimated fluxes associated with both the tricarboxylic acid cycle and the glycollic acid pathway.

Three methods were used to estimate the rate of photorespiration at high illuminance (8000 f.c.) and near-optimum temperatures ($30 \pm 0 \cdot 1$°C). All these methods are unsatisfactory, but as yet no suitable method is available which measures the total respiratory flux (Jackson and Volk 1970; Ludlow and Jarvis 1971).

(i) *CO_2 Efflux into CO_2-free Air*

CO_2 efflux was measured directly, and also determined by extrapolation of the relationship between C_i and P_N as described above. Even though a correction was made for intercellular reassimilation (Begg and Jarvis 1968), this value is an underestimate because intracellular reassimilation is not included (Ludlow and Jarvis 1971). Furthermore, if there is a direct linkage via common intermediates between photorespiration and photosynthesis, the photorespiratory flux at 0–10 μl l^{-1} will be less than at 300 μl l^{-1} CO_2.

(ii) *Oxygen or Warburg Effect*

When the oxygen concentration of ambient air is reduced from 21 to $0 \cdot 2\%$, net photosynthesis of some plants is stimulated by about 45% (Ludlow 1970). As the glycollic acid pathway is inhibited by the lack of oxygen it has been assumed that this stimulation is a measure of its activity (Ludlow and Jarvis 1971). However, part of the stimulation may be due to the removal of an inhibition of photosynthesis by oxygen, and is therefore probably an overestimate of glycollic acid pathway activity.

(iii) *Photorespiration Rate at the CO_2 Compensation Concentration*

The CO_2 compensation concentration was determined from the relationship between C_i and P_N as described. It can be converted to a flux (Ludlow and Jarvis 1971), and if the small dark-respiration flux from non-pigmented cells of the leaf such as the epidermis and the vascular tissue is neglected, photorespiration rate (R_L) at the compensation concentration is shown to be $2\Gamma/r_m$. Subject to the assumptions made in its derivation, this method is intended to account for both inter- and intracellular reassimilation but as with the CO_2 efflux method it has the disadvantage of being measured at low CO_2 concentrations and low rates of photosynthesis.

B. CONSEQUENCES OF DIFFERENCES IN LEAF NET PHOTOSYNTHETIC RATE

The transpiration ratio (weight of water transpired per unit of CO_2 fixed) was calculated for leaves of similar age (6–10 days after unrolling or unfolding) and environmental history (Ludlow and Wilson 1971*c*) from rates of net photosynthesis and transpiration measured under standard conditions.

Data on the effect of various environmental and physiological factors on transpiration ratio were calculated from published net photosynthetic rates (Ludlow and Wilson 1971*a*, 1971*b*, 1971*c*) and associated (but unpublished) transpiration rates.

III. Results and Discussion

A. Basis of Differences in Leaf Net Photosynthetic Rate

(a) *Minimum Resistances to CO_2 Uptake*

Stomatal resistances of grasses and legumes were similar, but the intracellular resistance of legumes was more than three times the value for grasses (Table 1). The similarity of stomatal resistance occurred despite large differences in stomatal density; grass leaves had approximately the same mean stomatal density on each surface (10,600 and 13,800 per square centimetre on the ad- and abaxial surfaces, respectively), whereas legumes had a greater number on the abaxial surface (9,200 and 24,400 per square centimetre). In addition, there was no correlation between P_N and r_s either between or within grass and legume groups, which is consistent with data from other amphistomatous species (El-Sharkawy and Hesketh 1965; Irvine 1967; Holmgren 1968).

Table 1

Minimum stomatal (r_s) and intracellular (r_i) resistances to CO_2 transfer, and mesophyll (r_m) and carboxylation (r_x) resistances of grass and legume leaves. Boundary layer resistance (r_a) is also given

Mesophyll and carboxylation resistances were measured under different conditions and in different experiments from intracellular resistance and therefore (r_m+r_x) and r_i are not comparable. Conditions for r_s and r_i: 8000 f.c., 0–200 μl l^{-1} CO_2 concentration, $30\pm0{\cdot}1$°C leaf temperature, 17 ± 3 mmHg leaf–area vapour pressure difference. Conditions for r_m and r_x: 4000–11,000 f.c., 300 ± 5 μl l^{-1} CO_2, $30\pm0{\cdot}1$°C leaf temperature, 17 ± 3 mmHg leaf–air vapour pressure difference

Species	CO_2 transfer resistances (sec cm^{-1})				
	r_a	r_s	r_i	r_m	r_x
Grasses					
Cenchrus ciliaris cv. Biloela	—	—	—	0·66	0·34
Panicum maximum var. *trichoglume* cv. Petrie	—	—	—	0·63	0·16
Panicum maximum cv. Hamil	0·95	0·73	0·63	0·50	0·32
Pennisetum purpureum Q5088	0·91	0·56	1·13	0·63	0·39
Sorghum almum cv. Crooble	0·90	1·25	1·36	0·49	0·09
Mean	0·92	0·85	1·04	0·58	0·32
Legumes					
Calopogonium mucunoides	0·67	1·08	2·98	3·46	0·24
Glycine wightii cv. Cooper	—	—	—	4·62	0·14
Phaseolus atropurpureus cv. Siratro	0·66	0·58	3·11	3·82	0·08
Vigna luteola cv. Dalrymple	0·62	0·47	3·73	2·97	0·16
Mean	0·65	0·71	3·27	3·72	0·15

A corollary of the proportionately larger stomatal component of total resistance in grasses is that stomatal resistance is a more important determinant of net photosynthetic rate than it is in legumes. Thus, the response of net photosynthesis of tropical grasses to different environmental and physiological conditions can largely be explained

by the response of stomata (CSIRO Aust. Div. Land Res. A. Rep. for 1968–69, pp. 84–6; Gifford and Musgrave 1970, 1972; Bull 1971; Gifford 1971; Ludlow and Wilson 1971*a*, 1971*b*, 1971*c*).

The large difference in r_i between grasses and legumes agrees with previously published data (Ludlow and Wilson 1971*a*, 1971*b*, 1971*c*; Ludlow 1971) and with other comparisons between C_4 and C_3 species (Hesketh and Baker 1967; Holmgren 1968; Bull 1969; Osmond, Troughton, and Goodchild 1969; Björkman, Pearcy, and Nobs 1971). The reason for the difference in net photosynthetic rate between these two groups, therefore, should be sought in the components of intracellular resistance.

Chartier's (1970*a*) technique is the only one available at present to separate the transport and the carboxylation processes. The assumptions which have to be made have been discussed (Chartier 1970*a*; Chartier, Chartier, and Čatský 1970; Ludlow 1971). Notwithstanding the limitations of the technique, r_m and r_x were calculated (Table 1). Because of the assumptions, and because the method of calculating CO_2 transfer resistances is a subtractive one which results in the remaining resistance containing the summation of all errors, no conclusion can be drawn about the relative sizes of the carboxylation resistances, except that they are small. Similarly, it would be unwise to draw any conclusions about the relative sizes of r_m and r_x for grasses. However, it is evident that r_m differs greatly between grasses and legumes, and that this difference appears to account for most, if not all, of the difference in intracellular resistance. The same conclusion was drawn for other data on pasture grasses and legumes (Ludlow 1971) and for the comparison of *Zea mays* L. and *Phaseolus vulgaris* L. (Chartier 1972).

In view of the different biochemical pathways of C_4 and C_3 species (Hatch, Osmond, and Slatyer 1971), it is surprising that the difference was not in r_x, rather than r_m. This matter has been fully discussed by Chartier (1972) and Ludlow (1971).*

(*b*) *Respiration*

Estimates of respiratory fluxes in light and darkness are shown in Table 2. No CO_2 release could be detected from grasses in the light, but the rate of dark respiration was appreciable in air with low or near-ambient CO_2 concentrations. In addition, the CO_2 compensation concentration was zero. This behaviour is consistent with that found for other C_4 grasses (Jackson and Volk 1970; Osmond 1971; Troughton 1971), and can be interpreted in two ways. In *S. almum* and *P. purpureum* which have little or no granal development in bundle sheath chloroplasts (determined from electron micrographs), and therefore little or no photosystem II or

* *Note added in proof.*—In a recent paper [Jones, H. G., and Slatyer, R. O., 1972, Estimation of the transport and carboxylation components of the intracellular limitation to leaf photosynthesis. *Pl. Physiol., Lancaster* **50**, 283–8], Chartier's method of calculating the component of intracellular resistance was criticized, and limitations of the resistance analogue approach in circumstances where the CO_2 response curve deviates from linearity were demonstrated. The CO_2 response curve of both grasses and legumes is linear up to and exceeding the CO_2 concentrations used in the present experiments (300 μl l^{-1}). Therefore although their model may allow data from gas-exchange and biochemical investigations, in general, to be rationalized, their comments do not invalidate the conclusions made in this paper. Furthermore, their conclusion that the transport resistance is the greater component of the intracellular resistance of cotton when measured on the linear portion of the CO_2 response curve agrees with our conclusions for tropical legumes.

glycollic acid pathway activity (Anderson, Woo, and Boardman 1971; Osmond 1971) only dark respiration may be operating and the CO_2 from this source is completely reassimilated. Alternatively, in *P. maximum* and *B. ruziziensis*, which have granal development in the bundle sheath chloroplasts and potential photosystem II and glycollic acid pathway activity, respiratory CO_2 from both sources is completely reassimilated.

TABLE 2

RATES OF PHOTORESPIRATION AND DARK RESPIRATION AND CO_2 COMPENSATION CONCENTRATION (Γ) OF GRASS AND LEGUME LEAVES

Conditions: 8000 f.c., $30 \pm 0{\cdot}1$°C leaf temperature, 17 ± 3 mmHg leaf–air vapour pressure difference

Species	Photorespiration rate (mg CO_2 $dm^{-2}hr^{-1}$)			Dark respiration rate (mg CO_2 $dm^{-2}hr^{-1}$)		Γ ($\mu l\ l^{-1}$)
	A*	B†	C‡	D§	E‖	
Grasses						
Brachiaria ruziziensis cv. Kennedy	0	0	0	2·62	3·87	—
P. maximum cv. Hamil	0	0	0	3·50	3·17	0
P. purpureum	0	0	0	2·84	5·48	0
S. almum	0	0	0	2·88	3·40	0
Mean	0	0	0	2·87	3·97	0
Legumes						
C. mucunoides	13·4	16·1	7·30	2·57	2·88	42
G. wightii	8·7	—	8·50	2·75	2·79	—
P. atropurpureus	19·7	12·5	6·87	3·22	2·73	36
V. luteola	16·8	14·7	6·22	2·95	2·94	33
Mean	14·7	14·4	7·22	2·87	2·83	37

* Measured by the oxygen effect at 300 $\mu l\ l^{-1}$ CO_2.

† Measured by a flux calculated at the CO_2 compensation concentration.

‡ Measured by CO_2 efflux into CO_2-free air, corrected for intercellular reassimilation.

§, ‖ Measured at 0–10 and *c.* 320 $\mu l\ l^{-1}$ CO_2 respectively.

The higher rates of leaf dark respiration (measured in normal air) of grasses compared with legumes shown in Table 2 support earlier data (Ludlow and Wilson 1971*a*, 1971*b*, 1971*c*), but the reason remains obscure. They are not associated with a higher dry weight per unit leaf area because the difference was still apparent when the rates given in Table 1 of Ludlow and Wilson (1971*a*) were expressed on a dry weight basis (mean values for grasses and legumes, respectively, were 16·6 and 9·6 mg CO_2 $g^{-1}hr^{-1}$). In addition, the higher respiration rates (on a leaf area basis) of grasses are also found at the whole plant level, whether calculated from dry weight changes (Ludlow and Wilson 1970) or measured directly by gas analysis (Heslehurst and Wilson, unpublished data).

Legumes, on the other hand, showed appreciable photorespiration, the value depending upon how it was measured (Table 2). This is demonstrated qualitatively by a

measurable CO_2 compensation concentration. The CO_2 efflux method yields the lowest estimate of photorespiration rate but because intracellular reassimilation is neglected and because of the possibility of photorespiration rate varying with photosynthetic rate, it is probably an underestimate. In contrast, the oxygen effect is known to be an overestimate because only a minor part of the stimulation of net photosynthesis is due to an inhibition of the glycollic acid pathway (Ludwig and Canvin 1971; Osmond and Björkman, personal communication). If we accept Ludwig and Canvin's value of one-third ($\equiv$ 4·9 mg CO_2 $dm^{-2}hr^{-1}$) and add to this 2·8 mg CO_2 $dm^{-2}hr^{-1}$ for dark respiration (which is unaffected by oxygen concentration within the range 0·2–21%), we obtain a value of 7·7 mg CO_2 $dm^{-2}hr^{-1}$ for the photorespiration rate which is similar to the estimate from the CO_2 efflux method. However, it is only half the value calculated for the flux at the CO_2 compensation concentration (Table 2) and a value calculated for soybeans using another technique (16 mg CO_2 $dm^{-2}hr^{-1}$, Samish *et al.* 1972). Both these methods attempt to make some estimate of intracellular reassimilation but, at present, it is not possible to determine if they overestimate the actual photorespiration rate.

TABLE 3

TRANSPIRATION RATIO OF FULLY EXPANDED GRASS AND LEGUME LEAVES

Values are means (±S.E.) of two measurements on two leaves of each species. Conditions: 10,000 f.c., 300±5 $\mu l\, l^{-1}$ CO_2, 31±0·5°C leaf temperature, 17·5±2·5 mmHg leaf–air vapour pressure difference. Leaf age: 6–10 days after unfolding

Species	Transpiration ratio*	Mean	Species	Transpiration ratio*	Mean
Grasses			Legumes		
P. purpureum	77·5±2·5	77·7	*C. mucunoides*	173±8·0	180
S. almum	78·2±0·6		*G. wightii*	187±6·6	

* Weight of water transpired (g) per gram of CO_2 fixed.

Because of the limitations of the various methods and the assumptions made in the calculations it is only possible to give a range (7–15 mg CO_2 $dm^{-2}hr^{-1}$) for the photorespiration rate of tropical legumes, which is about 2·5–5 times the rate of dark respiration and 25–50% of the net photosynthetic rate measured in bright light and at optimum temperature and ambient CO_2 levels (Ludlow and Wilson 1971*a*). This range is comparable with published values for other legumes (7–16 mg CO_2 $dm^{-2}hr^{-1}$: Begg and Jarvis 1968; Hofstra and Hesketh 1969; Bulley and Tregunna 1971; Hellmuth 1971; Samish *et al.* 1972), and for warm climate and temperate dicotyledons and temperate grasses (6–16 mg CO_2 $dm^{-2}hr^{-1}$: Hesketh 1967; Lake 1967; Hofstra and Hesketh 1969; Osmond, Troughton, and Goodchild 1969; Carlson *et al.* 1971).

Zelitch (1969) proposed that differences in rates of photorespiration account for differences in rates of net photosynthesis (measured in bright light, at optimum leaf temperature and at ambient CO_2 levels) between C_3 and C_4 species. This certainly does not apply to tropical grasses and tropical legumes because even when *average* net photosynthetic rates are compared (70 and 35 mg CO_2 $dm^{-2}hr^{-1}$ for grasses and legumes, respectively; Ludlow and Wilson 1971*a*, 1971*b*, 1971*c*), the difference in the rate of photorespiration between the groups (7–15 mg CO_2 $dm^{-2}hr^{-1}$) accounts for less

than half the difference in net photosynthetic rate. The remaining 20–28 mg CO_2 $dm^{-2}hr^{-1}$ is attributed to differences in intracellular resistance. In other instances such as when legumes (whose maximum rate rarely exceeds 45 mg CO_2 $dm^{-2}hr^{-1}$) are compared with grasses exhibiting rates of 100–120 mg CO_2 $dm^{-2}hr^{-1}$, the difference in photorespiration rate is of even less significance.

B. CONSEQUENCES OF DIFFERENCES IN LEAF NET PHOTOSYNTHETIC RATE

(*a*) *Growth*

In general, leaf net photosynthetic rates of tropical grasses measured under a wide range of environmental and physiological conditions are approximately twice those of tropical legumes (Ludlow and Wilson 1971*a*, 1971*b*, 1971*c*). The same applies to rates (on a leaf area basis) for whole plants when calculated from dry weight changes (Ludlow and Wilson 1970) or from gas-exchange measurements (Heslehurst and Wilson, unpublished data). Furthermore, the higher relative growth rates of grass plants arises from the greater net photosynthetic activity rather than a bigger photosynthetic system (Ludlow and Wilson 1970).

TABLE 4

TRANSPIRATION RATIOS OF GRASS AND LEGUME LEAVES AT NORMAL (21%) AND LOW (0·2%) OXYGEN CONCENTRATIONS

Conditions: 8000 f.c., 300±1 $\mu l\, l^{-1}$ CO_2, 30±0·1°C leaf temperature, 12±2 mmHg leaf–air vapour pressure difference

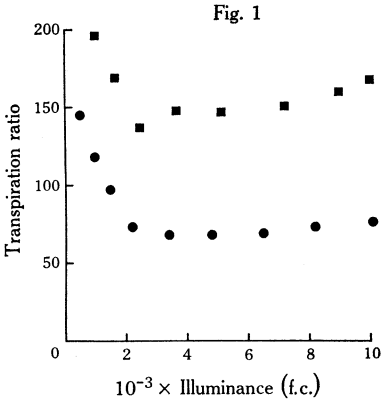
Species	Transpiration ratio*		Species	Transpiration ratio*	
	21% oxygen	0·2% oxygen		21% oxygen	0·2% oxygen
Grasses			Legumes		
B. ruziziensis	65	56	*C. mucunoides*	128	101
P. maximum cv. Hamil	72	79	*G. wightii*	119	90
P. purpureum	63	61	*P. atropurpureus*	120	89
S. almum	62	75	*V. luteola*	115	91
Mean	65	68	Mean	120	93

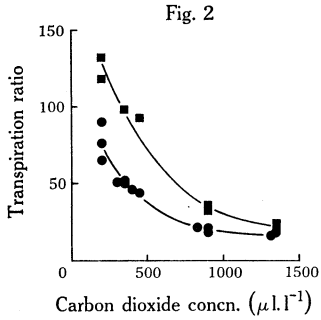
* Weight of water transpired (g) per gram of CO_2 fixed.

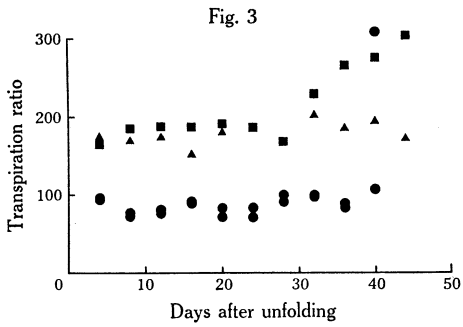
Pure grass swards have about twice the photosynthetic rate (on a leaf area basis) of pure legume swards, and Heslehurst and Wilson (1971) attributed this to superior leaf net photosynthetic characteristics. Grass swards fertilized with nitrogen also have higher crop growth rates than legume swards, arising from both higher net assimilation rates and higher leaf area indices (Stewart 1970; Heslehurst and Wilson 1971). The higher crop growth rates, and to some extent the longer growing season, result in annual dry matter yield of grass swards which are about twice those for legume swards (*c.* 20,000 versus *c.* 10,000 kg dry matter ha^{-1}: Henzell 1968; Riveros and Wilson 1970; Colman 1971; Jones, personal communication).

There appears to be a consistent relationship between the higher leaf photosynthetic rate, faster rates of growth, and higher annual dry matter yields of grass as

opposed to legume swards. However, the assimilatory rate may not always predominate in the growth of other C_4 and C_3 plants, as it does here for tropical grasses and legumes.







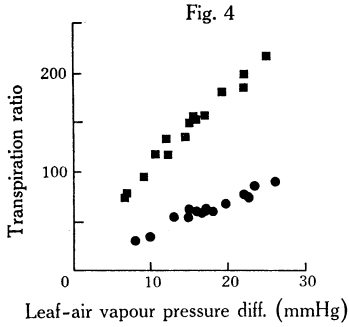


Fig. 1.—Effect of illuminance on the transpiration ratio of leaves of *C. mucunoides* (■) and *S. almum* (●). Conditions: 300±5 μl l^{-1} CO_2, 30±0·1°C leaf temperature, 17±3 mmHg leaf–air vapour pressure difference. [In Figures 1–4 transpiration ratio is expressed as grams of water transpired per gram CO_2 fixed.]

Fig. 2.—Effect of ambient CO_2 concentration on the transpiration ratio of leaves of three grasses (*P. maximum* cv. Hamil, *P. purpureum*, *S. almum*; ●) and three legumes (*C. mucunoides*, *P. atropurpureus*, *V. luteola*; ■). Conditions: 8500 f.c., 30±0·1°C leaf temperature, 17±3 mmHg leaf–air vapour pressure difference.

Fig. 3.—Relationship between leaf age and transpiration ratio of two grasses (*P. purpureum*, *S. almum*; ●) and two legumes (*C. mucunoides*, ■; *G. wightii*, ▲). Each point is the mean value for two leaves. Conditions: 10,000 f.c, 300±5 μl l^{-1} CO_2, 30±0·1°C leaf temperature, 17±3 mmHg leaf–air vapour pressure difference.

Fig. 4.—Effect of leaf–air vapour pressure difference on the transpiration ratio of leaves of *P. purpureum* (●) and *V. luteola* (■). Conditions: 9400 f.c., 300±5 μl l^{-1} CO_2, 30±0·1°C leaf temperature.

For example, Slatyer (1970) found that the lower net photosynthetic capacity of a C_3 *Atriplex* could be more than compensated by a larger leaf area and result in a higher growth rate than a C_4 *Atriplex* (see also Bull 1971).

(*b*) *Transpiration Ratio*

Grass leaves use water more efficiently than legumes (Table 3), the significantly lower transpiration ratios of grasses resulting almost entirely from higher rates of net photosynthesis (Ludlow and Wilson 1971*a*, 1971*b*, 1971*c*). This superiority is maintained over a range of illuminances (Fig. 1), at CO_2 concentrations less than 1500 μl l^{-1} (Fig. 2), at normal (21%) and low (0·2%) oxygen concentrations (Table 4), during leaf ontogeny (Fig. 3), and probably also over a range of leaf temperature

TABLE 5

EFFECT OF ILLUMINANCE AT WHICH LEAVES DEVELOPED ON THE TRANSPIRATION RATIO OF *P. MAXIMUM* AND *P. ATROPURPUREUS*

Conditions: 7000 f.c., 300±5 μl l^{-1} CO_2, 30±0·1°C leaf temperature, 17±3 mmHg leaf–area vapour pressure difference. Least significant differences (L.S.D.) at 5% level are shown

Species	Transpiration ratio* at relative illuminances of:			L.S.D.
	100	33	11	
P. maximum cv. Petrie	82	110	130	14
P. atropurpureus	151	200	244	32

* Weight of water transpired (g) per gram of CO_2 fixed.

(Downes 1970). The difference between grasses and legumes widens as leaf air vapour pressure difference increases (Fig. 4), when CO_2 concentration decreases (Fig. 2), and with age for some legumes (Fig. 3). The illuminance under which leaves develop has a pronounced effect on transpiration ratio, the ratio increasing as illuminance decreases (Table 5). On the other hand, the temperature regime during leaf development has no consistent effect.

TABLE 6

TRANSPIRATION RATIOS (AS WEIGHT OF WATER USED PER UNIT WEIGHT OF DRY MATTER PRODUCED) OF LEAVES, WHOLE PLANTS, AND SWARDS OF TROPICAL PASTURE GRASSES AND LEGUMES

	Transpiration ratios		
	Leaf*	Plant†	Sward‡
Grass	50	203	305–340
Legume	115	374	700

* Calculated from data in Table 3 assuming 1 g CO_2 = 0·64 g dry weight.

† Data for *Panicum maximum* (green panic) and *Glycine wightii* from Tow (1967).

‡ Data for *Pennisetum typhoides* and *Stylosanthes humilis* from J. E. Begg, personal communication.

Stems of both grasses and legumes used water more extravagantly than leaves because of the proportionately lower net photosynthetic rates (Ludlow and Wilson 1971*a*). Although there was considerable variation, the mean transpiration ratio of

stems was greater for legumes (av. 567; range 394–728) than for grasses (av. 278; range 134–461).

The magnitude of the difference in transpiration ratio between grasses and legumes shown here for leaves, also appears to be expressed at the plant and sward levels (Table 6). Similar differences in transpiration ratio between C_3 and C_4 plants have been reported for leaves (El-Sharkawy and Hesketh 1965; Hesketh 1968; Bull 1969; Osmond, Troughton, and Goodchild 1969; Downes 1970), and for individual plants in controlled environments (Downes 1969; Slatyer 1970) and in the field (Maximov 1929; Kato and Kamota 1969).

Thus the higher net photosynthetic rate of grass leaves compared with legumes results in lower transpiration ratios of leaves and plants, and is partly responsible via its influence on crop growth rate and dry matter yield for the lower transpiration ratio of swards in the field.

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