

Leaf Conductance in Relation to Assimilation in *Eucalyptus pauciflora* Sieb. ex Spreng

INFLUENCE OF IRRADIANCE AND PARTIAL PRESSURE OF CARBON DIOXIDE

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ABSTRACT

Rates of assimilation and transpiration in *Eucalyptus pauciflora* Sieb. ex Spreng were measured at various ambient partial pressures of CO₂ and various irradiances and were used to estimate leaf conductance and intercellular partial pressure of CO₂. The responses of leaf conductance and rate of assimilation to change in intercellular partial pressure of CO₂ were expressed in terms of feedback. They are small in the sense that their combined effect was to reduce disturbances in intercellular partial pressure of CO₂ by 30% only. The magnitude of the feedback had no influence on the system as affected by irradiance, because the direct responses of conductance and rate of assimilation to changes in irradiance in the range 0.25 to 2 millieinsteins per meter per second were such that intercellular partial pressure was maintained almost constant.

The notion of Scarth (10) that opening of stomata with increase in irradiance is due to stomatal sensitivity to reduction of partial pressure of CO₂ in the substomatal cavity has received some experimental support, particularly with *Zea mays* (8, 9). In contrast, stomata in epidermal strips of *Senecio odoris* responded to change in irradiance and not to change in partial pressure of CO₂ (7). Other experiments, both with epidermal strips (5) and with intact leaves (6), indicate that stomata respond both to changes in irradiance *per se* and to changes in partial pressure of CO₂ in the vicinity of the guard cells. It is surprising that there has been no attempt to analyze the relative roles of the two mechanisms in causing stomatal aperture to change with change in irradiance. This work aims to rectify that omission.

MATERIALS AND METHODS

Plant Material. Seeds of *Eucalyptus pauciflora* were collected from Sawpit Creek (elevation 1,215 m) in Kosciusko National Park, New South Wales, Australia. They were stratified at 4 C on moist filter paper for 30 days before germination. Seedlings were grown outdoors in spring and summer. They were brought into a glass house 1 month before the experiments. The plants were fertilized with Hoagland solution once a week. The day/night temperature regime in the glass house was 28/20 C. RH was between 50 and 60%. The plants were 8 months old at the time of the experiments.

Apparatus. Rates of transpiration of water vapor and assimilation of CO₂ were measured in a single attached leaf enclosed in a Plexiglas chamber. Illumination was provided by a water-cooled, high pressure, xenon lamp (Osram XBF 2500 W), the UV and IR components being removed with a Schott KG 2B filter. Irradiance

was varied by changing the distance of the lamp from the leaf, and by interposing copper screens having various mesh widths. Within the chamber, a fan circulated air past the leaf and through a heat exchanger supplied with water from an external temperature-controlled bath. The speed of air in the vicinity of the leaf was 7 m sec⁻¹. Mixing within the chamber as a whole was sufficiently rapid to ensure that the composition of the air was virtually uniform.

Air was passed through the chamber at a rate of 1.4 mmol sec⁻¹ (2 liter min⁻¹), monitored with a Hastings mass flow meter. It was obtained by mixing CO₂ and CO₂-free air using three sets of Wösthoff pumps (models SA 18/3, SA 27/3, and G 27/3F), and saturating the mixture at 12 C with water vapor, corresponding to 14.0 mbar vapor pressure. The partial pressures of CO₂ and water vapor in the air entering the chamber were measured with an IR analyzer (Hartmann and Braun URAS II) and a dew point hygrometer (Cambridge model 880), respectively. The same hygrometer was also used to measure the vapor pressure in the air expelled from the chamber. The difference in partial pressure of CO₂ in the ingoing and outgoing air streams was measured directly with a second IR analyzer (Beckman model 865). Leaf temperature was sensed by means of a copper-constantan thermocouple inserted into the leaf blade. The outputs of all sensors were continuously registered on a Rikadenki six-pen potentiometric recorder.

Technique. Experiments were carried out during normal photoperiods. A fully mature leaf (area 3.6 × 10⁻³ m²) was used on two successive days. The leaf temperature throughout was maintained at 25 ± 0.25 C corresponding to 30.7 ± 0.3 mbar water vapor pressure. The ambient vapor pressure deficit was between 10 and 16 mbar. Preliminary experiments showed that leaf conductance was insensitive to changes in the deficit within this range. During the 1st day of the experiment the leaf was irradiated at 0.25 and 0.96 mE m⁻² sec⁻¹, and during the second at 0.55 and 2.00 mE m⁻² sec⁻¹. At each level of irradiance the partial pressure of CO₂ in the gas supplied to the chamber was successively reduced in steps of 100 μbar from 400 to 100 μbar. The interval between each change was made sufficiently long (about 40 min) for the measured variables relating to gas exchange in the leaf to become steady. On the morning of the 2nd day one set of environmental circumstances that had been imposed during the 1st day was reproduced, in order to check that leaf characteristics had not changed.

Rate of transpiration per unit area of leaf was determined¹ as:

$$E = \frac{u(e_a - e_o)}{aP} \quad (1)$$

¹ The analysis of gas exchange is consistent with recent reviews (1, 4). The abbreviations and units used are: a (m²): leaf area (one side only); A

where u is molar flux of air through the chamber, e_a is vapor pressure in air expelled from the chamber (taken to be ambient vapor pressure), e_i is vapor pressure in gas entering the chamber, a is leaf area, and P is total air pressure. Rate of assimilation per unit leaf area was found from the analogous equation:

$$A = \frac{u(p_o - p_a)}{aP} \quad (2)$$

where p_o and p_a are the partial pressure of CO_2 in the air streams entering and leaving the chamber. To the extent that air is a mixture of approximately perfect gases the ratio p/P is identical with CO_2 concentration expressed as volume, or mole fraction. Conductance to vapor transfer was found as:

$$g = \frac{EP}{e_i - e_a} \quad (3)$$

with e_i , the vapor pressure in the intercellular spaces in the leaf, being taken as saturation vapor pressure at leaf temperature. Thus, the dimensions of g are the same as those of E , i.e. molar flux density (1, 4). As the conductance of the external boundary layer was at least 10 times the maximum magnitude of g , the conductance estimated from equation 3 was always dominated by the properties (stomatal and cuticular) of the leaf epidermes. We define it as leaf conductance. The partial pressure of CO_2 in the intercellular gas spaces was calculated as:

$$p_i = p_a - 1.6 PA/g \quad (4)$$

the numerical factor 1.6 being the ratio of the diffusivities of water vapor and CO_2 in air. As it is probable that some vapor transfer was sustained by the leaf cuticle whereas CO_2 transfer was not, there is an error inherent in the use of this relationship. Measurements of transpiration in the dark showed that cuticular conductance to vapor transfer was no more than $0.017 \text{ mol m}^{-2} \text{ sec}^{-1}$. The minimum conductance to vapor transfer determined in experiments in the light was more than 10 times greater. We calculate that p_i was overestimated by no more than $7 \mu\text{bar}$ in the worst possible case.

RESULTS

In Figure 1, p_i is plotted as a function of p_a . There is a nearly linear relationship, almost independent of irradiance. That is to say, the responses of g and A to irradiance are such that p_i is maintained nearly constant at a magnitude which increases linearly with p_a . In Figure 2, A is plotted as a function of p_i , the smooth curve being a quadratic defined by least squares regression. By substituting equation 4, A can be reexpressed as a function of g at any chosen ambient partial pressure of CO_2 , p_a . Figure 3 shows A as a function of g for $p_a = 320 \mu\text{bar}$. However g , also, is a function of p_i and I (Fig. 4). At any particular irradiance and ambient partial pressure A , g and p_i are uniquely defined. The magnitudes corresponding to $p_a = 320 \mu\text{bar}$ are indicated in Figures 2, 3, and 4. The increase of conductance with increase in irradiance is nearly sufficient to maintain p_i constant at $250 \mu\text{bar}$ (to be precise, p_i decreases from 257 to $243 \mu\text{bar}$) (Fig. 4).

The magnitudes of g and A corresponding to $p_i = 250 \mu\text{bar}$ are

($\text{mol m}^{-2} \text{ sec}^{-1}$): rate of assimilation of CO_2 per unit of leaf area; e_a (bar = 10^5 Pa): ambient vapor pressure; e_i (bar): vapor pressure in the intercellular spaces in the leaf; e_o (bar): vapor pressure in air entering the chamber; E ($\text{mol m}^{-2} \text{ sec}^{-1}$): rate of transpiration per unit of leaf area; g ($\text{mol m}^{-2} \text{ sec}^{-1}$): leaf conductance to vapor transfer; I ($\text{Em}^{-2} \text{ sec}^{-1}$): irradiance; K_A (dimensionless): gain of the opened feedback loop involving A and p_i ; K_R (dimensionless): gain of the opened feedback loop involving g and p_i ; p_a (bar): ambient partial pressure of CO_2 ; p_i (bar): partial pressure of CO_2 in the intercellular spaces; p_o (bar): partial pressure of CO_2 in air entering the chamber; P (bar): atmospheric pressure; u (mol sec^{-1}): rate of flow of air through chamber.

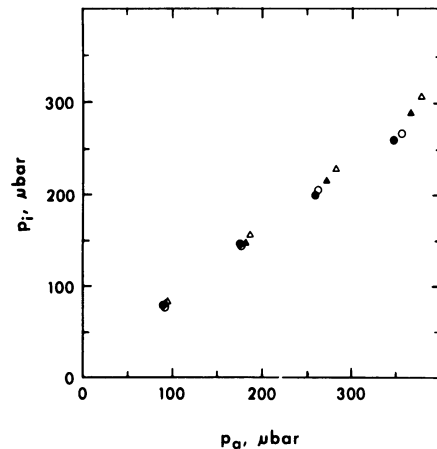


FIG. 1. Internal partial pressure of CO_2 , p_i , against ambient partial pressure of CO_2 , p_a , at four irradiances: Δ , $0.25 \text{ mEm}^{-2} \text{ sec}^{-1}$, and \circ , $0.96 \text{ mEm}^{-2} \text{ sec}^{-1}$ (imposed during 1st day of experiment); \square , $0.55 \text{ mEm}^{-2} \text{ sec}^{-1}$, and \bullet , $2 \text{ mEm}^{-2} \text{ sec}^{-1}$ (imposed during 2nd day).

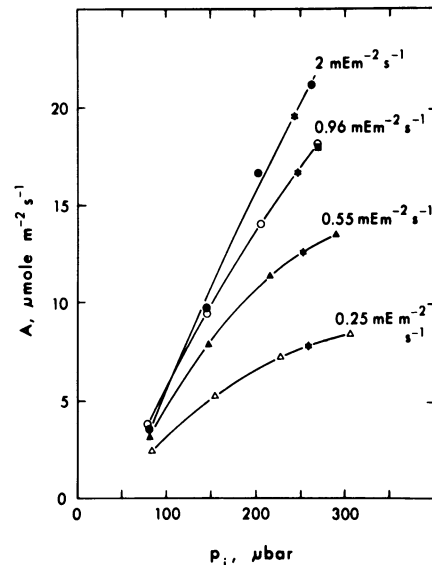


FIG. 2. Rate of assimilation, A , against internal partial pressure of CO_2 , p_i , at four irradiances, distinguished as in Figure 1. Data point shown as \star relates to $0.96 \text{ mEm}^{-2} \text{ sec}^{-1}$, but was obtained during 2nd day of experiment. Estimated values of A and p_i corresponding to $p_a = 320 \mu\text{bar}$ are indicated by \star . Smooth curves are quadratic functions obtained by least squares regression.

shown in Figure 5 as functions of irradiance. The fitted curves are hyperbolas having horizontal asymptotes at large irradiance.

ANALYSIS

Basic Relationships. We have assumed that g and A are functions of I and p_i , i.e.:

$$g = g(p_i, I) \quad (5)$$

$$A = A(p_i, I) \quad (6)$$

The interrelationships represented by equations 4, 5, and 6 are shown in Figure 6. The diagram depicts two interconnected feedback loops, the upper relating to the influence of p_i on g and the lower to the influence of p_i on A . The system may be perturbed by changes in the external variables p_a and I . Our problem is to analyze the role of feedback in the response of the system to such changes (1, 4). As the system is nonlinear we must concentrate

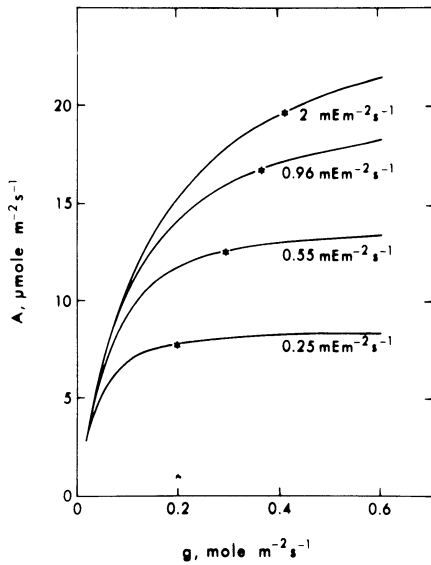


FIG. 3. Rate of assimilation, A, against leaf conductance, g. Actual values of A and g corresponding to $p_a = 320 \mu\text{bar}$ are indicated by ★. Curves represent the variation of A that would occur if g were independently perturbed.

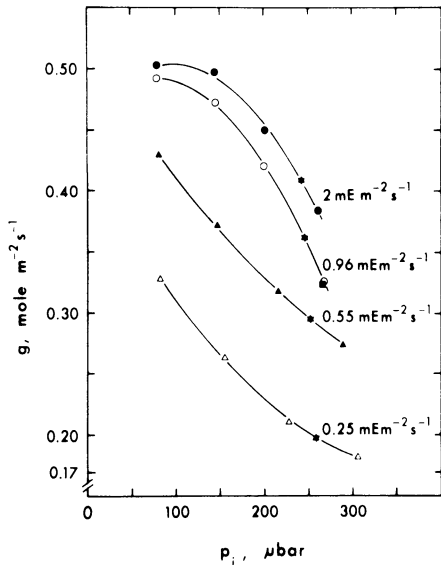


FIG. 4. Leaf conductance, g, against internal partial pressure of CO_2 , p_i , at four irradiances. Symbols have same significance as in Figure 2. Smooth curves are quadratic functions obtained by least squares regression.

attention on infinitesimal changes. Equations 4, 5, and 6 may be written:

$$dp_i = dp_a - \frac{p_a - p_i}{A} dA + \frac{p_a - p_i}{g} dg \quad (7)$$

$$dg = \left(\frac{\partial g}{\partial p_i}\right)_I dp_i + \left(\frac{\partial g}{\partial I}\right)_{p_i} dI \quad (8)$$

$$dA = \left(\frac{\partial A}{\partial p_i}\right)_I dp_i + \left(\frac{\partial A}{\partial I}\right)_{p_i} dI \quad (9)$$

The block diagram corresponding to these equations is shown in Figure 7. The coefficients $\partial g/\partial p_i$, $\partial g/\partial I$, $\partial A/\partial p_i$, and $\partial A/\partial I$ may be estimated by differentiation of the functions corresponding to the fitted curves in Figures 2, 4, and 5.

Change of p_i with Change in p_a . Using equations 8 and 9 to eliminate dg and dA from equation 7, and setting $dI = 0$, then:

$$\left(\frac{\partial p_i}{\partial p_a}\right)_I = \frac{1}{1 - K_g - K_A} \quad (10)$$

where

$$K_g = \frac{p_a - p_i}{g} \left(\frac{\partial g}{\partial p_i}\right)_I \quad (11)$$

and

$$K_A = -\frac{p_a - p_i}{A} \left(\frac{\partial A}{\partial p_i}\right)_I \quad (12)$$

The quantities K_g and K_A are the open loop gains of the feedback loops depicted in Figure 7. Their significance can best be appreciated by supposing that the output from the central summing junction in Figure 7 were severed, and that dp_i were an input independently imposed on the system. Then the outputs of the two loops (*i.e.* the signals entering the central summing junction)

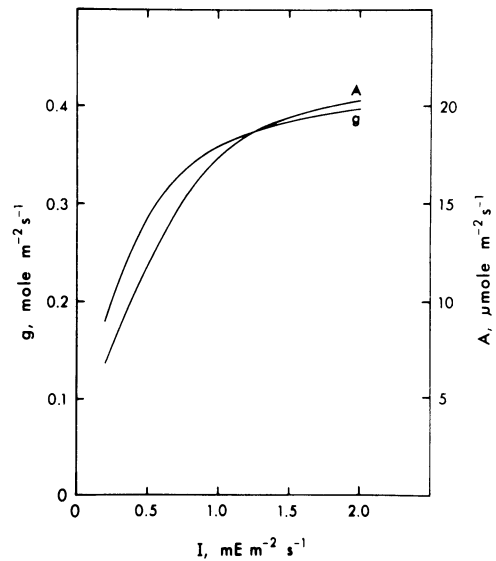


FIG. 5. Leaf conductance, g, and assimilation rate, A, as functions of irradiance with internal partial pressure of CO_2 , p_i , being $250 \mu\text{bar}$. Curves are hyperbolas having horizontal asymptotes at large irradiance.

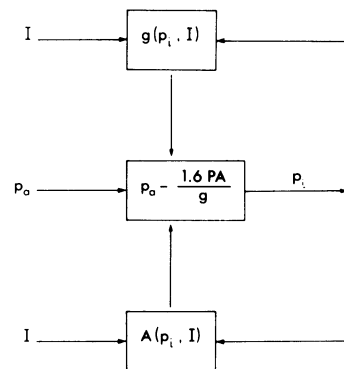


FIG. 6. Block diagram showing interrelationship between assimilation rate, A, leaf conductance, g, and irradiance, I, represented by equations 4, 5, and 6. Diagram depicts two interconnected feedback loops, the upper relating to the influence of internal partial pressure of CO_2 , p_i , on g and the lower to the influence of p_i on A. The system may be perturbed by changes in ambient partial pressure of CO_2 , p_a , and I.

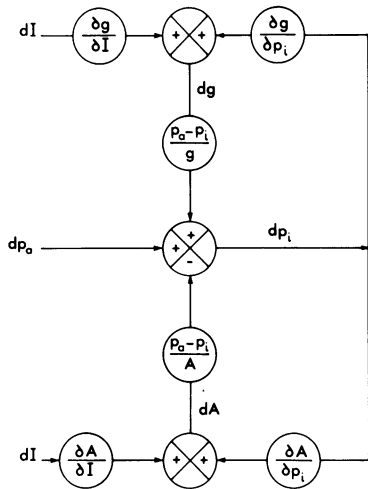


FIG. 7. Diagram showing interrelationships among assimilation rate, A, leaf conductance, g, and irradiance I, as represented by equations 7, 8, and 9. The coefficients $(p_a - p_i)/A$ and $(p_a - p_i)/g$ stem from the physical relationships among p_a , p_i , g, and A as expressed in equation 4. The coefficients $\partial g/\partial p_i$, $\partial g/\partial I$, $\partial A/\partial p_i$, and $\partial A/\partial I$ are dependent on processes in the guard cells and assimilatory tissues.

would be $K_r dp_i$ and $K_A dp_i$ for the upper and lower loops, respectively. Both of the open loop gains are negative and conspire in the intact system to reduce the change in partial pressure of CO₂ in the intercellular spaces, p_i , when the partial pressure in the ambient atmosphere, p_a , is changed. Their influence is formalized in equation 10. The magnitude of $\partial p_i/\partial p_a$ is the closed loop gain of the system. It is represented by the slope of a line drawn through the points in Figure 1 and has an average slope for all irradiances of about 0.7. Thus, the combined effects of both loops are to reduce disturbances in intercellular partial pressure of CO₂ by 30% only. The magnitudes of the closed loop gain and the open loop gains K_r and K_A at various irradiances are shown in Table I. Also shown are the quantities $1/(1 - K_r)$ and $1/(1 - K_A)$. These also are closed loop gains, being estimates of the magnitudes of $\partial p_i/\partial p_a$ that would obtain, respectively, if conductance alone and assimilation rate alone responded to change in partial pressure of CO₂.

Change of p_i with Change in I. The foregoing analysis describes the role of feedback in influencing responses to change in ambient partial pressure of CO₂, but its real significance is not in terms of change in p_a (such changes are small in the short term out-of-doors and in the remainder of our analysis p_a is taken as constant at 320 μ bar) but rather in terms of change in irradiance, I. As I increases, A tends also to increase and therefore to cause p_i to decrease. The depression in p_i is lessened because the stomata open partly as a result of the direct light response $(\partial g/\partial I)_p$ and partly as a result of the feedback response $(\partial g/\partial p_i)_I$. What are the relative roles of these two responses?

Setting $dp_a = 0$ in equation 7 and using equations 8 and 9 to eliminate dg and dA, we find:

$$\frac{dp_i}{dI} = \frac{\frac{p_a - p_i}{g} \left(\frac{\partial g}{\partial I} \right)_{p_i} - \frac{p_a - p_i}{A} \left(\frac{\partial A}{\partial I} \right)_{p_i}}{1 - K_r - K_A} \quad (13)$$

In order to evaluate this expression we need to have estimates of the partial derivatives $(\partial g/\partial I)_p$, $(\partial A/\partial I)_p$. Essentially these were obtained as slopes of the curves in Figure 5, but with appropriate allowance being made for the fact that p_i differed slightly from 250 μ bar at each particular magnitude of I.

If $(\partial g/\partial I)_p$ were zero then p_i would inevitably decrease with increase in I, however large the absolute magnitudes of K_r or K_A might be. In fact p_i does decrease with increase in I when $p_a = 320$

μ bar, as shown in Figures 2, 4, and 8. However, the decrease is small. That it is so is due to the near equality of the terms in the numerator of equation 13 (Fig. 8). The quantity dp_i/dI expressed by equation 13 is shown as curve (a). Curves (b) and (c) represent the same quantity, but with K_r and K_A , respectively, set to zero. It is evident that the feedback loops have a very small influence, only, on the functioning of the system. Curves (d) and (e) also represent dp_i/dI , but with $(\partial g/\partial I)_p$ and $(\partial A/\partial I)_p$, respectively, set to zero. Clearly the functioning of the system is dominated by the direct responses of conductance and rate of assimilation to irradiance.

Change of g and A with Change in I. Now that the quantity dp_i/dI has been evaluated the responses of g and A are readily found. From equations 8 and 9 they are:

$$\frac{dg}{dI} = \left(\frac{\partial g}{\partial I} \right)_{p_i} + \left(\frac{\partial g}{\partial p_i} \right)_{I} \frac{dp_i}{dI} \quad (14)$$

$$\frac{dA}{dI} = \left(\frac{\partial A}{\partial I} \right)_{p_i} + \left(\frac{\partial A}{\partial p_i} \right)_{I} \frac{dp_i}{dI} \quad (15)$$

They are shown as the curves (a) in Figure 9. Curves (b) and (c) represent the same quantities, but with K_r and K_A , respectively, set to zero. Again, the influence of feedback is seen to be small. Curves (d) and (e) also represent the quantities defined by equations 14 and 15, but with $(\partial g/\partial I)_p$ and $(\partial A/\partial I)_p$, respectively, set

Table I. The magnitude of various loop gains at four levels of irradiance

K_g and K_A are the open loop gains of the upper, conductance, loop and the lower, assimilation, loop depicted in Figure 7; $1/(1 - K_r)$ and $1/(1 - K_A)$ are the corresponding closed loop gains. The quantity $1/(1 - K_r - K_A)$ is an estimate of $\partial p_i/\partial p_a$, the sensitivity of internal partial pressure of CO₂ to change in ambient partial pressure of CO₂.

Loop gain	Irradiance				Mean
	0.25 (mE meter ⁻² sec ⁻¹)	0.55	0.96	2.0	
K_g	-0.14	-0.14	-0.31	-0.25	-0.21
K_A	-0.13	-0.15	-0.28	-0.37	-0.23
$1/(1 - K_g)$	0.88	0.88	0.76	0.80	0.83
$1/(1 - K_A)$	0.88	0.87	0.78	0.73	0.82
$1/(1 - K_g - K_A)$	0.79	0.78	0.63	0.62	0.70

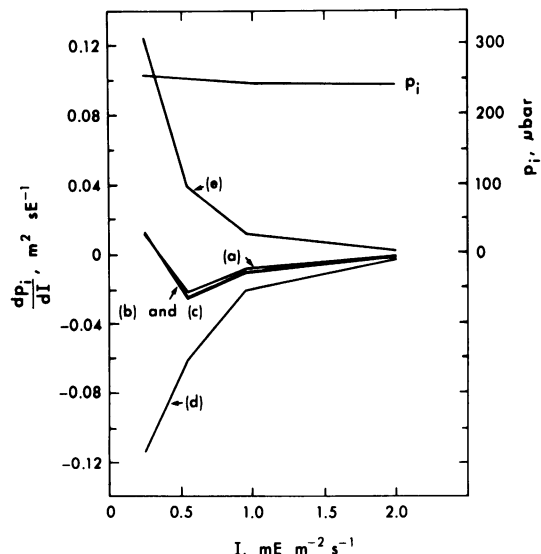


FIG. 8. Change in internal partial pressure of CO₂ with change in irradiance, plotted against irradiance. Line (a) relates to the intact leaf system and is computed using equation 13. Lines (b) and (c) are estimates which neglect the influence of internal partial pressure of CO₂ on leaf conductance and rate of assimilation, respectively. Lines (d) and (e) neglect the direct influence of irradiance on leaf conductance and rate of assimilation, respectively. Also shown are the absolute magnitudes of internal partial pressure of CO₂, p_i .

to zero. Stomatal opening with increase in irradiance is due primarily to the direct response of stomata to irradiance and increase in rate of assimilation with increase in irradiance is due primarily to the direct response of rate of assimilation to irradiance.

Figure 9 seems to imply that g has very little influence on A , for dA/dI is not much affected by setting $\partial g/\partial I = 0$. However, it is important to realize that this is because the integrated response to stomata to irradiance is so large that at each irradiance the stomata are sufficiently wide open to avoid appreciable restriction of rate of assimilation. The point is well illustrated by Figure 3.

DISCUSSION

Our analysis is based on the assumption that changes in leaf conductance were the result of stomatal responses to partial pressure of CO_2 inside the leaf and irradiance, only. The data are not inconsistent with this assumption. We have shown that leaf conductance in *E. pauciflora* increases with increase in irradiance at any fixed intercellular partial pressure of CO_2 , and decreases with increase in intercellular partial pressure of CO_2 at any fixed irradiance. The finding is similar to that of Heath and Russell (6), with wheat stomata, and numerous other workers since. However, ours is the first analysis of the relative importance of these two responses.

It has often been inferred that stomatal response to intercellular partial pressure of CO_2 is large, in the sense that it has a strong tendency, due to a process of negative feedback, to maintain intercellular partial pressure of CO_2 constant. Our results do not support this notion. The gain of the open feedback loop, K_g , was about -0.2 (varying somewhat with irradiance), corresponding to a closed loop gain of $1/(1 - K_g) = 0.83$. The stomatal response was sufficient to reduce perturbations in intercellular partial pressure of CO_2 by about only 17%. Our conclusions are relevant only to the range of irradiance 0.25 to $2 \text{ mE m}^{-2} \text{ sec}^{-1}$. Stomatal response to CO_2 may well be greater in other species, and in other plant growth conditions. We suspect that it tends to be greater in C_4 species, and it is worth noting that Farquhar *et al.* (4) found that the open loop gain in corn grown in a chamber was -3.6 . Dubbe *et al.* (3) found that the magnitude of the open loop gain increases in the presence of ABA.

A second implication of our data is that stomatal response to CO_2 had hardly any influence at all in causing leaf conductance to increase with increase in irradiance at normal ambient partial pressure of CO_2 —at least over the range of irradiance imposed in our experiment. The direct response of stomata to change in irradiance was sufficiently large to balance the influence of change in rate of assimilation and thus to maintain intercellular partial pressure of CO_2 substantially constant. It follows that the feedback loop associated with stomatal response to CO_2 was rendered inactive.

Is it fortuitous that leaf conductance and rate of assimilation should increase with irradiance in so nearly a similar fashion that the ratio of the two, and therefore intercellular partial pressure of CO_2 , is maintained almost constant? Perhaps the assumption underlying equation 5, restated at the beginning of this discussion is incorrect, and we should write:

$$g = g(p_i, I, A) \quad (16)$$

That is to say, the stomata respond not only to p_i and I but to a

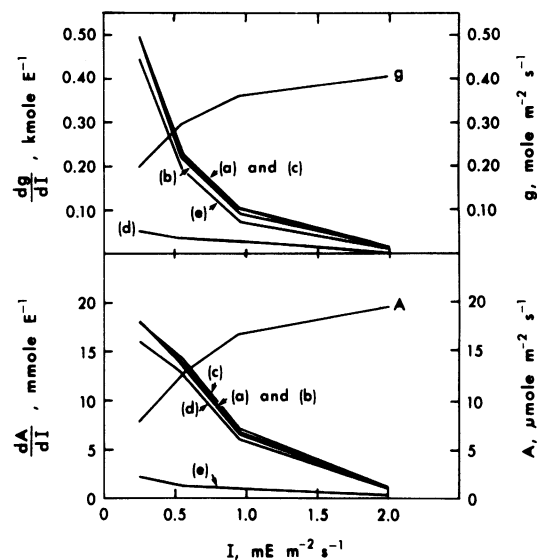


FIG. 9. Changes in leaf conductance and rate of assimilation with change in irradiance, plotted against irradiance. Line (a) relates to the intact leaf system and is computed using equations 14 and 15 in conjunction with equation 13. Lines (b) and (c) are estimates which neglect the influence of internal partial pressure of CO_2 on leaf conductance and rate of assimilation, respectively. Lines (d) and (e) neglect the direct influence of irradiance on leaf conductance and rate of assimilation, respectively. Also shown are leaf conductance, g , and assimilation rate, A , as functions of irradiance, I .

signal generated by the process of assimilation in the mesophyll and transmitted to the guard cells via the epidermis. We know of no evidence that can be invoked to discount this possibility, and indeed increasing evidence that metabolites are translocated to guard cells (2) tends to be concordant with it. It is a simple matter to take account of the implications of equation 16 in the formal description of CO_2 exchange in a leaf, but it will be a difficult problem to design experiments to test the hypothesis, let alone quantify the function in equation 16.

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