GAS EXCHANGE IN PLANT LEAVES HAVING DIFFERENT TRANSFER RESISTANCES THROUGH THEIR TWO SURFACES

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Abstract

An existing model for the internal pathways of gas exchange in anisolateral leaves is extended so as to include the feedback effects that different gas-exchange rates through the two surfaces of a leaf can have on the concentration differences driving the exchange. This "concentration effect" is analysed in detail, and graphs are presented which can be used to estimate the magnitude of error in estimates of the intracellular resistance to CO_2 uptake obtained from total leaf gas-exchange data.

In general, the concentration effect leads to underestimation of the intracellular resistance, the magnitude of this underestimation being greatest with a high degree of leaf anisolaterality, a high stomatal resistance, and a low intracellular resistance.

Measurements of the degree of anisolaterality in cotton indicate that the concentration effect will normally have significant effects on the usual estimates of intracellular resistance only if the stomatal resistance is high.

I. INTRODUCTION

Koller (1970) and Jones and Slatyer (1972a) have presented models for the internal pathways of gas exchange in leaves. These models are applicable to those leaves which have different resistances to gas exchange via their two surfaces (anisolateral leaves) when measurements are made in leaf chambers where the air passing over the two leaf surfaces is efficiently mixed. In this paper, the earlier model (Jones and Slatyer 1972a) is extended to allow its application to gas-exchange systems where the air streams passing over the two surfaces of a leaf are not well mixed during their passage over the leaf. This is commonly the case in single-leaf chambers of the opencircuit type (e.g. Bierhuizen and Slatyer 1964).

In such open-circuit chambers, the internal effects of anisolaterality (Koller 1970; Jones and Slatyer 1972*a*) influence the determination of the intracellular resistance, r_i . In addition, other errors can arise, since the rates of gas exchange through the two surfaces of such leaves are different. This leads to differences in gas concentrations over those surfaces, which in turn have feedback effects on the rates of gas exchange through the two surfaces. Overall gas-exchange measurements do not give appropriate averages in such a situation, so that resistances calculated from such measurements may be in error.

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This paper presents a theoretical treatment of this "concentration effect", and shows how factors such as degree of anisolaterality, leaf resistances, and vapour pressure differences within leaf chambers may be expected to affect estimates of r_i obtained from overall gas-exchange data. Data on the degree of anisolaterality commonly found in cotton leaves are also presented.



Fig. 1.—The models for leaf gas exchange used. (a) The transpiration pathways. (b) The CO_2 exchange pathways. (c) The transformation of the internal portion of (b).

II. THEORY

Consider a leaf chamber where the air streams over the two leaf surfaces are completely separated. The situation during steady-state water vapour exchange is illustrated in Figure 1(*a*). Typically, the incoming air stream is divided into two air streams, which then flow over the upper and lower surfaces at flow rates (cm³ s⁻¹) of v_1 and v_2 , respectively. The air streams are then remixed. The measurements of gas concentrations necessary for estimation of photosynthesis and transpiration are made on the pooled inlet and outlet air streams. The water vapour concentrations (ng cm⁻³)

 e_1 , e_2 , e_a , e_a , and e_s represent the concentrations above the leaf, below the leaf, in the inlet air stream, in the outlet air stream, and at the evaporating surfaces of the mesophyll cells respectively. The resistances to water vapour transfer (s cm⁻¹) through the upper and lower surfaces are represented by r_{g_1} and r_{g_2} , respectively. These resistances include any boundary layer and cuticular components. The corresponding transpiration rates (ng cm⁻² s⁻¹) are given by E_1 and E_2 .

In the system under consideration one can measure v_1 , v_2 , e_o , e_a , and e_s [which is assumed to equal the saturation water vapour concentration in air at the temperature of the mesophyll cells (Slatyer 1966; Jarvis and Slatyer 1970)]. Since v_1 and v_2 are generally not measured and are usually approximately equal, in the following development I shall consider the case where they are equal. I shall also assume that there is efficient stirring of the air each side of the leaf (Slatyer 1971). Another assumption is that transpiration is small compared with the volume flow rate through the chamber. The total transpiration $(E_1 + E_2)$ can be calculated from

$$E_1 + E_2 = 2v(e_a - e_o)/A,$$
 (1)

where A is the projected leaf area, and v is the flow rate over one side of the leaf. The overall estimate of the gas-phase resistance $[(r_g)^{est.}]$ is then obtained from the following form of Fick's law

$$(r_q)^{\text{est.}} = (e_s - e_a)/(E_1 + E_2).$$
 (2)

The true value of the overall gas phase resistance to water vapour $[(r_g)^{true}]$ is given by the parallel sum of r_{q_1} and r_{q_2}

$$(r_g)^{\text{true}} = (r_{g_1} r_{g_2}) / (r_{g_1} + r_{g_2}).$$
(3)

By applying the principle of continuity and Fick's law, one can write the following equations to describe the system shown in Figure 1(a):

$$E_1 = (e_s - e_1)/r_{g_1} \tag{4}$$

$$E_2 = (e_s - e_2)/r_{g_2} \tag{5}$$

$$e_1 = 2e_a - e_2 \tag{6}$$

$$E_1 = v(e_1 - e_o)/A$$
(7)

$$E_2 = v(e_2 - e_o)/A \tag{8}$$

By simple algebraic manipulation of equations 4–8 and by taking the smaller root of the resultant quadratic equation in e_2 one obtains

$$e_2 = \left[-b - (b^2 - 4ac)^{\frac{1}{2}}\right]/2a,\tag{9}$$

where

$$a = r_{g_1} - r_{g_2},$$

$$b = (e_o - e_s)(r_{g_1} + r_{g_2}) + 2e_a(r_{g_2} - r_{g_1}),$$

$$c = 2e_a e_s r_{g_1} + e_s e_o(r_{g_2} - r_{g_1}) - 2e_a e_o r_{g_2}.$$

It is now possible to obtain e_1 from equation 6, E_1 from equation 4, and E_2 from equation 5. The important value A/v can then be calculated from equations 7 or 8.

For any given set of values for e_o , e_a , e_s , r_{g_1} , and r_{g_2} the appropriate values of $(r_g)^{\text{est.}}$ and $(r_g)^{\text{true}}$ may therefore be obtained from equations 2 and 3. Therefore the error in estimates of the overall gas-phase resistance to transpiration may be estimated for any given situation.

The model used to describe the CO_2 pathway is similar to that used by Jones and Slatyer (1972*a*), though r'_{g_1} and r'_{g_2} refer to overall gas-phase resistances, including intercellular components. The model is illustrated in Figure 1(*b*), where the subscripts have the same meanings as above, *c* represents CO_2 concentrations (ng cm⁻³), *P* represents net photosynthetic rate (ng cm⁻² s⁻¹), Γ represents the CO_2 compensation concentration, and r'_{x_3} is the intercellular space resistance between upper and lower "effective sinks" (Jones and Slatyer 1972*a*). Primes are used throughout to indicate gas-phase resistances to CO_2 transfer. When applying this simplified model, care must be taken that conversion from water vapour resistances to CO_2 resistances takes account of any intercellular resistances that may occur. The assumptions involved in the internal model have been discussed in detail (Jones and Slatyer 1972*a*).

Calculation of r_i is usually from the equation

$$r_{i} = [(c_{a} - \Gamma)/P] - (r'_{g})^{\text{est.}},$$
(10)

where the symbols are as previously defined and $(c_a - \Gamma)/P$ represents the overall resistance to CO₂ uptake. This estimate of r_i , however, may be seriously in error since $(r'_g)^{\text{est.}}$ may be in error as shown above, while the overall resistance to CO₂ uptake may be similarly incorrect. In addition, one would not expect the overall resistance of an anisolateral leaf to be the simple sum of $(r'_g)^{\text{true}}$ and r_i (Jones and Slatyer 1972*a*). By the use of similar reasoning to that used above for water vapour exchange, one can estimate the error in estimates of r_i from overall gas-exchange data.

The internal portion of the model shown in Figure 1(b) may be transformed to give the network shown in Figure 1(c), where c_x , c_y , and c_z are the CO₂ concentrations at the indicated points within the network. The resistances r_a and r_c can be obtained from r_i and r'_{x_3} by means of the Delta–Wye transform (Guillemin 1953), and are given by

$$r_a = 2r_i r'_{x_3} / (4r_i + r'_{x_3}) \tag{11}$$

and

$$r_c = 4(r_i)^2 / (4r_i + r'_{x_3}).$$
⁽¹²⁾

Applying the usual transport equation and the condition of continuity to the network in Figure 1(c), one obtains the following

$$c_{z} = \Gamma + (P_{1} + P_{2})r_{c} = c_{1} - P_{1}(r'_{g_{1}} + r_{a}) = c_{2} - P_{2}(r'_{g_{2}} + r_{a}).$$
(13)

Also, as for water vapour exchange, one can write

$$P_1 = (c_o - c_1)v/A \tag{14}$$

$$P_2 = (c_o - c_2)v/A \tag{15}$$

$$c_2 = 2c_a - c_1 \tag{16}$$

From equations 11–16, one can derive the following expression for c_1 by means of suitable algebraic manipulation:

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$$c_{1} = \frac{2c_{a}[\Sigma_{1} + \Sigma_{1}\Sigma_{2}v/A - (r_{c})^{2}v/A + r_{c}] + \Gamma(\Sigma_{2} - \Sigma_{1})}{[\Sigma_{1} + \Sigma_{2} + 2\Sigma_{1}\Sigma_{2}v/A - 2(r_{c})^{2}v/A + 2r_{c}]},$$
(17)

where

and

 $\Sigma_1 = r_c + r_a + r'_{g_1}$

 $\Sigma_2 = r_c + r_a + r'_{g_2}.$

Substitution of this value for c_1 in equation 16 gives c_2 , while similar algebraic manipulation gives the following expression for c_0 :

$$c_o = A[c_1(1 + \Sigma_1 v/A) + c_2 r_c v/A - \Gamma]/[v(\Sigma_1 + r_c)]$$
(18)

which can then be evaluated. Equations 14 and 15 now give values for P_1 and P_2 after the appropriate substitution, and therefore the value of r_i estimated from overall gasexchange data $[(r_i)^{\text{est.}}]$ would then be given, using equation 10, by

$$(r_i)^{\text{est.}} = [A(c_a - \Gamma)/v(2c_o - c_1 - c_2)] - (r'_g)^{\text{est.}}$$
(19)

which can be compared with the true (i.e. assumed) value. The percentage error in $r_i(H)$ is given by

$$H = 100[(r_i)^{\text{est.}} - (r_i)^{\text{true}}]/(r_i)^{\text{true}}.$$
 (20)

For the present calculations, a value of $R(r_{g_1}/r_{g_2})$ of 1000 was used to approximate the situation in hypostomatous leaves.

The equations may be slightly simplified, since it can be shown that H is independent of the absolute values chosen for the various concentrations. This means that Γ can be replaced by zero throughout, without affecting the results. The complete equations are presented, however, for convenience.

III. MATERIALS AND METHODS

The plant material was cotton (Gossypium hirsutum L., cv. Deltapine Smoothleaf), grown in a controlled-environment cabinet. The photoperiod was 12.5 hr, at 90 W m⁻² (400–700 nm), provided by fluorescent tubes supplemented by incandescent lights. The day-night temperature regime was $30-25^{\circ}$ C, and the relative humidities were between 60 and 85%. Most measurements were made on 4-week-old plants grown in aerated Hoagland's solution, using the youngest fully expanded leaves. Some measurements were also made on soil-grown plants which had been stressed to a minimum diurnal relative water content of about 71%, for a period of 10 days, and rewatered immediately before measurement. The stress was imposed using osmotic soil cells (Painter 1966), with 5% polyethylene glycol (20M) in the external compartment. Further details are given by Jones (1972).

The gas-exchange properties of the control plants grown in solution were shown to be similar to those of control plants grown in soil.

Measurements were made of gas exchange from the two leaf surfaces, using the equipment described previously (Jones and Slatyer 1972*a*). The only difference was that the chamber insert was not used, therefore the projected leaf area was 34 cm^2 .

IV. RESULTS

(a) Theoretical Predictions

The dependence of error in overall estimates of r_i on values of the parameters involved in the present model is shown in Figures 2, 3, and 4. Only selected values are

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shown, where the variables were each altered in turn. The others were maintained at an arbitrary "standard state" where R = 3, $e_a/e_s = 0.74$ (which corresponds to a leaf-air vapour pressure deficit, at $24 \cdot 46^{\circ}$ C, of 6 mmHg), and $e_o/e_a = 0.9$. Each figure shows the effect of altering r_i , r_g , and r'_{x_3} . The error (H) in r_i is expressed throughout as a percentage of the true value.



Fig. 2.—The error (H) in estimates of r_i for various degrees of anisolaterality (R), and for different values of r_i . Each box shows the dependence of H on r'_{x_3} for r_g values of 1, 2, 4, 8, 16, and 32 s cm⁻¹ (the curves for higher resistances are omitted in some cases). The ratio e_o/e_a was maintained at 0.9 and that of e_a/e_s at 0.74.

Figure 2 illustrates the effect of R on H. As expected, the error increases with increasing anisolaterality. There is an increasing tendency to underestimate r_i as the stomatal resistance increases. Increases in r'_{x_3} from 0 to 5 s cm⁻¹ have a slight tendency



Fig. 3.—The dependence of H on the ratio of e_o/e_a . R was maintained at 3.0 and e_a/e_s at 0.74. Otherwise the figure is similar to Figure 2.

to reduce the degree of underestimation of r_i , and for high degrees of anisolaterality may even lead to a fairly large (20%) overestimation of r_i . Similar effects of changes in stomatal and intercellular resistances are observed in Figure 3 and 4. The effect on H of altering the ratio e_o/e_a is shown in Figure 3. The underestimation of r_i increases as the vapour pressure difference between the ingoing and outgoing air streams increases.

Figure 4 shows the dependence of H on the ratio of ambient to leaf vapour pressures (e_a/e_s) . The values of e_a/e_s shown represent leaf-air vapour pressure differences of approximately 3, 6, and 15 mmHg, for a leaf at 25°C. It can be seen that underestimation of r_i becomes more acute with small leaf-air vapour pressure differences. In general, variation of r'_{x_3} between 0 and 5 s cm⁻¹ has a small effect on the magnitude of error in r_i , while changes in stomatal resistance may have comparatively large effects.



Fig. 4.—The dependence of H on the ratio of e_a/e_s . R was maintained at $3 \cdot 0$ and e_o/e_a at $0 \cdot 9$. Otherwise the figure is similar to Figure 2.

(b) Cotton Anisolaterality Data

Table 1 shows the degree of anisolaterality found in cotton plants used for gas-exchange measurements in our laboratory (Jones 1972). The value of R was generally less than 3.0. For control plants 15% of the values of R were greater than

3.0, though if all the readings taken within 1 hr of placing a plant in the chamber were discounted, only 7% of the values were over 3.0. Most of the high readings were obtained from one plant. The stressed plants had significantly higher total resistances and ratios of r_{q_1}/r_{q_2} than the controls.

TABLE 1

DEGREE OF ANISOLATERALITY IN COTTON

Average values (\pm calculated standard errors) for stomatal resistances (r_g) and for the ratio of upper to lower resistances to water vapour (r_{g_1}/r_{g_2}) and CO₂ ($\Sigma r'_1/\Sigma r'_2$) for control and stressed cotton plants. Control values represent the average of 66 measurements (54 if those made in the first hour are omitted) on 10 plants, while stress values represent the average of 10 measurements on three plants

	Control plants*		Stressed
	A	В	plants
r_{g_1}/r_{g_2}	1·80 (±0·24)	1·59 (±0·51)	2·41 (±0·51)
$\Sigma r'_1 / \Sigma r'_2$	1·92 (±0·24)	1·72 (±0·47)	2·39 (±0·43)
r_{g} (s cm ⁻¹)	2·72 (±0·33)	2·50 (±0·38)	$3.6 (\pm 0.68)$

* A, averages of all measurements; B, averages, but omitting measurements made during the first hour.

There was no significant difference between the ratios of the upper to lower resistances for water vapour and CO_2 for any set of experiments. Therefore cotton does not appear to have significant anisolaterality in the intercellular pathways, though the data do not eliminate the possibility that there may be a significant intercellular space resistance to CO_2 uptake (Jones and Slatyer 1972*a*). In the absence of other evidence, however, the usual factor (K = 1.56, see McPherson 1970) has been taken as appropriate for the conversion of water vapour resistances to gas-phase CO_2 resistances.

V. DISCUSSION

This paper and the previous one (Jones and Slatyer 1972*a*) have considered only two classes of error affecting gas-exchange measurements of photosynthesis. In practice, other errors will tend to make these effects less clear-cut. For instance, Slatyer (1971) pointed out that if the chamber was not efficiently stirred the assumption that gas concentrations in the outgoing air stream represent average values over the whole leaf surface could be invalid. This effect can lead to positive or negative errors in r_i , depending on the relative values of leaf-air water vapour and CO₂ concentration differences. Commonly the effect tends to counter the anisolaterality effect described here, as long as the leaf-air vapour pressure difference is large. This effect also tends to increase with stomatal resistance. Although no good estimates for the efficiency of stirring are available, Slatyer (1971) suggested that e_o/e_a should be maintained at 0.9 or above to keep errors less than 10%.

Figure 4 suggests that leaf-air vapour pressure differences should be moderately large to reduce "concentration effect" errors, which fits with the requirements of the

above paragraph. Jarvis *et al.* (1971) suggested, however, that the leaf-air vapour pressure difference should be kept at less than 12 mmHg, and preferably less than 6 mmHg, to reduce leaf desiccation effects.

In practice, a balance must be maintained between considerations requiring large concentration differentials (such as the constraint imposed by instrument sensitivity) and the need for small concentration differentials arising from the effects mentioned above. By suitable manipulation of the conditions it may be possible to reduce the errors in r_i to low levels, if the degree of anisolaterality, and the efficiency of stirring, are known. In this context, it is particularly interesting to note that the concentration effect model presented here predicts that, in general, r_i will be underestimated in anisolateral leaves. This is in direct contrast to the predictions of the simple anisolaterality model (Koller 1970; Jones and Slatyer 1972*a*). The two models behave similarly, in that the magnitude of the error increases with decreasing r_i and with increasing r_g ; however, the effects are in opposite directions. In a typical opencircuit leaf chamber with small leaves, where separation of the two air streams is incomplete, the two opposing effects may tend to cancel out.

It is apparent from Figures 2, 3, and 4 that anisolaterality errors can be significant, even under normal leaf chamber conditions, if simple open-circuit systems are used. For cotton, however, where R is rarely greater than 3, and assuming an r_i of $3 \cdot 0$ s cm⁻¹ (Jones and Slatyer 1972b) and an r'_{x_3} of $1 \cdot 0$ s cm⁻¹ (Jones 1972), overall estimates of r_i are only likely to be more than 5% in error if stomatal resistances are greater than 8 s cm⁻¹, though the error could approach 30% if stomatal resistance is as high as 30 s cm⁻¹ (using standard leaf chamber conditions of $e_o/e_a = 0.9$ and $e_a/e_s = 0.74$). Many C₄ dicarboxylic acid pathway plants have intracellular resistances less than $1 \cdot 0$ s cm⁻¹ (Hatch *et al.* 1971), so that with the same degree of anisolaterality and similar measurement conditions, the underestimation of r_i could be as high as 30% with a stomatal resistance of only 8 s cm⁻¹. The standard conditions chosen may not necessarily be optimal but they do take into account some of the conflicting considerations mentioned above. By suitable manipulation it may be possible to further reduce these anisolaterality errors.

The model could also have relevance to photosynthetic measurements in wholeplant chambers, where the "anisolaterality" could be due to different stomatal resistances of leaves at different levels in the canopy, a phenomenon which has been demonstrated by several workers (e.g. Stevenson and Shaw 1971; Teare and Kanemasu 1972). The appropriate form of the model for such a situation is likely to be intermediate between that given by Jones and Slatyer (1972*a*), and that presented here, so that the errors would tend to cancel out. Also, other heterogeneity effects may be dominant in practice.

Although in many situations the anisolaterality errors may be negligible, for accurate work the best diffusive estimates of intracellular properties can still be obtained by means of simultaneous gas-exchange measurements for each surface of the leaf. Alternatively, anisolaterality errors may be either allowed for (by using independent estimates of R, e_o/e_a , and e_a/e_s , in conjunction with Figs. 2, 3, and 4), or else eliminated by using the "through-flow" measurement technique (Lake and Slatyer 1970).

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VI. ACKNOWLEDGMENTS

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