

RESPIRATION OF LEAVES DURING PHOTOSYNTHESIS

I. ESTIMATES FROM AN ELECTRICAL ANALOGUE

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Summary

A new analogue for the gas exchange of leaves takes account of respiratory CO₂. During light-saturated photosynthesis, the rate of respiratory CO₂ production by some dicotyledons was at least double that occurring in darkness. That this was apparently not so for three grasses, two tropical and one temperate, may be explained morphologically as well as biochemically.

I. INTRODUCTION

This paper lends new support to the possibility that respiration is greater during CO₂ assimilation than it is in darkness; "a nightmare oppressing all who are concerned with the exact measurement of photosynthesis" (Rabinowitch 1945). This possibility is important in relation to Warburg's controversial hypothesis concerning the quantum yield of the photochemical process (Good 1965), but it also has implications for the estimation of resistances to the transport of CO₂ within photosynthetic cells (Lake 1967).

Although much work still appears to support the notion that respiration rate is nearly the same in the light as in darkness (Good 1965), a current hypothesis is that dark respiration is inhibited in the light and replaced in most plants except the tropical grasses by a different respiratory process (Hoch, Owens, and Kok 1963; Ozbun, Volk, and Jackson 1964; El Sharkawy and Hesketh 1965; Forrester, Krotkov, and Nelson 1966; Tregunna 1966). The rate of this latter process has sometimes appeared much greater than the rate of dark respiration (Decker 1957, 1959; Ozbun, Volk, and Jackson 1964). However, the results of experiments in this field are often open to several conflicting interpretations (Decker 1957, 1958) and few authors have stated fully, in an algebraic form, the assumptions and method of calculation on which their own conclusions are based, although some (Hoch, Owens and Kok 1963; Forrester, Krotkov, and Nelson 1966) promise forthcoming papers to fill this gap.

Electrical analogues are of great assistance in studies of the gas exchange of leaves (Gaastra 1963; Monteith 1963) but they have not, so far, been used in the present context.† Only one existing analogue (Monteith 1963) takes account of respiration explicitly. It makes no distinction between the contributions from the tissues with and without chloroplasts and does not allow for the possibility that the respiration rate of some tissues increases with photosynthesis.

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† *Note added in proof.*—Since this paper was prepared, Moss (1966) has published an alternative electrical analogue, but he has not developed it algebraically. It is like the present one in that three different intracellular resistances are identified and it can be used to reach conclusions similar to those of the present paper.

II. THE ELECTRICAL ANALOGUE

Suppose that the photosynthetic cells (and any tissues, the respiratory CO_2 of which must pass through photosynthetic cells before escaping from the leaf), respire at a rate, B_r , per unit area circumscribed by the leaf outline, when photosynthesis is light-saturated. In the paths between the sites of this respiration, the chloroplasts, and the walls of the photosynthetic cells the mean resistances to CO_2 flux are r_{wc} , r_{rw} , and r_{rc} (Fig. 1). The dimensions of B are $\text{ML}^{-2}\text{T}^{-1}$ and those of r are L^{-1}T .

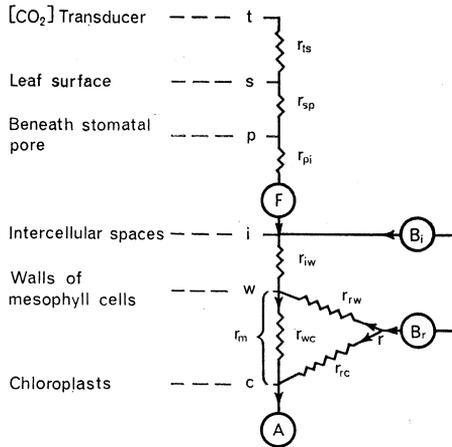


Fig. 1.—Electrical analogue of the gas exchange of a photosynthesizing leaf. Fluxes are taken as positive when they are in the directions indicated by the arrows.

Suppose, also, that the non-photosynthesizing cells release CO_2 into the intercellular spaces at a rate, B_i , per unit leaf area, independent of the concentration in those spaces. Carbon dioxide from this source must pass through a part, r_{iw} , of the mean intercellular space resistance r_{pw} before reaching the surfaces of the photosynthesizing cells. To reach the chloroplasts, it must pass through the mesophyll resistance, r_m , and in the notation of Figure 1,

$$1/r_m = 1/r_{wc} + 1/(r_{rw} + r_{rc}). \quad (1)$$

If the photosynthetic process is light-saturated and limited by the rate of supply of CO_2 , the concentration of CO_2 at the chloroplasts, c_c , may be taken as zero. Then if c_r is the mean equilibrium CO_2 concentration (dimensions ML^{-3}) at the site of release of B_r , the flux in the resistance r_{rc} is given by c_r/r_{rc} and the flux in r_{wc} is then

$$B_i + F + B_r - c_r/r_{rc} = c_w/r_{wc}, \quad (2)$$

where c_w is the mean equilibrium concentration at the surface of the mesophyll cells. The net flux of CO_2 into the leaf, F , is the rate of CO_2 uptake per unit leaf area and has the dimensions $\text{ML}^{-2}\text{T}^{-1}$. The flux in r_{rw} is

$$B_r - c_r/r_{rc} = (c_r - c_w)/r_{rw}. \quad (3)$$

Eliminating c_r and r_{wc} from (1), (2), and (3),

$$B_i + F + B_r r_{rc}/(r_{rw} + r_{rc}) = c_w/r_m. \quad (4)$$

The total resistance in the path between the transducer measuring the CO_2 concentration in the ambient air and the chloroplasts comprises aerial, stomatal, intercellular space, and mesophyll components, r_{ts} , r_{sp} , r_{pw} , and r_m . If c_t is the CO_2 concentration in the ambient air, the concentration at the site of release of B_i is $c_t - Fr_{ti}$, so that the flux in r_{tw} is

$$F + B_i = (c_t - Fr_{ti} - c_w) / r_{tw},$$

or

$$c_w = c_t - Fr_{tw} - B_i r_{tw}. \quad (5)$$

Eliminating c_w from equations (4) and (5),

$$B_i(r_m + r_{tw}) / r_m + B_r r_{rc} / (r_{rw} + r_{rc}) = [c_t - (r_{tw} + r_m)F] / r_m. \quad (6)$$

The tissues contributing to B_i usually form only a small proportion of the total leaf mass, so that B_i is small compared with B_r . The resistance r_{pw} is usually taken to be small and is included in r_{sp} or r_m by most workers (Gaastra 1963; Monteith 1963); r_{tw} can therefore be neglected compared with r_m and the coefficient of B_i taken as unity. The coefficient of $B_r \leq 1$, so we can write equation (6) in the form

$$\beta B = [c_t - (r_{tw} + r_m)F] / r_m, \quad (7)$$

where $B = B_i + B_r$ and $\beta \leq 1$.

If r_m does not vary with F and conditions are chosen such that r_{sp} remains constant, differentiation of equation (7) gives

$$r_m \beta (dB/dF) = (dc_t/dF) - r_{tw} - r_m. \quad (8)$$

If, as is usually taken to be the case, B is constant, or if it increases with F (Decker 1958) the left-hand side of equation (8) becomes ≥ 0 and

$$r_{tw} + r_m \leq dc_t/dF. \quad (9)$$

Eliminating r_m from equations (7) and (9),

$$\beta B \geq \frac{c_t - F(dc_t/dF)}{(dc_t/dF) - r_{tw}}. \quad (10)$$

III. SOME ESTIMATES OF RESPIRATION RATE

As $\beta \leq 1$, equations (7) and (10) can be used to calculate from published data minimum values of B or of the ratio B/B^* , where B^* is the rate of respiration in darkness.

Holmgren, Jarvis, and Jarvis (1965) measured light-saturated values of F and dc_t/dF with r_{sp} held constant and with c_t between 370 and 550 $\mu\text{g}/\text{l}$ (200 and 300 p.p.m. by volume at 20°C and 760 mmHg). From their Table 1 it is possible to recalculate the data they obtained for leaves of six dicotyledons. They also estimated r_{tw} from transpiration measurements, so all the terms on the right of equation (10) can be calculated from their data and minimum values of B found. These values (Table 1) exceed one-fifth of the rate of light-saturated gross photosynthesis, A , in most cases, whereas values of B^* are usually less than one-tenth of A (Gaastra 1963).

Begg and Jarvis (unpublished data) made similar observations with shoots of *Stylosanthes humilis*, but c_i was only 6 $\mu\text{g/l}$ when F was measured and varied from 6 to 160 $\mu\text{g/l}$ for the measurement of dc_i/dF . They also measured B^* and found that it appeared to depend on c_i (cf. Forrester, Krotkov, and Nelson 1966). Using their greatest value of B^* , obtained when $c_i = 9 \mu\text{g/l}$, and calculating the minimum value of B from equation (10), gives $B/B^* \geq 1.8$, i.e. the minimum rate of respiration when photosynthesis was light-saturated was nearly twice the greatest value measured in darkness.

TABLE 1

MINIMUM RATES OF LIGHT-SATURATED GROSS PHOTOSYNTHESIS AND GROSS RESPIRATION
Leaf temperature 22°C. Calculated from data of Holmgren, Jarvis, and Jarvis (1965)

Plant	Leaf	Light-saturated Gross Photosynthesis ($\text{mg dm}^{-2} \text{ hr}^{-1}$)	Gross Respiration ($\text{mg dm}^{-2} \text{ hr}^{-1}$)
<i>Populus tremula</i>	1	14.6	2.4
	2	14.0	2.2
	3	19.3	5.0
<i>Betula verrucosa</i>	1	22.8	7.4
	2	19.9	6.7
	3	19.9	5.9
<i>Quercus robur</i>	1	8.4	1.2
	2	9.2	1.7
<i>Acer platanoides</i>	1	13.2	4.4
	2	13.2	5.3
	3	5.6	0.3
<i>Lamium galeobdolon</i>	4	7.4	2.2
<i>Helianthus annuus</i>	1	47.3	11.6
	2	47.0	12.4
	3	48.6	11.0

Moss (1962) measured F_{180}/F_{550} , F_{550}/B^* , and the CO_2 compensation point, c_i ($F = 0$) or Γ , for several species. The subscripts to F indicate the values ($\mu\text{g/l}$) of c_i at which it was determined. The value of c_i used during the determination of B^* was not given.

Now, from equation (7),

$$F_{180} = (180 - r_m \beta B_{180}) / (r_{tw,180} + r_m), \quad (11)$$

where the terms with the subscript 180 may vary with c_i . When $F = 0$, equation (7) becomes

$$\Gamma = r_m \beta B_\Gamma, \quad (12)$$

where B_Γ is the respiration rate at the CO_2 compensation point. The data Moss

(1962) gives for *Acer* are not complete enough for use here, but for his other species Γ was less than 180 $\mu\text{g/l}$, so equations (11) and (12) give

$$\frac{B_r}{B^*} \geq \frac{\Gamma}{180 - \Gamma} \cdot \frac{F_{550}}{B^*} \cdot \frac{F_{180}}{F_{550}} \quad (13)$$

For the three dicotyledons, the minimum values of B_r/B^* (Table 2) agree well with the value of B/B^* found for *Stylosanthes humilis*.

TABLE 2

VALUES OF THE CO_2 COMPENSATION POINT (Γ) AND RATIO OF THE MINIMUM RATE OF RESPIRATION OF SHOOTS WHEN PHOTOSYNTHESIS WAS LIGHT-SATURATED (B_r) AND THE MEASURED RATE OF RESPIRATION IN THE DARK (B^*)
Temperature 23°C. Calculated from data of Moss (1962)

Plant	Γ ($\mu\text{g/l}$)	B_r/B^*
<i>Zea mays</i>	17	0.2
<i>Saccharum officinarum</i>	13	0.3
<i>Dactylis glomerata</i>	110	0.5
<i>Nicotiana tabacum</i>	110	2.2
<i>Pelargonium</i> sp.	120	2.7
<i>Lycopersicon esculentum</i>	138	1.9

IV. DISCUSSION

Thus for most of the dicotyledons considered, the rate of production of respiratory CO_2 during light-saturated photosynthesis has exceeded the measured or expected rate of dark respiration by a factor of two or more. Part of this effect could possibly be attributed to photo-oxidation in the experiments where very low values of c_i were used, but this was not so in the experiments of Holmgren *et al.* For species with a high value of A , the corresponding value of B also tended to be high (Table 1). However, the data do not show whether, when the respiration rate of a particular species increased compared with the dark value, it was because of a direct effect of illumination, as would be implied by the term "photorespiration" (Tregunna 1966), or because of a correlation between the rates of respiration and gross photosynthesis (Decker 1958). In either case, the effect is likely to be associated with B_r rather than with B_i .

Others who have studied photosynthesis (Hatch and Slack 1967), respiration (Tregunna 1966), or both (Forrester, Krotkov, and Nelson 1966; El Sharkawy and Hesketh 1965) have distinguished between the tropical grasses and other monocotyledons. In the present paper only minimum values of B/B^* have been calculated, so that one cannot with certainty infer from the comparison in Table 2 that there is no distinction between the tropical grasses and *Dactylis glomerata*. Nor can one be sure, from the low values obtained for all three grasses, that the process of dark respiration was inhibited in the light.

The possibility that dark respiration of both dicotyledons and grasses is inhibited in the light is strongly supported by the observation of Forrester, Krotkov, and Nelson (1966) that the value of Γ was linearly related to the concentration of oxygen in the ambient air, extrapolating to zero when the oxygen concentration was zero. B_r must also have become zero in this case [equation (12)], whereas Forrester, Krotkov, and Nelson (1966) found that in darkness respiration continued almost unimpaired at oxygen concentrations near zero. However, the corollary that the respiratory process which occurs in the light is lacking in tropical grasses is poorly supported. Equation II of Forrester, Krotkov, and Nelson (1966) can be written

$$B = \Gamma(dF/dc_t), \quad (14)$$

whereas equation (10) above gives

$$B \geq \Gamma(dF/dc_t)/[1 - r_{tw}(dF/dc_t)], \quad (15)$$

so that Forrester, Krotkov, and Nelson (1966) underestimated the rate of respiration in the light and also appeared to neglect the possibility that it may vary with the rate of photosynthesis.

Tregunna (1966) found that the increase in Γ which occurred when leaves of *Zea mays* were treated with flavin mononucleotide (FMN) was an order of magnitude greater than that calculated by assuming that FMN had no effect on B and inserting in equation (14) his measured value of the FMN-induced decrease in dF/dc_t . He therefore concluded that the FMN treatment had greatly increased B and that the leaves normally failed to respire in the light because of a lack of FMN. However, equation (14) is not an appropriate equation to use and equation (15) is only appropriate if the effect of FMN was to increase r_m . If the effect was to inhibit the photosynthetic mechanism, c_c will have risen above zero by some unknown amount and it appears difficult to draw a conclusion from the observations reported.

A simple morphological explanation for what has been observed is that in the tropical grasses, if not in all others, most of the respiratory CO_2 is trapped by the chloroplasts before it escapes from the leaf (El Sharkawy and Hesketh 1965), or as can now be written more explicitly, B_i and r_{rc} both approach zero.

This electrical analogue is appropriate not only to CO_2 but to $^{14}\text{CO}_2$. If an additional intracellular resistance is placed in the path of B_i , the analogue also becomes appropriate to oxygen and its isotopes.

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