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MESOPHYLL RESISTANCE AND CO_2 COMPENSATION CONCENTRATION IN LEAF PHOTOSYNTHESIS MODELS[1)]

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Abstract

Net CO_2 assimilation of leaves at saturating irradiance is often described as the difference between the CO_2-concentration in the intercellular spaces and the CO_2 compensation concentration, divided by a mesophyll resistance. In this paper the value of the mesophyll resistance at full light is derived directly from the biochemical properties of the carboxylating enzymes and the geometry of cell and leaf. This calculation correctly accounts for the difference between C_3 and C_4 plants and gives also values for the mesophyll resistance that are in the right order of magnitude. It appears that for cell sizes up to $1.1\ 10^{-3}$ cm and $0.4\ 10^{-3}$ cm for C_3 and C_4 plants, respectively, the CO_2-gradients within the cells are negligible, and that the disadvantage of larger cells may be overcome by vacuole formation.

The factors that govern the CO_2-compensation concentration at saturation irradiance are identified and discussed.

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List of symbols

name	meaning	dimension
a	air filled fraction	-
C	CO_2 concentration in the cell	$g\ cm^{-3}$
C_a	CO_2 concentration in ambient air	$g\ cm^{-3}$
C_i	CO_2 concentration in intercellular air spaces	$g\ cm^{-3}$
D	diffusion coefficient	$cm^2\ s^{-1}$
G	geometrical factor	-
K_c	Michaelis-Menten constant for carboxylation	$g\ cm^{-3}$
K_o	Michaelis-Menten constant for photorespiratory O_2 uptake	$g\ cm^{-3}$
L	thickness of carboxylating slab	cm
M	coefficient for the vacuole effect	-
O	oxygen concentration in cell	$g\ cm^{-3}$
P_g	gross CO_2 assimilation per leaf area	$g\ cm^{-2}\ s^{-1}$
P_n	net CO_2 assimilation per leaf area	$g\ cm^{-2}\ s^{-1}$
R_d	respiratory CO_2 dissimilation per leaf area	$g\ cm^{-2}\ s^{-1}$
R	radius of the cell	cm
R_v	radius of the vacuole	cm
r	distance from the centre of the cell	cm
r_a	boundary layer resistance	$s\ cm^{-1}$
r_c	cellular resistance	$s\ cm^{-1}$
r_m	mesophyll resistance	$s\ cm^{-1}$
r_s	leaf resistance	$s\ cm^{-1}$
S	ratio of exposed cell wall area to leaf area	-
T	leaf thickness	cm
t	photorespiratory fraction	-
V_l	cell volume per leaf area	$cm^3\ s^{-1}$
V_c	maximum velocity of carboxylation	$g\ cm^{-3}\ s^{-1}$
V_o	maximum velocity of photorespiratory O_2 uptake	$g\ cm^{-3}\ s^{-1}$
α	carboxylation coefficient	cm^{-1}
Γ	CO_2 compensation point	$g\ cm^{-3}$
ϕ	net CO_2 uptake per cell volume	$g\ cm^{-3}\ s^{-1}$
ϕ_{chl}	gross CO_2 uptake per cell volume	$g\ cm^{-3}\ s^{-1}$
ϕ_{dr}	rate of dark respiration per cell volume	$g\ cm^{-3}\ s^{-1}$
ϕ_{pr}	rate of photorespiration per cell colume	$g\ cm^{-3}\ s^{-1}$
ϕ_r	rate of respiration per cell volume	$g\ cm^{-3}\ s^{-1}$
ψ	net CO_2 uptake per cell area	$g\ cm^{-2}\ s^{-1}$

Introduction

Net CO_2-assimilation (P_n) per unit leaf area is often assumed to be the difference between gross assimilation (P_g) and respiratory CO_2-dissimilation (R_d):

$$P_n = P_g - R_d \tag{1}$$

This equation has been further elucidated by using the resistance analog to the flow of CO_2 in the assimilation process (De Wit, 1958; Gaastra, 1959; Chartier, 1966; Jarvis, 1971). Net assimilation is then represented as:

$$P_n = (C_a - C_i)/(r_a + r_s) \tag{2}$$

in which C_a and C_i are the CO_2 concentrations in the ambient air and the intercellular air spaces, and r_a and r_s the boundary layer and epidermal (stomatal) resistance against diffusion.

Similarly, the gross assimilation is here defined as

$$P_g = C_i/r_m \tag{3}$$

in which r_m is the so called mesophyll resistance for the transfer of CO_2 from the intercellular air spaces to the first biochemical products of photosynthesis. It will be shown later on that this definition is consistent with definitions that are based on net photosynthesis and compensation concentration. The magnitude of this mesophyll resistance is in general calculated as a closing entry from assimilation, r_a and r_s being estimated from concurrent leaf transpiration and temperature measurements.

Since it seems, that assimilation is also controlled by this mesophyll resistance, many attempts have been made (Chartier, 1970; Jones and Slatyer, 1972) to segregate this mesophyll resistance into a transport component in the aqueous phase from the intercellular air spaces to the sites of carboxylation and a carboxylation component. Apart from appropriate assumptions, this analysis is based on detailed studies of assimilation data in dependence of light intensity and CO_2 concentration. In general transport resistances were found to be much larger than carboxylation resistances, at least at high irradiance. However, the analysis is based on the assumption of linear first order diffusion of CO_2 in series, but the actual situation is much more diverse.

Once CO_2 has entered the cytoplasm, there is no finite distance of diffusion to the carboxylation sites, because they are distributed throughout the cytoplasm. Transport and carboxylation resistances cannot be separated in this case by assuming that both are in series. This may be otherwise for very small cells or for a distinct ordering of the chloroplasts along the cell wall, in which the so called transport resistances are minimal.

It will be shown that the mesophyll resistance is better understood by assuming at first that the carboxylation sites are uniformly distributed throughout the cytoplasm and then considering limit situations. This allows the computation of mesophyll resistances from several important morphological and biochemical characteristics of the leaves without using assimilation data and suggests further methods of experimentation and analyses.

Theory

An idealized configuration of spherical photosynthesizing cells fully surrounded by intercellular air spaces within leaves is used in this analysis (Fig. 1). This allows a description of CO_2 uptake in the cells with the following second-order differential equation

$$\phi = \frac{D}{r^2} \frac{d}{dr} \left(r^2 \frac{dC}{dr}\right) \qquad (4)$$

in which
ϕ is the net CO_2 uptake (g cm^{-3} s^{-1})
D is the diffusion coefficient (cm^2 s^{-1})
C is the CO_2 concentration (g cm^{-3})
r is the distance from the centre of the cell (cm)

In analogy of equation (1), the net CO_2 uptake is here also divided into a sink and a source term. The sink term represents the carboxylation in the chloroplasts and the source term results from at least two decarboxylation processes. First, cells carry on metabolic respiration which is identified as dark respiration and secondly there may be photorespiration which is associated with carboxylation. Therefore the net uptake of CO_2 per unit volume can be defined

$$\phi = \phi_{chl} - \phi_r \qquad (5)$$

in which ϕ_{chl} is the gross CO_2 fixation rate in the chloroplasts and ϕ_r is

$$\phi_r = \phi_{dr} + \phi_{pr} \qquad (6)$$

the rate of dark respiration plus photorespiration which are assumed to take place in the same cells.

The net assimilation rate ϕ may be eliminated from equation (4) and equation (5) if it is assumed that the chloroplasts are small and uniformly distributed, an assumption which will be considered in more detail later on. Since the value of ϕ_{chl}, the gross uptake by the chloroplasts is certainly dependent on the CO_2 concentration, it is necessary to expand this expression further. This is done here on the basis of the work by Charles-Edwards and Ludwig (1973), Peisker (1974) and Laing, Ogren and Hageman (1974), who consider the carboxylation and photorespiratory decarboxylation of C_3 plants on the biochemical level. These analyses show competitive inhibition between CO_2-fixation and photorespiration. Although differing in details, they arrive at similar expressions for assimilation and photorespiration per unit cytoplasm at high light intensity and low CO_2 concentrations. Using the symbols of Laing et al., which are most directly vizualized in biochemical terms, these are:

$$\phi_{chl} = \frac{V_c}{K_c} \quad \frac{K_o\, C}{(K_o+0)} \tag{7}$$

$$\phi_{pr} = \frac{t\, V_o\, 0}{(K_o+0)} \tag{8}$$

in which

C and 0 are the carbon dioxide and oxygen concentration at the sites of carboxylation,

V_c and K_c are the maximum enzymatic velocity of carboxylation and the Michaelis-Menten constant for carboxylation,

V_o and K_o are the similar constants for the oxygenase reaction and the constant t(=0.25) is the fraction of glycolate carbon that is released in photorespiration.

The CO_2-concentration at the site of carboxylation may be considerable different from the CO_2-concentration in the air. The O_2-concentration in the air is, however, so large that the relation between the O_2-concentration in the air and at the carboxylation sites is negligible.

In this formulation photorespiration is independent of the CO_2 concentration and assimilation proportional to the CO_2 concentration within the intercellular spaces. Because of stomatal regulation of this CO_2 concentration (Raschke, 1975), this does not imply that assimilation is also proportional to the CO_2-concentration of the air. In the case of C_4 plants, K_o is infinite, photorespiration

is then absent (eq. 8) and the term $K_o/(K_o+0)$ is one in eq. (7).

The differential equation for the spherical cells is now

$$\frac{D}{r^2}\ \frac{d}{dr}\ (r^2\ \frac{dC}{dr}) - \frac{V_c\ K_o\ C}{K_c(K_o+0)} = -\phi_{dr} - \frac{t\ V_o\ 0}{(K_o + 0)} \qquad (9)$$

The solution for a cell with radius R and a vacuole with radius R_v is obtained by assuming that at the cell surface the CO_2 concentration is equal to that in the intercellular airspace (i.e. $C_{(r=R)} = C_i$) and that at the tonoplast there is no CO_2 gradient (i.e. $(\frac{dc}{dr})_{r=R_v} = 0$).

$$C = (C_i - \Gamma)\ (\frac{\cosh(\alpha r) + M\ \sinh(\alpha r)}{\cosh(\alpha r) + M\ \sinh(\alpha r)})\ \frac{R}{r} + \Gamma \qquad (10)$$

with

$$\Gamma = \frac{(K_o + 0)}{K_o}\qquad \frac{K_c}{V_c}\qquad \phi_{dr} \qquad (11)$$

and

$$\alpha = (\ \frac{V_c\ \ K_o}{D\ K_c\ (K_o+0)}\ )^{0.5} \qquad (12)$$

and

$$M = \frac{\cosh(\alpha R_v) - \alpha R_v \sinh(\alpha R_v)}{\alpha R_v \cosh(\alpha R_v) - \sinh(\alpha R_v)} \qquad (13)$$

The net CO_2 flux ψ into the cells is given by $(D.dC/dr)_{r=R}$. The solution in g cm^{-2} s^{-1} is:

$$\psi = (C_i - \Gamma)\alpha D\ (\ \frac{\tanh(\alpha R) + M}{1 + M\tanh(\alpha R)}\ - \frac{1}{\alpha R}\ ) \qquad (14)$$

This expression may be presented by

$$\psi = (C_i - \Gamma)/r_c \qquad (15)$$

in which the cellular resistance r_c equals

$$r_c = \left(\frac{K_c (K_o+0)}{V_c D K_o} \right)^{0.5} / G \qquad (16)$$

The geometrical factor G is given by

$$G = \frac{\tanh(\alpha R)+M}{1+M \tanh(\alpha R)} - \frac{1}{\alpha R} \qquad (17)$$

G varies from zero to one, as will be discussed later.

Assuming that all cells in the leaves are equally productive, the net assimilation rate of the whole leaf is obtained by multiplying the net assimilation of the cells by the ratio S of the cell wall area exposed to the air in the intercellular space to the external leaf area, which results in

$$P_n = (C_i - \Gamma)\, S/r_c \qquad (18)$$

This equation is similar to equation (1), so that the mesophyll resistance defined in equation (3) is given by:

$$r_m = r_c/S = \left(\frac{K_c(K_o + 0)}{V_c D K_o} \right)^{0.5} / (G S) \qquad (19)$$

In this way the mesophyll resistances and CO_2-compensation points in the CO_2-dependent, but light independent range of assimilation are fully expressed in biochemical, geometrical and structural parameters which may be determined in principle independently of any direct measurement of assimilation.

Biochemical aspects

Apart from the geometrical factor, G, the mesophyll resistance is governed by the parameters: D, V_c, K_c, K_o and the oxygen concentration. For C_4-plants and for C_3-plants at near zero oxygen concentration $(K_o+0)/K_o$ vanishes or approaches one. It was calculated by Laing et al. that at normal temperatures K_o is equivalent with 29 percent oxygen in the air, so that at normal oxygen concentrations $(K_o+0)/K_o=(29+21)/29 = 1.7$. From the data of Charles-Edward and Ludwig, a value of 72 percent oxygen is calculated, so that this ratio is then 1.3. because

r_m depends only on the square root of this ratio, its value is relatively less affected by the uncertainty in the value of the constant K_o.

Since it is the purpose, to estimate r_m independently of CO_2 assimilation measurements from geometrical and biochemical data, the other constants are obtained from in vitro measurements. The diffusion coefficient is assumed to be the diffusion coefficient of CO_2 in water and equals 1.8×10^{-5} cm^2 s^{-1}. To obtain the M-M constant of carboxylation, it is assumed that ribulose diphosphate (RuDP) carboxylase catalyses the carboxylation reaction and that molecular CO_2 is the reactive substrate species. Recently Bahr and Jensen (1974) extracted from tobacco and spinach leaves RuDP carboxylase with a K value of 7.10^{-7} g cm^{-3}, which they assumed to be the active form of RuDP in vivo. Chen et al. (1971) found in vitro a maximum carboxylase rate of RuDP carboxylase extracted from C_3-plants of about 4×10^{-6} g CO_2 s^{-1} (mg chl)$^{-1}$. Assuming a chloroplyll concentration of about 7 mg cm^{-3} cytoplasm, V_c equals roughly 3.10^{-5} g CO_2 s^{-1} cm^{-3} cytoplasm.

Hence for C_3-plants, it is estimated that

$$r_m \, G \, S = \left(\frac{K_c (K_o + 0)}{V_c \, D \, K_o} \right)^{0.5} = 49 \text{ s cm}^{-1} \quad (C_3 \text{ plants}) \tag{20}$$

Since in vitro determinations of V_c are almost certainly too small compared with in vivo determinations, this is a maximum estimate. However, this is not the place to review critically methods and results of determining Michaelis-Menten constants and maximum carboxylation velocities. It suffices to state that it may be done and that there is scope for improvement of methods.

For C_4-plants it is currently hypothesized that molecular CO_2 is initially fixed into an organic acid by a reaction mediated by phosphoenol pyruvate (PEP) carboxylase (Black, 1974) which has a low K_c value. This is an obvious advantage. Maryoma et al. (1966) and Waygood et al. (1969) reported K_c values of 3.10^{-7} g cm^{-3}. Chen et al. (1971) observed again in vitro that the activity of this enzyme in C_4-plants is as high as 9×10^{-6} g CO_2 s^{-1} (mg chl)$^{-1}$. Assuming the same chlorophyll concentration as before for C_3-plants, V_c is about 6.10^{-5} g CO_2 s^{-1} cm^{-3} cytoplasm,

$$r_m G \, S = \left(\frac{K_c}{V_c \, D} \right)^{0.5} = 17 \text{ s cm}^{-1} \quad (C_4 \text{ plants}) \tag{21}$$

which is more than a factor 2 lower than for C_3-plants. Of course the value may be also too high because the in vivo maximum carboxylation rates

are also probably underestimated by in vitro determinations.

For further analyses of the geometrical factor G the value of

$$\alpha = \left(\frac{V_c \; K_o}{DK_c(K_o + 0)} \right)^{0.5} \qquad (22)$$

is also needed. Substituting the above values it is found that

$\alpha = 1.1\ 10^3\ cm^{-1}$ for C_3 plants

and $\alpha = 3.0\ 10^3\ cm^{-1}$ for C_4 plants

These are minimum values because in vitro maximum carboxylation rates are almost surely an underestimate of in vivo activity.

Cell geometry and mesophyll resistance

According to eq. 19, the mesophyll resistance of the leaf may be found by dividing the minimum cellular resistance by the product GS.

The value of S is unequivocably defined as the exposed surface of the cells per unit leaf area. Assuming that the cells of the leaves touch each other, so that the exposed and total surface of the cells are the same, its value may be derived also by multiplying the measured cell volume per unit leaf area with 3/R, since the surface-volume ratio of spheres is $4\pi R^2/(4/3\pi R^3)$. The volume (V) per unit leaf area is equal to the thickness T of the leaf times one minus the air filled fraction a, i.e.:

$$S = (3/R)V = (3/R)T(1-a) \qquad (23)$$

As for G, its general expression in equation 17, may be simplified for the case of cells with large vacuoles and for small cells.

For cells with a large vacuole, the layer of cytoplasm approaches the shape of a plane. The equation for G for a plane may be found by a series development in $(R-R_v)$ of the general expression (eq. 17) or more directly by solving eq. 4 for linear geometry. This leads to

$$G = \tanh(\alpha L) \qquad (24)$$

with L the thickness of the layer in which CO_2 can enter only at one side. For vacuolated cells L equals $R-R_v$. The simple eq. (24) is accurate within 10 percent when either R_v/R is larger than 0.9 or αR is larger than 10.

For non vacuolated cells ($R_v=0$), G is given by

$$G = \coth(\alpha R) - 1/\alpha R \qquad (25)$$

since M goes to infinity for R_v approaching zero. This relation is graphically presented in Fig. 2. For αR larger than 10, G is within 10 percent of 1. For small cell radii eq. 25 can be approximated by

$$G = \alpha R/3 \qquad (26)$$

This approximation is accurate within 10 percent for αR less than 1.2 as can be seen in Fig. 2.

Combining equation 23 and 26 it follows that for these small cells the product GS equals

$$GS = \alpha T(1-a) \qquad (27)$$

For larger cells, but at the same leaf thickness, GS is always smaller and the mesophyll resistance accordingly larger, since G in eq. 25 increases less than proportional with R. Hence eq. 27 gives the maximum value of GS for a given volume of cytoplasm per leaf area. According to El-Sharkawy and Hesketh (1965), leaf thickness is of the order of 20.10^{-3} cm for C_3 plants and 10.10^{-3} cm for C_4 plants. The air filled fraction (a) was about 0.4 for both groups of species.

The estimated minimum values for the mesophyll resistance, obtained by combining eq. 20 and 21 with eq. 27 are therefore

$r_m = 49/(1.1\ 10^3 \times 20.10^{-3} \times 0.6) = 3.7$ s cm^{-1} (C_3 plants)

$r_m = 17/(3.10^3 \times 10.10^{-3} \times 0.6) = 0.95$ s cm^{-1} (C_4 plants)

Cell radii according to El-Sharkawy and Hesketh are about $0.5\ 10^{-3}$ and $0.35\ 10^{-3}$ cm for C_3 and C_4 plants. With the previous estimates of α, αR is thus still below 1.2, so that the assumption leading to eq. 26 is satisfied.

Even though the estimated mesophyll resistances are close to the actual mesophyll resistances there are still some problems which are related to the value of S. According to eq. 23, which is implicitely used in eq. 27, the values of S are 72 and 52 for C_3 and C_4 plants, respectively. Experimental values in literature consider the area of both top and bottom external leaf surfaces, whereas assimilation rates are expressed per unit leaf area. Taking this into account, it appears from Turrell's (1936) measurement that S is 13.6 to 19.8 for shade leaves, 23.2 to 38.4 for mesomorphic leaves and 34.4 to 62.6 for xeromorphic leaves. El-Sharkawy and Hesketh found values of S ranging from 12 to 32 for C_3 plants and from 14 to 20 for C_4 plants. All these values are considerably smaller than those calculated by assuming spherical cells. Hence it could be concluded that more than half of the cell surfaces touch each other to such an extent that they are not exposed to the air. However, it may be as well that the exposed cell surface is considerably underestimated in anatomical studies because of the finite thickness of the slices that are analysed.

For values of G larger than 0.5 or αR larger than 0.8, the geometrical distribution of the chloroplasts can be improved by vacuole formation. Using the previous estimate of α, the critical cell radii correspond to $1.6\ 10^{-3}$ and $0.6\ 10^{-3}$ cm for C_3 and C_4 plants respectively, which are large compared with observed radii. However, the estimated values of α are probably too small, so that vacuole formation may be advantageous at cell radii within the observed range. The layer of cytoplasm between a large vacuole and the cell wall can be approximated as a linear system (eq. 24). If, moreover, $\alpha(R-R_v)$ is smaller than 0.5, then G is equal to $\alpha(R-R_v)$, (Fig. 2). This means that further contraction of the cytoplasm layer by vacuole formation becomes useless when the layer is thinner than $0.45\ 10^{-3}$ cm for C_3 plants and $0.17\ 10^{-3}$ cm for C_4 plants. It must be noted that this value for C_4 plants is also the thickness of the chloroplasts so that further contraction is not only useless but even impossible.

This advantage of vacuole formation is due to the efficient positioning of the available carboxylating enzymes. By just creating more enzymes and also using them in the centre of the cell, mesophyll resistance could be reduced even further. However, any advantage could be nullified by higher maintenance costs.

Discussion

The purpose of this paper is the development of methods to estimate mesophyll resistances that are independent of photosynthesis measurements. At this stage of knowledge, this can be done only approximately, but the results should be at least in the right order of magnitude. This is indeed the case.

Using the data of the previous sections, the calculated mesophyll resistances are:

$3.7\ s\ cm^{-1}$ for C_3 species and $0.95\ s\ cm^{-1}$ for C_4 species

The difference between both species is in accordance with observations, and the absolute values are only slightly too high.

However, it should be taken into account that the estimates of the maximum carboxylation velocity and the oxygen term $(K_o/(K_o+0)$ introduce considerable uncertainties. Moreover, K_o is derived from photosynthesis measurements, which is against the principle of the present approach.

The respiratory term of the net assimilation of the leaves is according to eq. 18 equal to:

(28)

$$R_d = \Gamma\ S/r_c$$

This term also contains the cellular resistance r_c. For small spherical cells, the cellular resistance is according to eqs. 16 and 26 equal to

$$r_c = \frac{3\ K_c\ (K_o+0)}{R\ V_c K_o} \tag{29}$$

so that the respiration in this case equals

$$R_d = \phi_r\ S\ R/3 = \phi_r\ T(1-a) \tag{30}$$

Only in this situation is respiration proportional to the volume T(1-a). Net assimilation, photorespiration and dark respiration may then be added to obtain gross assimilation. In general, the cellular resistance is given by eq. 16 so that the respiration equals

$$R_d = \phi_r SG\left(\frac{K_c D(K_o+0)}{V_c\ K_o}\right)^{0.5} = \phi_r\ S\ G/\alpha \tag{31}$$

Compared with the previous situation, the importance of the respiratory term is now smaller by the dimensionless factor $3G/(\alpha R)$ which reflects the internal cycling of the respiratory released CO_2 in the cell.

Although photorespiration is absent in the absence of oxygen, (equation (8)), it is not justified under these conditions to state that photorespiration of a leaf equals the difference between assimilation with and without oxygen, or to assume that dark respiration manifests itself fully under light.

Another implication of the present treatment is the interpretation of the CO_2 compensation concentration Γ in equation 11:

$$\Gamma = \frac{(K_o+0)\ K_c}{K_o\ V_c}\ (\phi_{dr} + \phi_{pr}) \tag{32}$$

This equation suggests that the CO_2 compensation concentration is not only a function of the presence or absence of photorespiration (ϕ_{pr}), but also of the biochemical properties that determine CO_2 assimilation in full light. Geometrical aspects play no role, because no transport of CO_2 is involved. The difference in compensation concentration between C_3 and C_4 plants is partly due to the difference in the ratio (K_c/V_c), but mainly a result of the presence or absence of photorespiration and through the presence or absence of the multiplication term $(K_o+0)/K_o$ of the dark respiration.

The equation signifies also that substantial differences of mesophyll resistances among cultivars attributable to biochemical characteristics should be reflected in Γ or $(\phi_{dr} + \phi_{pr})$. Moss (1971) observed CO_2 compensation points of plants grown under similar conditions and found Γ remarkably the same for genotypes within species. The carboxylating enzyme is assumed to be the same among genotypes, so that variations in $r_c (=S.r_m)$ and the constancy of Γ suggest that V_c and $(\phi_{dr} + \phi_{pr})$ vary proportionally (eq. 32). And this suggests (compare eq. 29) that dark respiration and photosynthesis under high irradiance are proportional for leaves with the same morphology.

The functional relationship between mesophyll resistance and leaf morphology (eq. 27) predicts a positive relation between maximum photosynthesis and leaf thickness, which was actually observed by Wilson and Cooper (1967) for grass leaves and also by Louwerse and Van der Zweerde (1975) for bean leaves and maize leaves. A constant value of the product of leaf thickness and mesophyll resistance implies that in case of thicker leaves, the amount of carboxylation enzymes per unit surface is increased accordingly. This increase is not necessarily reflected in an increased chlorophyll content per unit surface.

Sun and shade leaves differ in their amount of carboxylating enzymes and in their morphology. Once mature, only the biochemical composition may adapt to new conditions and this explains why r_m is not fully adapted by changing shade leaves to sunny conditions and sun leaves to shady conditions (Wassink et al., 1956; Bjorkman, 1963). In fact such experiments are a tool to distinguish structural and biochemical effects on r_m.

Finally it should be recognized that eq. 18 for the net photosynthesis of leaves has been derived without assuming a linear first order diffusion pathway. It forms the basis to determine experimentally the mesophyll resistance, the gross assimilation and the respiratory components in an unambigeous way.

References

Bahr, J.T. and R.G. Jensen, 1974: Ribulose dephosphate carboxylase from freshly ruptured spinach chloroplasts having an in vivo K_m (CO_2). Pl. Physiol. 53: 39-44.

Björkman, O. and P. Holmgren, 1963: Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. Physiol. Plant. 16, 889-914.

Black, C.C., Jr., 1973: Photosynthetic carbon fixation in relation to net CO_2 uptake. Ann. Rev. Plant Physiol. 24: 253-286.

Charles-Edwards, D.A., and L.J. Ludwig, 1974: A model for leaf photosynthesis by C_3 plants. Ann. of Bot. 38, 921-930.

Chartier, P., 1966: Étude théorique de l'assimilation brute de la feuille. Ann. Physiol. vég. 8: 167-196.

Chartier, P., 1970: A model of CO_2 assimilation in a leaf. In: Prediction and Measurement of Photosynthetic Productivity. Proceedings of the IBP/PP Technical Meeting, Trebon, 1969. Pudoc, Wageningen. pp. 307-315.

Chen, T.M., R.H. Brown and C.C. Black, Jr., 1971: Photosynthetic $^{14}CO_2$ fixation products and activities of enzymes related to photosynthesis in Bermudagrass and other plants. Pl. Physiol. 47: 199-203.

Dornhoff, G.M. and R.M. Shibles, 1970: Varietal differences in net photosynthesis of soybean leaves. Crop Sci. 10: 42-45.

El-Sharkawy, N. and J. Hesketh, 1965: Photosynthesis among species in relation to characteristics of leaf anatomy and CO_2 diffusion resistance. Crop Sci. 5: 517-521.

Gaastra, P., 1959: Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature, and stomatal diffusion resistance. Meded. Landbouw-hogesch. Wageningen, 59: 1-68.

Holmgren, P. and P.G. Jarvis, 1967: Carbon dioxide efflux from leaves in light and darkness. Physiol. Plant. 20: 1045-1051.

Jarvis, P.G., 1971: The estimation of resistances to carbon dioxide transfer. In: Z. Sestak, J. Catsky and P.G. Jarvis, eds. Plant Photosynthetic Production, Manual of Methods, W. Junk, The Hague, pp. 556-631.

Jones, H.G. and R.O. Slatyer, 1972: Estimation of the transport and carboxylation components of the intracellular limitation to leaf photosynthesis. Pl. Physiol. 50: 283-288.

Laing, W.A., W.L. Ogren and R.H. Hageman, 1974: Regulation of soybean net photosynthetic CO_2-fixation by the interaction of CO_2, O_2, and Ribulose 1,5-diphosphate carboxylase. Plant Phys. 54: 678-685.

Louwerse, W. and W. van der Zweerde: Photosynthesis, transpiration and leaf morphology in artificial and sunlight. Submitted to Photosyntetica.

Maruyama, H., R.L. Easterday, Hoei-Che Chong, and M.D. Lane, 1966: The enzymatic carboxylation of phosphoenolpyruvate. I. Purification and properties of phosphoenolpyruvate carboxylase. J. Biol. Chem. 241: 2405-2412.

Moss, D.N., 1971: Carbon dioxide compensation in plants with C_4 characteristics. In: Photosynthesis and Photorespiration, Ed. M.D. Hatch, C.B. Osmond, and R.O. Slatyer, p. 120-123.

Pearce, R.B., G.E. Carlson, D.K. Barnes, R.H. Hart, and C.H. Hanson, 1969: Specific leaf weight and photosynthesis in alfalfa. Crop Sci. 9: 423-426.

Peisker, M., 1974: A model describing the influence of oxygen on photosynthetic carboxylation. Photosynthetica 8(1), 47-50.

Wassink, E.C., S.O. Richardson and G.A. Pieters, 1956: Photosynthetic adaptation to light intensity in leaves of Acer pseudoplatanus. Acta Bot. Neerl. 5, 247-256.

Waygood, E.R., R. Noche, and C.K. Tan, 1969: Carbon dioxide, the substrate for phosphoenolpyruvate carboxylase from leaves of maize. Can. J. Bot. 47: 1455-1458.

Wilson, D. and J.P. Cooper, 1967: Assimilation of Lolium in relation to leaf mesophyll. Nature: 989-992.