An Evaluation of the Recycling in Measurements of Photorespiration

ALAIN GERBAUD* AND MARCEL ANDRE
Laboratoire de Chimie Biologique et de Photophysio-
logie, INRA 78850 Thiverval-Grignon, France (A.G.),
and Service de Radioagronomie, Centre d’Etudes
Nucleaires de Cadarache, BP 1, 13108 Saint Paul lez
Durance, France (A.G., M.A.)

ABSTRACT

All measurements of photorespiration and gross photosynthesis in
leaves, whether using isotopes or not, are underestimated because of the
recycling of O₂ or CO₂. On the basis of a simple diffusion model, we
propose a method for the calculation of the recycling and the corre-
sponding underestimation of the measurements. This procedure can be
applied when the stomatal resistance is known, and allows for a correction
of certain results in the literature. It is found that measurements of the
photorespiratory CO₂ release are usually underestimated by 20 to 100%,
which sets the estimated rate of CO₂ photorespired at 30 to 50% of the
net photosynthesis in C3 plants under normal conditions. In water stress
studies, the correction of the photorespiration is still more important
(1.5-3.3) because the stomata are closed more. Analysis of the diffusion
of O₂ shows that its recycling is low and that the underestimation of
photorespiration with ^18O₂ is negligible.

It is difficult to measure the gas exchanges of photorespiration because
they are masked by opposite photosynthetic gas exchanges which occurs
at a higher rate. Various aspects of the problem have been reviewed by
Jackson and Volk (10). One approach is to measure photorespiration by
suppressing photosynthesis, either measuring the CO₂ release in CO₂-free
air or the temporary CO₂ outburst upon darkening. Another approach is
to use isotopes, mainly ^18O₂ and ^14CO₂, which allow one to
distinguish between photosynthetic and photorespiratory gas
fluxes.

Neither of these methods enables one to distinguish between
photorespiration and the dark respiration which continues in
light. The measured fluxes are always the sum of the two proc-
esses, so that the measurements should be corrected for dark
respiration in so far as its rate in light is known.

Another drawback of these methods is that they overlook the
recycling of gas fluxes. Recycling is the phenomenon whereby
CO₂ released by photorespiration is taken up by photosynthesis
instead of leaving the leaves, or whereby O₂ released by
photosynthesis is taken up by photorespiration. The fluxes that are
recycled are 'invisible' from outside the leaf and are therefore
not measured. This results in underestimation of the measure-
ments of photorespiration and gross (or true) photosynthesis.
The occurrence of recycling has been known for years (18) but
estimates of its magnitude vary widely from zero to 100% of the
photorespiratory flux (7, 16, 18), so that it is usually disregarded.

The object of this paper is to show that recycling can be
calculated—at least a minimum estimation of it—whenever the
stomatal resistance is known. This is the case in many recent
studies where stomatal resistance is deduced from water vapor
exchange and temperature measurements and is used for the
calculation of the internal CO₂ concentration (3, 11).

A simple theory of gas exchanges, taking diffusion in account,
is presented and applied to the correction of some measurements
of gross photosynthesis and photorespiration found in the liter-
ature. The cases of ^18O₂ and ^14CO₂ practically are shown to be
quite different, as there is little recycling of O₂.

THEORY

Most measurements of gas exchanges in plants refer to the fol-
lowing principles: the plant is enclosed in a chamber and its
exchanges are calculated from the variation of gas concentra-
tion in the chamber. The plant air spaces are assumed to constitute
a homogenous gas compartment, from which CO₂ is taken up by
photosynthesis and to which it is supplied by photorespiration.
The plant internal air space is separated from the chamber
atmosphere by the epidermis; resistance to diffusion is deter-
mined by the sum of stomatal and boundary layer resistances.

Plant gas exchanges occur at two levels: between the cell
organelles and the air spaces, and between the air spaces and
the atmosphere. The problem is that the measurement of gas con-
centrations in the atmosphere allows the calculation of gas
exchanges between plant and atmosphere, which are only the
resultant of several physiological fluxes occurring inside the plant, in
which we are interested. The supplementary information given
by isotopes allows to trace back the internal gas flows, provided
that they follow a simple model.

Measurements with Carbon Isotopes. Just as the measurement of
^13CO₂ concentration with an IR gas analyzer allows one to
measure only the net CO₂ flux F (Fig. 1) from the chamber to
the plant, the measurement of ^14CO₂ with an ionization chamber
gives the net ^14CO₂ flux F*, which is in this case identical to the
gross ^14CO₂ flow, as long as there is no ^14CO₂ coming out of
the plant. This condition imposes very fast measurements because
the photosynthetic CO₂ becomes labeled after only 30 s of
photosynthesis in the presence of ^14CO₂ (16). From the gross
flow of ^14CO₂ into the plant, the total gross flow GPA of CO₂
into the plant can be deduced by a simple proportion. The value
obtained differs from the true (or gross) photosynthesis by the
amount of PR that is recycled (Fig. 1).

Usually the external concentration of the labeled CO₂, Ce*, is
low compared to the unlabeled, C, and the fluxes of ^13CO₂ are
dominant. Only the net fluxes of CO₂ into the plant, F* and F,
are measurable. A part of photorespiration contributes to the
flow of CO₂ into the chloroplasts F' through recycling and
another part is released out of the plant, although the net ^14CO₂
flux is usually into the leaf.
The law for gas diffusion can be written for each isotope

\[ F^* = \frac{(Ce^* - Ci^*)}{R} \]  

\[ F = \frac{Ce - Ci}{R}. \]  

The two isotopes encounter the same resistance to carboxylation:

\[ F'/F^* = Ci/Ci^* \]  

and in the steady state there is no accumulation of 12CO2 in the air space:

\[ F' = F + PR. \]  

With these equations one can calculate the remaining parameters using values of \( F, F^*, Ce, Ce^*, \) and \( R \) as known variables:

\[ Ci^* = Ce^* - F^* \cdot R \]  

\[ Ci = Ce - F \cdot R \]  

\[ F' = \frac{F^* \cdot Ci}{Ci^*} = \frac{F^* \cdot Ce - F \cdot R}{Ce^* - F^* \cdot R} \]  

Gross photosynthesis can be obtained by the obvious relations:

\[ GP = F^* + F' = F^* \left( 1 + \frac{Ce - F \cdot R}{Ce^* - F^* \cdot R} \right) \]  

and \( PR = GP - NP. \) Let us use \( te \) and \( ti \) as the labels for the external and internal CO2, respectively:

\[ te = \frac{Ce^*}{Ce^* + Ce}, \]  

\[ ti = \frac{Ci^*}{Ci^* + Ci}. \]  

then

\[ GP = \frac{F^*}{te}. \]  

The Usual Approximation. In many cases when \( R \) or \( ti \) are not known, the above resolution is not possible. Authors approximate \( ti \) by \( te \) and calculate approximations of \( GP \) and \( PR \) which we shall call \( GPA \) and \( PRA. \) The approximation of \( ti \) by \( te \) is equivalent to the assumption that there is no recycling: \( ti \) is less than \( te \) because of the resistance \( R \) to the diffusion between the interior and exterior spaces. Actually there would be no recycling if there were no resistance.

Equation 9 is replaced by

\[ GPA = \frac{F^*}{te}, \]  

hence

\[ PRA = \frac{F^*}{te} - NP. \]  

These equations are well known. Our interest in calculating them with reference to the exact equations 8 and 9 is that we can then recalculate \( PR \) and \( GP \) as functions of \( PRA \) and \( GPA. \) The only supplementary information needed is the value of \( R. \)

Calculation of the Corrected Values of Gross Photosynthesis and Photorespiration as Functions of the Approximated Values \( GPA \) and \( PRA. \) Comparison of equations 9 and 10 shows that

\[ GP = GPA \frac{Ce}{te}, \]  

\[ PR = GPA \frac{Ce - R \cdot NP}{Ce - R \cdot GPA}. \]  

These equations show clearly that \( PRA \) and \( GPA \) would be equal to the real values if \( R \) was zero. We shall use equations 13 and 14 for recalculating corrected values of \( PR \) and \( GP \) from the values \( PRA \) and \( GPA \) found in the literature.

Analysis of the Oxygen Exchanges. Because of the analogy between the exchanges of \( O_2 \) and \( CO_2, \) we can dispense with doing the same series of calculations again. It is enough to replace the \( CO_2 \) fluxes by the corresponding \( O_2 \) fluxes in the equations, keeping in mind that the equivalent of \( PR \) is \( GP \) and vice versa (Fig. 2), and \( NP \) is replaced by \( -NP \) because it is counted positively in the opposite direction.

Transforming equations 10 and 11 gives the values for \( O_2 \) uptake and true photosynthesis obtained by neglecting the recycling:

\[ PRA_0 = \frac{F^*_0}{te_0}, \]  

\[ GPA_0 = \frac{F^*_0}{te_0} + NP_0. \]  

and the true exchanges can be calculated by transforming equations 13 and 14:

\[ GP_0 = GPA_0 \frac{Ce_0}{Ce_0 - R \cdot PRA_0}, \]  

\[ PR_0 = PRA_0 \frac{Ce_0 + R \cdot NP_0}{Ce_0 - R \cdot PRA_0} = PRA_0 \frac{Ci_0}{Ce_0 - R \cdot PRA_0}. \]
These equations will be used to compare the errors arising from the recycling of O₂ or CO₂.

**APPLICATION**

Comparison of the Errors Due to the Recycling of O₂ and CO₂. Although the formulas for O₂ and CO₂ are almost identical, they lead to different numerical results for the correction ratios PR/PRA and PR0/PRA0, respectively, equal to Ce/(Ce - R.GPA) and Ci0/(Ce0 - R.PRA0). The main difference arises from the fact that the CO₂ concentration is small and often of the same order of magnitude as the "gradient" R.GPA (frequently around 100 𝜇L⁻¹), whereas the O₂ concentration is much larger (20% is 606 times 330 𝜇L⁻¹) and the gradient term R.PRA0 is negligible. In other words, the concentration of CO₂ limits its diffusion, but this is not the case with O₂.

For example, if we assume that the internal CO₂ concentration is 230 𝜇L⁻¹ for an external concentration of 330 𝜇L⁻¹, the gradient R.NP = 100 𝜇L⁻¹. Taking the usual ratio of 1.2 for GPA/NP, R.GPA would be 120 𝜇L⁻¹, so that the correction for photosynthesis would be 330/(330 - 120) = 1.5.

For O₂, if PRA0 is about the same as NP (2.8) and if the resistance to diffusion is approximately the same as for CO₂, we get R.PRA0 near 100 𝜇L⁻¹, but Ce is equal to 20.6% or 206000 𝜇L⁻¹ hence Ci0 = Ce0 + R.NP0 = 206100 𝜇L⁻¹ and Ci0/(Ce0 - R.PRA0) will be very near one with an error of 5%. At worst, the difference between O₂ and CO₂ fluxes can be illustrated if we represent the CO₂ and O₂ exchanges with unidirectional fluxes drawn on a realistic scale (Fig. 3). The unidirectional fluxes Fi and Fe follow the law of diffusion and are respectively equal to Ci/R and Ce/R. Their difference (Ci - Ce)/R is the net flux. If we consider that the ratio of recycling is the probability that a CO₂ molecule coming from photosynthesis is taken up in GP rather than in Fi, it is obvious that this probability is small if the unidirectional flux Fi is large. As Fi equals Ci/R, the probability of recycling is inversely related to the internal concentration. We can calculate that even in the less favorable case when the external O₂ concentration is reduced (for example to 1%), the recycling of O₂ will be negligible.

**RESULTS AND DISCUSSION**

We have applied the preceding calculations to the correction of measurements of gross photosynthesis and photorespiration found in the literature, where stomatal conductances were recorded. The data analyzed concern measurements with ^14CO₂ published by Ludwig and Canvin (17), Lawlor and Fock (14), Krampitz et al. (13), Fock et al. (5), and measurements of CO₂ evolution in CO₂ free air of Lawlor (15).

Measurements using ^14CO₂ are corrected on the basis of formulas 13 and 14:

\[ PR = \frac{PR0}{PRA0}, \]
\[ GP = \frac{GP0}{GPA0}, \]

where PR and GPA are the underestimated measurements of photorespiration and gross photosynthesis; R is the stomatal + boundary layer resistance to CO₂ diffusion, and Ce the external concentration of CO₂. Ce is usually expressed in μL/L. For homogeneity of units, R.GPA was multiplied by a conversion factor (1.4 when GPA is in mg CO₂ dm⁻² h⁻¹). Table I gives the results of the corrections. Analysis of the measurements of photorespiration in Helianthus annuus by Fock et al. (5)(not shown), gives similar results: the correction factor is around 1.6 independent of the level of CO₂ or temperature.

We also applied similar reasoning to the correction of an example of measurement of photorespiration by the CO₂ release in CO₂-free air. We took data from Lawlor (15) on wheat submitted to water stress. Since both the stomatal (c₁) and mesophyll (cₕ) conductances were given, the calculation of the correction is straightforward, because in CO₂ free air the ratio of recycled to released CO₂ flux is cₕ/cₑₑ where cₑₑ is the conductance of the stomata with the air layer. It is equal to c₁·cₑₑ/(c₁ + cₑₑ). PRA is the flux of released CO₂ and

\[ PR = \frac{PRA}{1 + cₚ/cₑₑ}. \]

The results are shown in Table II. The underestimation due to the recycling ranges from 1.15 to 3.3, which shows that recycling should rarely be considered as negligible. The accuracy of its calculation is mostly dependent on the accuracy of the diffusion resistance R, especially in the case of severe water stress, when R is large and the denominators

![Diagram of O₂ gas exchanges](image-url)
Table I. Correction of the Recycling in Measurements of Photorespiration with $^{14}$CO$_2$
Wet stress experiments were made using PEG 4000 as osmoticum.

<table>
<thead>
<tr>
<th>Type of Experiment</th>
<th>$R$</th>
<th>$NP$</th>
<th>PRA</th>
<th>GPA</th>
<th>PR</th>
<th>GP</th>
<th>CO$_2$</th>
<th>Correction Factor $(PR/PR^*)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>SUNFLOWER, $Ce$, $\mu$L</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Variation of $Ce$</td>
<td>50</td>
<td>0.68</td>
<td>1.2</td>
<td>5.8</td>
<td>7</td>
<td>6.7</td>
<td>7.9</td>
<td>49</td>
</tr>
<tr>
<td>Concentration</td>
<td>130</td>
<td>0.73</td>
<td>12</td>
<td>6.5</td>
<td>17.5</td>
<td>6.4</td>
<td>18.4</td>
<td>118</td>
</tr>
<tr>
<td>700 $\mu$E m$^{-2}$ s$^{-1}$</td>
<td>250</td>
<td>0.78</td>
<td>26</td>
<td>6</td>
<td>32</td>
<td>7</td>
<td>33</td>
<td>222</td>
</tr>
<tr>
<td>Data from Ref. 17</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SNOTFLOWER, $\Psi$, bar</td>
<td>$-6$</td>
<td>2.24</td>
<td>11.6</td>
<td>5.0</td>
<td>16.9</td>
<td>6.1</td>
<td>17.7</td>
<td>294</td>
</tr>
<tr>
<td>Water stress</td>
<td>$-9.5$</td>
<td>5.8</td>
<td>9</td>
<td>3.2</td>
<td>11.9</td>
<td>4.9</td>
<td>13.9</td>
<td>257</td>
</tr>
<tr>
<td>400 $\mu$E m$^{-2}$ s$^{-1}$</td>
<td>$-13.5$</td>
<td>6.8</td>
<td>6.5</td>
<td>3.2</td>
<td>8.3</td>
<td>4.3</td>
<td>10.8</td>
<td>268</td>
</tr>
<tr>
<td>Data from Ref. 14</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SNOTFLOWER</td>
<td>$-6$</td>
<td>2.9</td>
<td>30.8</td>
<td>8</td>
<td>39.6</td>
<td>15.8</td>
<td>46.6</td>
<td>205</td>
</tr>
<tr>
<td>Water stress</td>
<td>$-9$</td>
<td>3.6</td>
<td>24.5</td>
<td>8</td>
<td>31.7</td>
<td>15.8</td>
<td>40.3</td>
<td>205</td>
</tr>
<tr>
<td>1000 $\mu$E m$^{-2}$ s$^{-1}$</td>
<td>$-13$</td>
<td>6.8</td>
<td>12.7</td>
<td>7</td>
<td>19.8</td>
<td>16.7</td>
<td>29.4</td>
<td>210</td>
</tr>
<tr>
<td>Data from Ref. 13</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BEAN</td>
<td>$-5.5$</td>
<td>3.7</td>
<td>16.6</td>
<td>7.1</td>
<td>23.7</td>
<td>11.4</td>
<td>28</td>
<td>245</td>
</tr>
<tr>
<td>Water stress</td>
<td>$-6.4$</td>
<td>5.8</td>
<td>13.5</td>
<td>6.3</td>
<td>19.8</td>
<td>12.3</td>
<td>26.5</td>
<td>215</td>
</tr>
<tr>
<td>1000 $\mu$E m$^{-2}$ s$^{-1}$</td>
<td>$-8$</td>
<td>7.1</td>
<td>9.2</td>
<td>5.5</td>
<td>14.7</td>
<td>10.1</td>
<td>19.3</td>
<td>240</td>
</tr>
<tr>
<td>Data from Ref 15</td>
<td>$-9$</td>
<td>12.5</td>
<td>6.5</td>
<td>4.7</td>
<td>11.2</td>
<td>11.6</td>
<td>18.1</td>
<td>216</td>
</tr>
</tbody>
</table>

* $R$, stomatal + boundary layer resistance $s$-cm$^{-1}$; $NP$, net photosynthesis. All gas exchanges are in mg CO$_2$, dm$^{-2}$ h$^{-1}$; PRA, apparent photorespiration (CO$_2$ evolution calculated without correction of the recycling); GPA, apparent gross photosynthesis; PR, corrected photorespiratory CO$_2$ evolution; GP, corrected gross photosynthesis; $Ce$, external CO$_2$ concentration; $Ct$, internal CO$_2$ concentration; $\Psi$, leaf water potential.

Table II. Correction of the Recycling in Measurements in CO$_2$-Free Air

Symbols are as in Table I, except PIB, post-illumination burst; $c_s$, stomatal conductance; $c_m$, mesophyll conductance. Calculations are made with the hypothesis that the boundary layer resistance is $ra = 0.6$ s$^{-1}$ cm$^{-1}$.

The data are from wheat from Ref. 15.

<table>
<thead>
<tr>
<th>Bar</th>
<th>$c_s$</th>
<th>$c_m$</th>
<th>PIB</th>
<th>PRA</th>
<th>PR</th>
<th>Corr</th>
<th>NP</th>
</tr>
</thead>
<tbody>
<tr>
<td>$-5$</td>
<td>0.52</td>
<td>0.27</td>
<td>10.1</td>
<td>5.7</td>
<td>10</td>
<td>1.78</td>
<td>27.5</td>
</tr>
<tr>
<td>$-8$</td>
<td>0.29</td>
<td>0.23</td>
<td>8.6</td>
<td>4.6</td>
<td>9.2</td>
<td>2.0</td>
<td>21.2</td>
</tr>
<tr>
<td>$-12$</td>
<td>0.13</td>
<td>0.15</td>
<td>6.6</td>
<td>3.2</td>
<td>7.4</td>
<td>2.3</td>
<td>13</td>
</tr>
<tr>
<td>$-16$</td>
<td>0.065</td>
<td>0.072</td>
<td>4.5</td>
<td>1.7</td>
<td>3.7</td>
<td>2.2</td>
<td>4.3</td>
</tr>
</tbody>
</table>

in formulas 13 and 14 are small. Krampitz et al. (13) give standard deviations for conductance measurements. Although deviations are smaller at low water potentials where conductances are low (and resistances high), the relative deviations become very large, which causes a high relative uncertainty in the correction factors. Errors on $R$ in other conditions would cause only moderate errors on the correction factors (2.5% at $-6$ bar in Krampitz' data for sunflower). Measurements made by Ludwig and Canvin (17) appear as the least underestimated (correction factor 1.15) because of the very low boundary layer + stomatal resistance of 0.78. Minimal values of stomatal resistance found in the literature range from 0.6 to 2.2 for young plants, but the most frequent values are between 2 and 4 (12), to which should be added the value of the boundary layer resistance; this value depends on experimental conditions and common ranges from 1.8 s$^{-1}$ cm$^{-1}$ (14) to 0.6 s$^{-1}$ cm$^{-1}$ (15). The range of variation of the diffusion resistances is considerable, but the recycling varies certainly much less because it is the product R.GPA which is the variable factor in formula 14, and GPA is usually negatively correlated with $R$. Körner et al. (12) showed a linear relationship between the photosynthetic capacity of well-watered leaves and their stomatal conductance.

Measurements of the rate of CO$_2$ evolution in CO$_2$-free air suffer from similar underestimation values (Table II).

The literature offers few estimations of the recycling. Samish and Koller (18) describe a model and calculate corrections for the recycling ranging from 1.3 to 2.3. However they could not make the full calculation of the correction factor because they do not dispose of photorespiration measurements. In a later paper (19), factors of 2 to 3 are given for measurements of photorespiration in soybean by CO$_2$ evolution in CO$_2$-free air. The values are higher than ours due to higher stomatal resistances. D'Aoust and Canvin (4) have estimated, from the difference between the rate of CO$_2$ evolution measured with $^{14}$CO$_2$ and the post-illumination burst (PIB) which is little subject to recycling, that the recycling would be around 30 to 40%, but this remained hypothetical, as the PIB itself can be underestimated for other reasons. It may be noticed that the PIB gives values that are probably quite near the true rate of photorespiration.

The validity of the correction for recycling is dependent on the validity of the model for the diffusion of O$_2$ and CO$_2$ (Fig. 1). The main objection to that scheme is that it overlooks the direct recycling of dissolved gases inside the cells. This type of recycling should be added to recycling through the air spaces, which would make the underestimation of the measurements even greater. Although we do not know the internal diffusion resistances and concentrations, we can attempt to evaluate its magnitude compared with air-space recycling. The probability for a CO$_2$ molecule released from a mitochondria of reaching directly a chloroplast, instead of going to the air space, is pro-

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portional to the ratio

‘Diffusion to the air space’ resistance

‘Diffusion to the chloroplast + carboxylation’ resistance’

The following argument suggests that this ratio would not be considerable. Although diffusion through liquid is much slower than through the gas phase, this is partly compensated for CO₂ by a high solubility (due to the formation of HCO₃⁻), and distances are short, so that the carboxylation resistance would be dominant. The same argument holds for O₂: the fact that the internal concentration is nearly equilibrated with the external air means that the flux is limited by the photosynthetic capacity of the chloroplasts, not by the diffusion rate.

In spite of the number of untested assumptions involved, we shall consider that the direct recycling is small and that the error committed by neglecting it does not affect the overall validity of the calculations presented. In any case the corrections calculated are minimal ones.

CONCLUSION

A primary consequence of the proposed correction is that it increases the ratio of photorespiration (as CO₂ evolution) to net photosynthesis. Whereas 20 to 30% of NP is a commonly cited figure (1, 5, 14, 17), corrected ratios would be in the range from 30 to 50% in nonstressed conditions. These figures fit better with measurements of O₂ uptake made with ¹⁸O₂ (9) and the accepted stoichiometry of the glycolate pathway. Tolbert (20) proposed a ratio of O₂ uptake to CO₂ evolution of three, and O₂ uptake would be 80 to 100% of NP. If this O₂ uptake is composed of about 15% of dark respiration, and 65 to 85% of photorespiratory O₂ uptake, then photorespiratory CO₂ evolution would be 20 to 30% of PN. Adding 15% for dark respiration, we come to a total CO₂ evolution of 35 to 45% of PN which fits well with our evaluation of photorespiration.

It is a problem that the CO₂ evolution does not seem to vary or may even increase with the CO₂ concentration (1, 5, 17). It has been hypothesized that this is due to decrease of the recycling with increasing CO₂ concentration (1), but Table I shows that this is not the case. This is also confirmed by the analysis of the results of Fock et al. (5) (data not shown), which shows that the correction factor is not affected by the CO₂ level. As it is known that O₂ uptake increases with decreasing CO₂ concentration (2, 8), photorespiratory CO₂ evolution should vary similarly, according to the model of the glycolate pathway. It follows that at high CO₂ level there is more CO₂ evolution than predicted by the model, but less at low CO₂ level. The last point could be explained by the occurrence of other O₂ uptake reactions, such as the Mehler reaction (6).

Although the correction changes the values taken for photorespiration appreciably, and to a lesser degree the values of gross photosynthesis, it does not change very much the qualitative aspects of the response to water stress. The decrease of PR with water stress in Lawlor’s results is conserved, but the slight decrease of PR in the Kramptitz et al. (13) data is changed to a slight increase. In all cases the increase in the ratio of PR to photosynthesis cannot be due to the variation of the internal CO₂ concentration, as this is quite stable. How this ratio can be modified otherwise than through the CO₂ concentration is an open question. It can be envisioned that the dark respiration increases during stress, but it would require rates of dark respiration as high as 30% of normal net photosynthesis to explain the conservation of the CO₂ evolution when photosynthesis goes to zero. On the other hand, in water stressed plants, or whenever stomata are closed, the recycling could be considerable, causing an important underestimation of measurements of photorespiration; at the same time correction of the results becomes unfeasible because the uncertainty of values of high stomatal resistances is very large.

It appears that the problems of the measurement, as well as of the nature, of photorespiration are still far from solved.

LITERATURE CITED


4. D’Aoust AL, DT Canvin 1974 Caractéristiques du ¹³C₀₂ dégagé à la lumière et à l'obscurité par des feuilles de haricot, de radis, de tabac et de tournesol pendant et après une photosynthèse en présence de ¹³C₀₂. Physiol Veg 12: 545-556


