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An Evaluation of the Recycling in Measurements of Photorespiration

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ABSTRACT

All measurements of photorespiration and gross photosynthesis in leaves, whether using isotopes or not, are underestimated because of the recycling of O_2 or CO_2. On the basis of a simple diffusion model, we propose a method for the calculation of the recycling and the corresponding 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 CO_2 release are usually underestimated by 20 to 100%, which sets the estimated rate of CO_2 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 O_2 shows that its recycling is low and that the underestimation of photorespiration with $^{18}O_2$ is negligible.

It is difficult to measure the gas exchanges of photorespiration because they are masked by opposite photosynthetic gas exchanges which occur 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 CO_2 release in CO_2-free air or the temporary CO_2 outburst upon darkening. Another approach is to use isotopes, mainly $^{18}O_2$ and $^{14}CO_2$, 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 processes, 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 CO_2 released by photorespiration is taken up by photosynthesis instead of leaving the leaves, or whereby O_2 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 measurements 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 CO_2 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 literature. The cases of $^{18}O_2$ and $^{14}CO_2$ practically are shown to be quite different, as there is little recycling of O_2.

THEORY

Most measurements of gas exchanges in plants refer to the following principles: the plant is enclosed in a chamber and its exchanges are calculated from the variation of gas concentration in the chamber. The plant air spaces are assumed to constitute a homogenous gas compartment, from which CO_2 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 determined 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 concentrations 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 $^{12}CO_2$ concentration with an IR gas analyzer allows one to measure only the net CO_2 flux F (Fig. 1) from the chamber to the plant, the measurement of $^{14}CO_2$ with an ionization chamber gives the net $^{14}CO_2$ flux F^*, which is in this case identical to the gross $^{14}CO_2$ flow, as long as there is no $^{14}CO_2$ coming out of the plant. This condition imposes very fast measurements because the photorespiratory CO_2 becomes labeled after only 30 s of photosynthesis in the presence of $^{14}CO_2$ (16). From the gross flow of $^{14}CO_2$ into the plant, the total gross flow GPA of CO_2 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 CO_2, Ce^*, is low compared to the unlabeled, Ce, and the fluxes of $^{12}CO_2$ are dominant. Only the net fluxes of CO_2 into the plant, F^* and F, are measurable. A part of photorespiration contributes to the flow of CO_2 into the chloroplasts F' through recycling and another part is released out of the plant, although the net $^{12}CO_2$ flux is usually into the leaf.

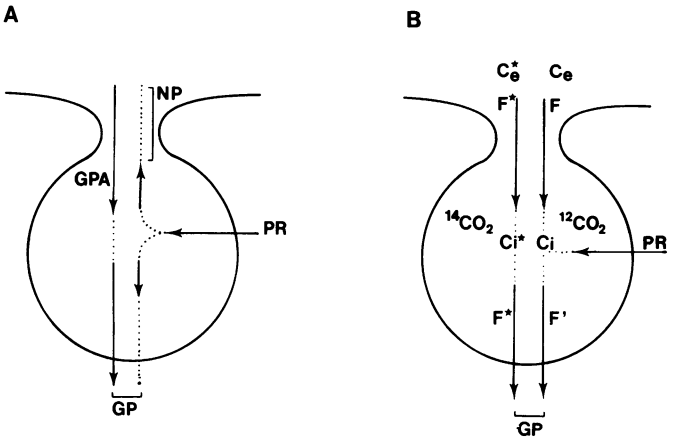

FIG. 1. Scheme of the photosynthetic CO_2 exchanges inside a leaf. A, Physiologically defined fluxes; B, physical fluxes of the isotopes. The cavity figures all internal air spaces. *PR*, photorespiration; *NP*, net photosynthesis; *GP*, gross photosynthesis; *, indicates labeled CO_2; *F*, net CO_2 flow into the leaf; *F'*, gross (or true) flow of CO_2; *Ce*, *Ci*, external and internal CO_2 concentrations. The size of the arrows is not proportional to the actual fluxes.

The law for gas diffusion can be written for each isotope

$$F^* = \frac{(Ce^* - Ci^*)}{R} \tag{1}$$

$$F = \frac{Ce - Ci}{R}. \tag{2}$$

The two isotopes encounter the same resistance to carboxylation:

$$F'/F^* = Ci/Ci^* \tag{3}$$

and in the steady state there is no accumulation of $^{12}CO_2$ in the air space:

$$F' = F + PR. \tag{4}$$

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

$$Ci^* = Ce^* - F^* \cdot R \tag{5}$$

$$Ci = Ce - F \cdot R \tag{6}$$

$$F' = \frac{F^* \cdot Ci}{Ci^*} = F^* \frac{Ce - F \cdot R}{Ce^* - F^* \cdot R} \tag{7}$$

Gross photosynthesis can be obtained by the obvious relations:

$$GP = F^* + F' = F^* \left(1 + \frac{Ce - F \cdot R}{Ce^* - F^* \cdot R}\right) \tag{8}$$

and $PR = GP - NP$. Let us use *te* and *ti* as the labels for the external and internal CO_2, respectively:

$$te = \frac{Ce^*}{Ce^* + Ce}, \qquad ti = \frac{Ci^*}{Ci^* + Ci}$$

then

$$GP = \frac{F^*}{ti}. \tag{9}$$

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

$$GPA = \frac{F^*}{te}, \tag{10}$$

hence

$$PRA = \frac{F^*}{te} - NP. \tag{11}$$

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

$$GP = GPA\ te/ti. \tag{12}$$

As the isotope concentration is very low ($Ci^* \ll Ci$), the expression of *ti* can be approximated by Ci^*/Ci. Let us replace Ci^* and *Ci* by their values from equations 5 and 6, then equation 12 can be written as:

$$GP = GPA\ te \frac{Ci}{Ci^*} = GPA\ te \frac{Ce - F \cdot R}{Ce^* - F^* \cdot R}$$

$$= GPA \frac{Ce - F \cdot R}{Ce^*/te - F^* \cdot R/te}$$

or, approximating *F* by *NP*:

$$GP = GPA \frac{Ce - R \cdot NP}{Ce - R \cdot GPA}. \tag{13}$$

In a similar way we get

$$PR = PRA \frac{Ce}{Ce - R \cdot GPA}. \tag{14}$$

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_0 and vice versa (Fig. 2), and *NP* is replaced by $-NP_0$ 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:

$$PRA_0 = \frac{F_0^*}{te_0} \tag{15}$$

$$GPA_0 = \frac{F_0^*}{te_0} + NP_0 \tag{16}$$

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

$$GP_0 = GPA_0 \frac{Ce_0}{Ce_0 - R \cdot PRA_0} \tag{17}$$

$$PR_0 = PRA_0 \frac{Ce_0 + R \cdot NP_0}{Ce_0 - R \cdot PRA_0} = PRA_0 \frac{Ci_0}{Ce_0 - R \cdot PRA_0}. \tag{18}$$

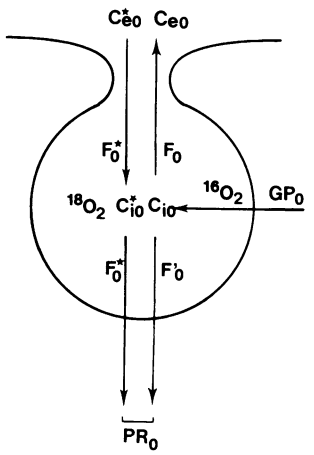

FIG. 2. Diagram of O_2 gas exchanges (indexed 0) when labeled O_2 is used, showing the equivalence with CO_2 (Fig. 1B) by substituting PR_0 for GP and GP_0 for PR.

These equations will be used to compare the errors arising from the recycling of O_2 or CO_2.

APPLICATION

Comparison of the Errors Due to the Recycling of O_2 and CO_2. Although the formulas for O_2 and CO_2 are almost identical, they lead to different numerical results for the correction ratios PR/PRA and PR_0/PRA_0, respectively, equal to $Ce/(Ce - R\cdot GPA)$ and $Ci_0/(Ce_0 - R\cdot PRA_0)$. The main difference arises from the fact that the CO_2 concentration is small and often of the same order of magnitude as the "gradient" R·GPA (frequently around 100 $\mu l\cdot L^{-1}$), whereas the O_2 concentration is much larger (20% is 606 times 330 $\mu l\cdot L^{-1}$) and the gradient term $R\cdot PRA_0$ is negligible. In other words, the concentration of CO_2 limits its diffusion, but this is not the case with O_2.

For example, if we assume that the internal CO_2 concentration is 230 $\mu l\cdot L^{-1}$ for an external concentration of 330 $\mu l\cdot L^{-1}$, the gradient R·NP is 100 $\mu l\cdot L^{-1}$. Taking the usual ratio of 1.2 for GPA/NP, $R\cdot GPA$ would be 120 $\mu l\cdot L^{-1}$, so that the correction for photorespiration would be 330/(330 − 120) = 1.5.

For O_2, if PRA_0 is about the same as NP (2, 8) and if the resistance to diffusion is approximately the same as for CO_2, we get R·PRA$_0$ near 100 $\mu l\cdot L^{-1}$, but Ce is equal to 20.6% or 206000 $\mu l\cdot L^{-1}$ hence $Ci_0 = Ce_0 + R\cdot NP_0 = 206100$ $\mu l\cdot L^{-1}$ and $Ci_0/(Ce_0 - R\cdot PRA_0)$ will be very near one with an error of 5%. At worst.

The difference between O_2 and CO_2 fluxes can be illustrated if we represent the CO_2 and O_2 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 CO_2 molecule coming from photorespiration 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 O_2 concentration is reduced (for example to 1%), the recycling of O_2 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 $^{14}CO_2$ published by Ludwig and Canvin (17), Lawlor and Fock (14), Krampitz *et al.* (13), Fock *et al.* (5), and measurements of CO_2 evolution in CO_2 free air of Lawlor (15).

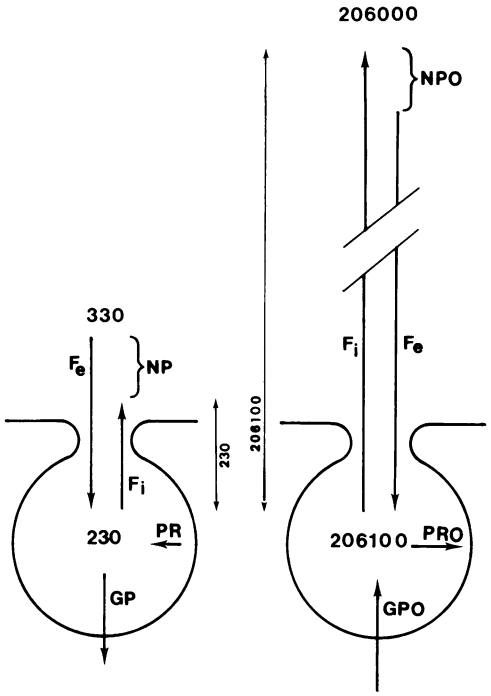

FIG. 3. Photosynthetic gas fluxes drawn at a realistic scale (for normal conditions and a C3 plant). Diffusional fluxes F_i and F_e, which are proportional to gas concentrations, are overwhelming in the case of O_2, compared to photosynthetic and photorespiratory fluxes. The consequence is that the recycling of O_2, proportional to FP_0/F_i, is negligible.

Measurements using $^{14}CO_2$ are corrected on the basis of formulas 13 and 14:

$$PR = PRA\cdot Ce/(Ce - R\cdot GPA),$$

$$GP = GPA\cdot Ci/(Ce - R\cdot GPA)$$

where PRA and GPA are the underestimated measurements of photorespiration and gross photosynthesis; R is the stomatal + boundary layer resistance to CO_2 diffusion, and Ce the outer concentration of CO_2. Ce is usually expressed in $\mu l/L$. For homogeneity of units, $R\cdot GPA$ was multiplied by a conversion factor (1.4 when GPA is in mg CO_2 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 CO_2 or temperature.

We also applied similar reasoning to the correction of an example of measurement of photorespiration by the CO_2 release in CO_2-free air. We took data from Lawlor (15) on wheat submitted to water stress. Since both the stomatal (c_s) and mesophyll (c_m) conductances were given, the calculation of the correction is straightforward, because in CO_2 free air the ratio of recycled to released CO_2 flux is c_m/c_{s+a} where c_{s+a} is the conductance of the stomata with the air layer. It is equal to $c_s\cdot c_a/(c_s + c_a)$. PRA is the flux of released CO_2 and

$$PR = PRA\ (1 + c_a/c_{s+a}).$$

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

Table I. *Correction of the Recycling in Measurements of Photorespiration with $^{14}CO_2$*[a]
Water stress experiments were made using PEG 4000 as osmoticum.

Type of Experiment		*R*	*NP*	*PRA*	*GPA*	*PR*	*GP*	CO_2	Correction Factor *(PR/PRA)*
SUNFLOWER, *Ce*, μl/L									
Variation of CO_2	50	0.68	1.2	5.8	7	6.7	7.9	49	1.15
Concentration	130	0.73	12	6.5	17.5	6.4	18.4	118	1.16
700 $\mu E \cdot m^{-2} s^{-1}$	250	0.78	26	6	32	7	33	222	1.16
Data from Ref. 17									
SUNFLOWER, Ψ, bar	−6	2.24	11.6	5.0	16.9	6.1	17.7	294	1.22
Water stress	−9.5	5.8	9	3.2	11.9	4.9	13.9	257	1.5
400 $\mu E \cdot m^{-2} s^{-1}$	−13.5	6.8	6.5	3.2	8.3	4.3	10.8	268	1.35
Data from Ref. 14									
SUNFLOWER	−6	2.9	30.8	8	39.6	15.8	46.6	205	2
Water stress	−9	3.6	24.5	8	31.7	15.8	40.3	205	2
1000 $\mu E \cdot m^{-2} s^{-1}$	−13	6.8	12.7	7	19.8	16.7	29.4	210	2.4
	−15	12.9	6.4	6.3	12.6	20.8	27.2	216	3.3
	−18	51.8	1.3	4.7	6.3	?	?	210	?
Data from Ref. 13									
BEAN	−5.5	3.7	16.6	7.1	23.7	11.4	28	245	1.6
Water stress	−6.4	5.8	13.5	6.3	19.8	12.3	26.5	215	1.9
1000 $\mu E \cdot m^{-2} s^{-1}$	−8	7.1	9.2	5.5	14.7	10.1	19.3	240	1.8
Data from Ref 13	−9	12.5	6.5	4.7	11.2	11.6	18.1	216	2.5

[a] *R*, stomatal + boundary layer resistance $s \cdot cm^{-1}$; *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; *Ci*, internal CO_2 concentration; Ψ, leaf water potential.

Table II. *Correction of the Recycling in Measurements in CO_2-Free Air*[a]
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 $ra = 0.6\ s \cdot cm^{-1}$. The data are from wheat from Ref. 15.

Bar	c_s	c_m	*PIB*	*PRA*	*PR*	Corr	*NP*
−5	0.52	0.27	10.1	5.7	10	1.78	27.5
−8	0.29	0.23	8.6	4.6	9.2	2.0	21.2
−12	0.13	0.15	6.6	3.2	7.4	2.3	13
−16	0.065	0.072	4.5	1.7	3.7	2.2	4.3

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 $s \cdot cm^{-1}$ (14) to 0.6 $s \cdot cm^{-1}$ (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 relation 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, (Table II).

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-

portional to the ratio

$$\frac{\text{'Diffusion to the air space' resistance}}{\text{'Diffusion to the chloroplast + carboxylation' resistance}}.$$

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 CO_2 by a high solubility (due to the formation of HCO_3^-), and distances are short, so that the carboxylation resistance would be dominant. The same argument holds for O_2: 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 CO_2 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 nonstress conditions. These figures fit better with measurements of O_2 uptake made with $^{18}O_2$ (9) and the accepted stoichiometry of the glycolate pathway. Tolbert (20) proposed a ratio of O_2 uptake to CO_2 evolution of three, and O_2 uptake would be 80 to 100% of *NP*. If this O_2 uptake is composed of about 15% of dark respiration, and 65 to 85% of photorespiratory O_2 uptake, then photorespiratory CO_2 evolution would be 20 to 30% of *PN*. Adding 15% for dark respiration, we come to a total CO_2 evolution of 35 to 45% of *PN* which fits well with our evaluation of photorespiration.

It is a problem that the CO_2 evolution does not seem to vary or may even increase with the CO_2 concentration (1, 5, 17). It has been hypothesized that this is due to decrease of the recycling with increasing CO_2 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 CO_2 level. As it is known that O_2 uptake increases with decreasing CO_2 concentration (2, 8), photorespiratory CO_2 evolution should vary similarly, according to the model of the glycolate pathway. It follows that at high CO_2 level there is more CO_2 evolution than predicted by the model, but less at low CO_2 level. The last point could be explained by the occurrence of other O_2 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 Krampitz *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 CO_2 concentration, as this is quite stable. How this ratio can be modified otherwise than through the CO_2 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 CO_2 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.

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