

Photosynthesis of Grass Species Differing in Carbon Dioxide Fixation Pathways¹

VI. DIFFERENTIAL EFFECTS OF TEMPERATURE AND LIGHT INTENSITY ON PHOTORESPIRATION IN C₃, C₄, AND INTERMEDIATE SPECIES

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ABSTRACT

The effects of temperature and photosynthetically active radiation levels on photorespiration were investigated in *Panicum milioides* Nees ex Trin. and *Panicum schenckii* Hack., species known to have low photorespiration rates and other characteristics intermediate between C₃ and C₄ species. Comparisons were made with the C₃ grass species tall fescue (*Festuca arundinacea* Schreb.). An increase in temperature from 20 to 35 C raised photorespiration from 7.3 to 10.2 milligrams per square decimeter per hour in tall fescue, but the increase in *P. schenckii* was less than 1 milligram per square decimeter per hour. Increases in temperature caused much less change in CO₂ compensation concentration in *P. milioides* and *P. schenckii* than in tall fescue, values of 160 microliters per liter being obtained in tall fescue at 40 C compared to about 40 microliters per liter for *P. milioides* and *P. schenckii*. Photorespiration in *P. schenckii* increased by only about 1 milligram CO₂ per square decimeter per hour as the photosynthetically active radiation level was raised from 100 to 2,000 microEinsteins per square meter per second. Loss of CO₂ into CO₂-free air actually decreased from 2.2 to 1.0 milligrams per square decimeter per hour as the radiation level was raised from 100 to 1,100 microEinsteins per square meter per second but tended to rise again at 2,000 microEinsteins per square meter per second. In contrast, photorespiration in tall fescue tripled with radiation level over the same range, reaching a maximum value of 7.2 milligrams per square decimeter per hour as determined by extrapolation of the CO₂ response curves to zero CO₂. The CO₂ compensation concentration in tall fescue was nearly insensitive to photosynthetically active radiation above 140 microEinsteins per square meter per second but, in *P. milioides* and *P. schenckii*, it decreased from values of 69 and 62 microliters per liter, respectively, to values of 21 and 16 as the radiation level was increased from 50 to 1075 microEinsteins per square meter per second. Interpolation of CO₂-response curves showed that an increase in photosynthetically active radiation level from 100 to 2,000 microEinsteins per square meter per second reduced the CO₂ compensation value of *P. schenckii* from 38 to 19 microliters per liter. Data from these experiments indicate reduced photorespiration or a CO₂-recycling mechanism in *P. milioides* and *P. schenckii* which causes apparent photorespiration to be nearly insensitive to temperature in the 20 to 35 C range and to decrease at high radiation intensities.

reduction in carboxylation of RuBP because O₂ competes with CO₂ for carboxylation sites and (b) the production and oxidation of glycolate to produce CO₂ (13, 21). This oxidation of glycolate and resulting loss of CO₂ is known as PR. The PR component of O₂ inhibition of AP appears to be the smaller of the two. Ku and Edwards (10) estimated that PR made up a larger proportion of O₂ inhibition in wheat as temperature was increased from 25 to 35 C but, even at the higher temperature, it constituted less than 30% of the total inhibition at 300 μl l⁻¹ of CO₂. Ludwig and Canvin (14) found that PR accounted for one-third of the inhibition of AP by 21% O₂ in sunflower.

Increases in temperature cause PR to rise in C₃ species as shown by CO₂ loss in CO₂-free air in the light (7), extrapolation of CO₂-response curves to zero CO₂ concentration (10), and the postillumination CO₂ burst (6). The increase in PR was attributed by Ku and Edwards (10) to an increase in the solubility ratio of O₂/CO₂, but Laing *et al.* (13) reported a decreased affinity of RuBP carboxylase for CO₂ and an increased affinity for O₂ as temperature increased. Increases in PR with increased light intensity would be expected through its effects on RuBP regeneration (4) and from the current views on the mechanism of action of RuBP carboxylase/oxygenase (13). Stimulation of PR by light intensity has been shown by the techniques mentioned above for temperature effects (6, 20). Increases in PR at high temperatures are accompanied by steep increases in Γ, whereas light intensity above the compensation point has very little effect on Γ (6, 20).

Panicum milioides, *Panicum schenckii*, and *Panicum decipiens* have been shown to exhibit less O₂ inhibition of AP by 21% O₂ than C₃ species (1, 2, 8, 11, 15). This reduced O₂ inhibition has been ascribed to low photorespiration rates rather than reduced O₂ sensitivity of carboxylation efficiency (2, 15). Photorespiration estimated from the extrapolation of the CO₂-response curves of AP was low and nearly insensitive to O₂ in *P. milioides* and *P. schenckii*, whereas the slope of the CO₂-response curve (carboxylation efficiency) was reduced by a similar amount in the two *Panicum* species and tall fescue, a C₃ species (2). The similar reduction in carboxylation efficiency at 21% O₂ indicates C₃ photosynthesis in *P. milioides* and *P. schenckii*. Keck and Ogren (8), however, found less sensitivity of carboxylation efficiency to O₂ in *P. milioides* than in the C₃ plant soybean (*Glycine max* [L.] Merr.). Rathnam and Chollet (16-18) have concluded from (a) enzyme localization, (b) increased O₂ sensitivity of photosynthesis upon inhibition of phosphoenolpyruvate carboxylase, and (c) initial products of ¹⁴CO₂ assimilation that reduced O₂ sensitivity in *P. milioides* is due to a limited C₄ cycle.

Whatever the reason for reduced O₂ inhibition of AP, *P. milioides* and *P. schenckii* have been shown to have Γ values between those of C₄ and C₃ species and lower PR (loss of CO₂ in CO₂-free air) than the C₃ species tall fescue (1, 2, 15).

The inhibition of AP² by 21% O₂ in C₃ species is due to (a) the

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² Abbreviations: AP, apparent photosynthesis; RuBP, ribulose biphosphate; Γ, CO₂ compensation concentration; PR, photorespiration.

Inasmuch as increases in temperature and light intensity are known to stimulate PR in C_3 species, experiments were conducted to examine effects of these environmental factors on photorespiratory loss of CO_2 in *P. milioides* and *P. schenckii*. Comparisons were made with the C_3 species tall fescue (*Festuca arundinacea* Schreb.) and, in some experiments, with the C_4 species *Panicum maximum* Jacq.

MATERIALS AND METHODS

Plants of *P. milioides*, *P. schenckii*, *P. maximum*, and tall fescue were grown in the greenhouse at maximum daytime temperatures of 25 to 35 C and night-time minima of 15 to 20 C. Supplemental lighting from 1500-w multivapor lamps was used to provide at least $1,500 \mu E m^{-2} s^{-1}$ of PAR during midday at plant height. Tillers were transplanted to pots containing a soil/peat/Perlite mixture and were fertilized with complete Hoagland solution. When plants were well-established, the following experiments were conducted.

Temperature Effects on PR and Γ . PR in *P. schenckii* and tall fescue was estimated from measurements of AP at CO_2 concentrations entering the leaf chamber of 3, 37, 62, 115, and $165 \mu l l^{-1}$ and leaf temperatures of 20 and 35 C. The youngest fully expanded leaf on a tiller was placed in a small leaf chamber and AP was measured. Measurements of AP and transpiration and calculation of substomatal CO_2 concentrations were as described earlier (2). PAR at the leaf surface was $2,000 \mu E m^{-2} s^{-1}$. Estimates of PR were made by extrapolating the AP-intercellular CO_2 concentration regression line to zero CO_2 . Estimates of Γ were made from the regression equation at AP = 0.

Effects of temperature on Γ were determined in a separate experiment by the Mylar bag technique of Goldworthy and Day (5). In this experiment, measurements were made on *P. milioides*, *P. schenckii*, *P. maximum*, and tall fescue. Temperatures inside the bags were maintained at 15, 25, 35, and 40 C by setting the growth chamber in which the bags were placed at the appropriate temperatures. PAR inside the bags was $1,600 \mu E m^{-2} s^{-1}$. Three replications of measurements were made for each temperature and species.

Light Intensity Effects on PR and Γ . Estimates of PR were made for *P. schenckii* and tall fescue at PAR levels of 100 and $2,000 \mu E m^{-2} s^{-1}$ by measuring AP at these intensities and at CO_2 concentrations used in the temperature experiments described above. Leaf temperature was maintained at 30 C. Photorespiration and Γ were calculated from CO_2 -response curves as described in the previous section.

Dark respiration and PR were also estimated by measuring CO_2 evolution in CO_2 -free air for *P. schenckii*, *P. maximum*, and tall fescue. Young, fully expanded leaves were enclosed in the leaf chambers and exposed to PAR levels of 0, 100, 300, 600, 1,100, and $2,000 \mu E m^{-2} s^{-1}$. At each PAR level, leaves were exposed to air containing $300 \mu l l^{-1} CO_2$ until AP or dark respiration reached a steady level. The leaf then was flushed with CO_2 -free air and CO_2 evolution was measured until an equilibrium was reached, usually 5 to 10 min. Concentrations of CO_2 in the exhaust of the leaf chamber ranged from zero to $10 \mu l l^{-1}$. For some leaves, measurements were made in sequences from lowest to highest PAR levels, and for others the sequence was reversed. The sequence did not appear to affect the response of CO_2 evolution to light intensity. Leaves were maintained at 30 C during measurements.

Measurements of Γ were made on *P. milioides*, *P. schenckii*, *P. maximum*, and tall fescue using a modification of the Mylar bag technique (5). Leaf sections were floated on water in two Petri dishes which were placed in Mylar bags. The bags then were inflated with air or with N_2 containing 3.7% O_2 . Each Mylar bag was fitted with a rubber septum from which 20-ml samples were withdrawn with a hypodermic syringe. Samples were injected into

a flowing N_2 stream which passed through the sample cell of an IR gas analyzer. N_2 was passed through the reference cell also. The analyzer was calibrated by injecting into the sample N_2 stream 20-ml samples of air with known CO_2 concentrations in the range of 0 to $100 \mu l l^{-1}$. Determinations were made at 50, 140, 225, 450, and $1,100 \mu E m^{-2} s^{-1}$. The lower PAR levels were attained by shading the Mylar bags with plastic shade screens; the highest level was the full PAR level in the growth chamber.

The bags were placed in a growth chamber at $1,100 \mu E m^{-2} s^{-1}$ and allowed to reach an equilibrium CO_2 concentration (Γ). Air temperature inside the bags was maintained at 30 C by adjusting temperature of the growth chamber. After the determination was made at $1,100 \mu E m^{-2} s^{-1}$, the bags were shaded to produce the next lower illumination level, chamber temperature was again adjusted, and bags allowed to reach CO_2 equilibrium.

RESULTS

Temperature Effects on PR and Γ . Photorespiration in tall fescue estimated from extrapolation of plots of substomatal CO_2 concentrations against AP increased from 7.3 to $10.2 mg dm^{-2} h^{-1}$ as temperature was raised from 20 to 35 C (Fig. 1). The slopes of the CO_2 -response curves of tall fescue were not changed by increased temperature, indicating that reductions in AP at 35 C compared to 20 C are mainly due to increased PR. In *P. schenckii*, PR was increased only slightly, from 2.5 to $3.3 mg dm^{-2} h^{-1}$ at 35 C compared to 20 C. The slope of the CO_2 -response curve was increased slightly at the higher temperature, indicating a higher carboxylation efficiency.

The intercepts of the CO_2 -response curves at AP = 0 show that Γ was responsive to temperature in tall fescue, but not in *P. schenckii*. Whereas Γ was not changed in *P. schenckii*, it was increased from 43 to $62 \mu l l^{-1}$ in tall fescue as temperature was raised from 20 to 35 C. Data in Figure 2 also show a contrast among species in the response of Γ to temperature. In tall fescue, Γ increased from 40 to $160 \mu l l^{-1}$ as temperature was increased from 15 to 40 C but, in *P. schenckii* and *P. milioides*, Γ increased from 8 to only $39 \mu l l^{-1}$ over the same temperature range. In contrast to the lack of temperature response for these species in Figure 1, Γ rose $12 \mu l l^{-1}$ as temperature was increased from 20 to 35 C in Figure 2. In the C_4 species *P. maximum*, Γ responded only slightly to temperature, rising to about $10 \mu l l^{-1}$ at 40 C.

Effects of Light Intensity on PR and Γ . PR in tall fescue estimated from extrapolation of the CO_2 -response curve increased from 2.4 to $7.2 mg dm^{-2} h^{-1}$ as PAR was increased from 100 to $2,000 \mu E m^{-2} s^{-1}$ (Fig. 3). The slope of the CO_2 -response curve

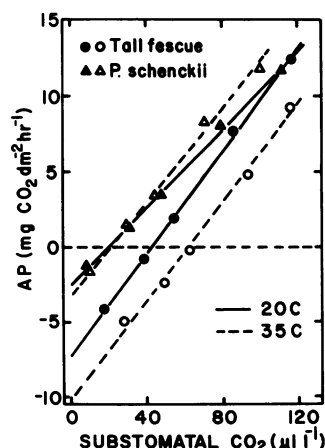


FIG. 1. Relationships between AP and substomatal CO_2 concentrations for tall fescue and *P. schenckii* at 20 and 35 C. Data are averages of five measurements.

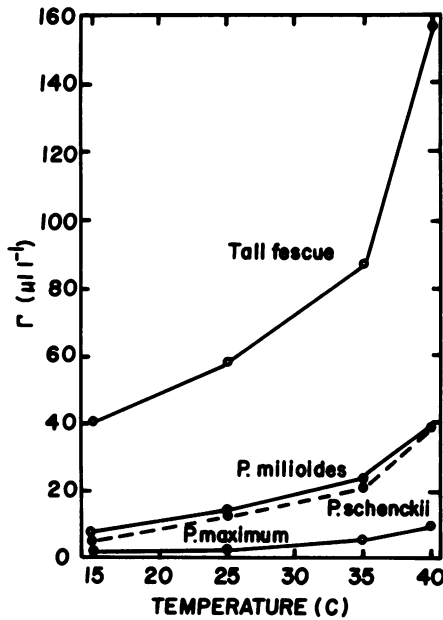


FIG. 2. Effect of temperature on the CO_2 compensation concentration (Γ) of tall fescue, *P. milioides*, *P. schenckii*, and *P. maximum*. Data are averages of three determinations.

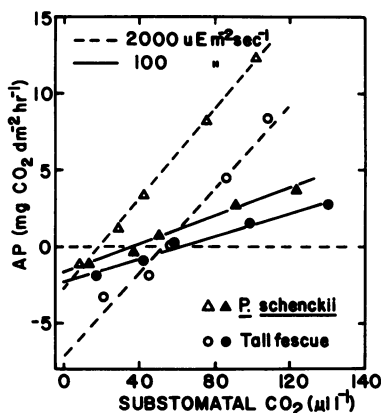


FIG. 3. Relationships between AP and substomatal CO_2 concentrations for tall fescue and *P. schenckii* at PAR levels of 100 and $2000 \mu\text{E m}^{-2} \text{s}^{-1}$. Data are averages of five measurements.

was greatly increased at the higher intensity, and the curves for the two intensities intersected near the compensation point. Thus, although PR was greatly increased by high PAR levels, Γ was affected only slightly. In *P. schenckii*, PR was only $2.8 \text{ mg dm}^{-2} \text{ h}^{-1}$ at $2,000 \mu\text{E m}^{-2} \text{ s}^{-1}$ and was reduced by only $1 \text{ mg dm}^{-2} \text{ h}^{-1}$ by lowering the PAR level to $100 \mu\text{E m}^{-2} \text{ s}^{-1}$. In contrast to tall fescue, Γ in *P. schenckii* was increased at the low PAR level from 19 to $38 \mu\text{l l}^{-1}$.

Evolution of CO_2 into CO_2 -free air increased in tall fescue with increases in PAR levels from $2.4 \text{ mg dm}^{-2} \text{ h}^{-1}$ in darkness to $4.3 \text{ mg dm}^{-2} \text{ h}^{-1}$ at $2,000 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Fig. 4). Estimates of PR in this experiment are lower than in Figure 3 because the estimate is of CO_2 evolved from the leaf, whereas in Figure 3, CO_2 evolution into intercellular spaces is estimated. A portion of the CO_2 evolved into intercellular spaces would be recycled reducing CO_2 evolution from the leaf. In contrast to the response in tall fescue, PR was decreased in *P. schenckii* as PAR levels were increased to $1,100 \mu\text{E m}^{-2} \text{ s}^{-1}$ and then rose again as PAR was increased further to $2,000 \mu\text{E m}^{-2} \text{ s}^{-1}$. Estimates of PR from extrapolation of CO_2 -response curves were higher at $2000 \mu\text{E m}^{-2} \text{ s}^{-1}$ than at $100 \mu\text{E m}^{-2} \text{ s}^{-1}$, whereas estimates from flushing with air showed a reverse

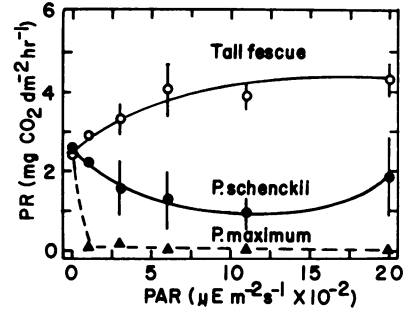


FIG. 4. Loss of CO_2 in CO_2 -free air (PR) as a function of PAR levels for tall fescue, *P. schenckii* and *P. maximum*. Data are averages of six measurements for *P. schenckii* and four each for tall fescue and *P. maximum*. Vertical lines are ± 1 SD.

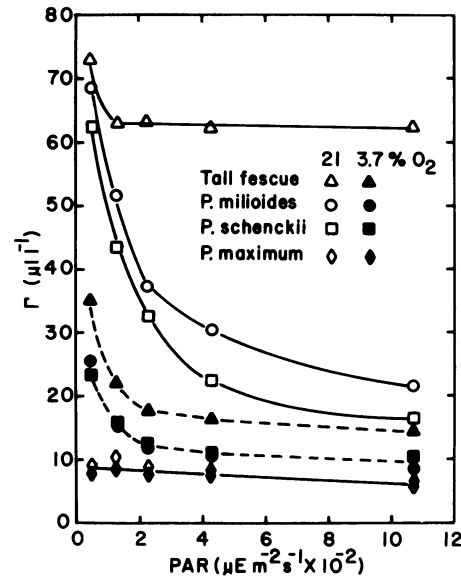


FIG. 5. Effect of PAR level and O_2 concentration on CO_2 compensation concentrations (Γ) in tall fescue, *P. milioides*, *P. schenckii*, and *P. maximum*. Data are averages of four determinations.

trend. Nevertheless, PR rates at the high and low PAR levels were low and varied only about $1 \text{ mg dm}^{-2} \text{ h}^{-1}$. Minimum PR for *P. schenckii* was $1 \text{ mg dm}^{-2} \text{ h}^{-1}$ at $1,100 \mu\text{E m}^{-2} \text{ s}^{-1}$ and, at the same PAR level, PR in tall fescue was approximately 4 times as great. Evolution of CO_2 in *P. maximum* dropped from $2.4 \text{ mg dm}^{-2} \text{ h}^{-1}$ in darkness to near zero at $100 \mu\text{E m}^{-2} \text{ s}^{-1}$ and remained very low at all higher PAR levels.

Measurement of Γ by the Mylar bag technique resulted in responses at 21% O_2 similar to those shown in Figure 3; that is, Γ changed little in tall fescue from a value of $62 \mu\text{l l}^{-1}$ as PAR level was increased from 140 to $1075 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Fig. 5). There was a rise to $73 \mu\text{l l}^{-1}$ when the PAR level was reduced to $50 \mu\text{E m}^{-2} \text{ s}^{-1}$. The Γ values of *P. milioides* and *P. schenckii* at 21% O_2 decreased from 69 and $62 \mu\text{l l}^{-1}$ at $50 \mu\text{E m}^{-2} \text{ s}^{-1}$ to 21 and $16 \mu\text{l l}^{-1}$ at $1,075 \mu\text{E m}^{-2} \text{ s}^{-1}$, respectively. At 3.7% O_2 , Γ in tall fescue, *P. milioides*, and *P. schenckii* decreased with increased PAR in a similar pattern, the decrease being steep from 50 to $225 \mu\text{E m}^{-2} \text{ s}^{-1}$ and only slight from 225 to $1,075 \mu\text{E m}^{-2} \text{ s}^{-1}$. In *P. maximum*, Γ was not affected by O_2 and the decrease from 50 to $1,075 \mu\text{E m}^{-2} \text{ s}^{-1}$ was only from 8.5 to $6 \mu\text{l l}^{-1}$.

An estimate of the effect of O_2 on Γ was made by subtracting those values obtained at 3.7% from those at 21% (data not shown). The O_2 effect was similar in *P. milioides*, *P. schenckii*, and tall fescue at $50 \mu\text{E m}^{-2} \text{ s}^{-1}$, with Γ being 38 to $44 \mu\text{l l}^{-1}$ higher at 21 than at 3.7% O_2 . Whereas the O_2 effect on Γ in tall fescue increased

from 38 to 48 $\mu\text{l l}^{-1}$ with increased PAR level, O_2 effect on Γ in *P. milioides* and *P. schenckii* decreased by 31 and 32 $\mu\text{l l}^{-1}$, respectively.

DISCUSSION

In previous reports (2, 15) it was suggested that the reduced O_2 sensitivity of AP in *P. milioides* and *P. schenckii* was due to a low PR rate rather than reduced sensitivity of carboxylation to O_2 . Experiments reported here confirm the low PR in *P. milioides* and *P. schenckii*, although the rates are not as low as those reported by Brown (2). The low PR rates were not very sensitive to temperature nor light intensity, factors which exert a striking influence on PR on C_3 species. O_2 has also been shown to have a relatively small effect on PR in *P. milioides* and *P. schenckii* (2, 11, 15) compared to its influence on PR in C_3 species.

The low PR rate in *P. schenckii* and *P. milioides* could be due to low CO_2 production or more efficient re-fixation of CO_2 than in C_3 species. More efficient re-fixation might be indicated by the decrease in PR and Γ as light intensity was increased. Data in Figures 4 and 5 indicate that PR in *P. milioides* and *P. schenckii* is similar to that in the C_3 species tall fescue, at low light intensities, but differences in PR increase with PAR levels up to about 1,100 $\mu\text{E m}^{-2} \text{s}^{-1}$. If the difference in Γ at the two O_2 concentrations can be attributed to PR, then it is obvious that light intensity has a quite different effect on the photorespiratory component of Γ in the C_3 and intermediate species. This difference in response of PR and Γ to light is compatible with data presented earlier (2) showing similar O_2 inhibition of AP at low light intensities for the three species mentioned above, but reduced inhibition in *P. milioides* and *P. schenckii* compared to tall fescue at high intensities.

Since PR has been shown to increase with light intensity in C_3 species (6, 20, 21), presumably due to increased RuBP levels (4), and since photosynthesis in *P. milioides* and *P. schenckii* is apparently predominantly C_3 , the production and oxidation of glycolate in these species may also be expected to increase with light intensity. If such an increase occurs, a light-dependent, CO_2 -recycling mechanism must operate and become more efficient with increased light intensity. If a limited C_4 cycle operates in these intermediate species, as suggested by data of Rathnam and Chollet (16-18), it apparently becomes more influential on total CO_2 exchange with increased light intensity. It is not clear why a low level of C_4 metabolism should exert a relatively stronger effect on gas exchange as light intensity increases. Perhaps CO_2 concentration in the bundle sheath cells increases at higher light intensities, reducing O_2 inhibition of RuBP carboxylation. This could explain the reduced formation of glycolate in *P. milioides* compared to the C_3 species *Hordeum vulgare* L. observed by Servaites *et al.* (19) at 1,500 $\mu\text{E m}^{-2} \text{s}^{-1}$. It is not consistent, however, with the observation of carboxylation efficiencies in *P. milioides* and *P. schenckii* similar to those of C_3 species (2, 11). In fact, the lack of traits associated with C_4 photosynthesis at atmospheric CO_2 and O_2 levels, such as high AP rates, increased H_2O use efficiency, and low $^{13}\text{C}/^{12}\text{C}$ ratios compared to C_3 species (1-3, 20), may mean that the CO_2 concentrating mechanism is ineffectual in these species. Disagreement over the extent of ^{14}C labeling of initial products of the C_4 cycle (9, 12, 18) and compartmentation of enzymes involved in the two phases of C_4 photosynthesis (12, 16, 18) leaves open the question of C_4 cycle activity in *P. milioides*

and *P. schenckii*.

The low PR rates in *P. milioides* and *P. schenckii* have been confirmed in these experiments and have been found to be much less sensitive to temperature and light intensity than in C_3 species. The low sensitivity of PR to temperature, light intensity, and O_2 and its decrease, at least up to PAR levels of about one-half of full sunlight, indicates some carbon metabolism different from that typical of C_3 plants. Perhaps phosphoenolpyruvate carboxylase plays a role in recycling of photorespired CO_2 as suggested earlier (8, 9, 12) but without a CO_2 concentrating mechanism similar to C_4 plants to raise carboxylation efficiency.

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