

# Photosynthesis of Grass Species Differing in Carbon Dioxide Fixation Pathways

## IV. ANALYSIS OF REDUCED OXYGEN RESPONSE IN *PANICUM MILIOIDES* AND *PANICUM SCHENCKII*<sup>1</sup>

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### ABSTRACT

Reduced photorespiration has been reported in *Panicum milioides* on the basis of lower CO<sub>2</sub> compensation concentrations than in C<sub>3</sub> species, lower CO<sub>2</sub> evolution in the light, and less response of apparent photosynthesis to O<sub>2</sub> concentration. The lower response to O<sub>2</sub> in *P. milioides* could be due to reduced O<sub>2</sub> competition with CO<sub>2</sub> for reaction with ribulose 1,5-bisphosphate, to a reduced loss of CO<sub>2</sub>, or to an initial fixation of CO<sub>2</sub> by phosphoenolpyruvate carboxylase. Experiments were carried out with *Panicum maximum* Jacq., a C<sub>4</sub> species having no apparent photorespiration; tall fescue (*Festuca arundinacea* Schreb.), a C<sub>3</sub> species; *P. milioides* Nees ex Trin.; and *Panicum schenckii* Hack. The latter two species are closely related and have low photorespiration rates. CO<sub>2</sub> exchange was measured at five CO<sub>2</sub> concentrations ranging from 0 to 260 microliters per liter at both 2 and 21% O<sub>2</sub>. Mesophyll conductance or carboxylation efficiency was estimated by plotting substomatal CO<sub>2</sub> concentrations against apparent photosynthesis. In the C<sub>4</sub> species *P. maximum*, mesophyll conductance was 0.96 centimeters per second and was unaffected by O<sub>2</sub> concentration. At 21% O<sub>2</sub> mesophyll conductance of tall fescue was decreased 32% below the value at 2% O<sub>2</sub>. Decreases in mesophyll conductance at 21% O<sub>2</sub> for *P. milioides* and *P. schenckii* were similar to that for tall fescue. On the other hand, loss of CO<sub>2</sub> in CO<sub>2</sub>-free air, estimated by extrapolating the CO<sub>2</sub> response curve to zero CO<sub>2</sub>, was increased from 1.8 to 6.5 milligrams per square decimeter per hour in tall fescue as O<sub>2</sub> was raised from 2-21%. Loss of CO<sub>2</sub> was less than 1 milligram per square decimeter per hour for *P. milioides* and *P. schenckii* and was unaffected by O<sub>2</sub>. The results suggest that the reduced O<sub>2</sub> response in *P. milioides* and *P. schenckii* is due to a lower loss of CO<sub>2</sub> in the light rather than less inhibition of carboxylation by O<sub>2</sub>, since the decrease in carboxylation efficiency at 21% O<sub>2</sub> was similar for *P. milioides*, *P. schenckii*, and tall fescue. The inhibition of apparent photosynthesis by 21% O<sub>2</sub> in these three species at low light intensities was similar at 31 to 36% which also indicates similar O<sub>2</sub> effects on carboxylation. Apparent photosynthesis at high light intensity was inhibited less by 21% O<sub>2</sub> in *P. milioides* (16.8%) and *P. schenckii* (23.8%) than in tall fescue (28.4%). This lower inhibition in the *Panicum* species may have been due to a higher degree of recycling of photorespired CO<sub>2</sub> in these species than in tall fescue.

glycolate pathway (3, 4). In C<sub>4</sub> species, O<sub>2</sub> concentration does not affect AP greatly, apparently because: (a) CO<sub>2</sub> is concentrated in the bundle sheath cells favoring the reaction of RuBP with CO<sub>2</sub> rather than O<sub>2</sub> (12); and (b) CO<sub>2</sub> which may be generated in photorespiration is refixed by PEPC in the mesophyll cells, preventing its evolution from the leaf (24).

When the O<sub>2</sub> concentration in the atmosphere around a C<sub>3</sub> leaf is increased from near zero to 21%, AP is reduced by about 30%. This effect has been shown by Björkman (1) to be similar at limiting and saturating light intensities, but others (17) have found the O<sub>2</sub> effect to diminish at high light intensities. This inhibition of AP at 21% O<sub>2</sub> is apparently due to a stimulation of photorespiration (20) and inhibition of carboxylation of RuBP (18). Stimulation of photorespiration by O<sub>2</sub> may be shown by a rise in  $\Gamma$  or an increase in the loss of CO<sub>2</sub> in CO<sub>2</sub>-free air (13). Inhibition of carboxylation may be inferred in gas exchange measurements by a reduction in  $g_m$  (19).

*Panicum milioides* Nees ex Trin. is a species which is adapted from the tropics to subtropical and temperate areas of North and South America. It has been reported to have reduced photorespiration based on lower response of AP and growth to O<sub>2</sub> compared to C<sub>3</sub> species and lower  $\Gamma$  than C<sub>3</sub> species (6, 15, 22). Also, it has been reported to have some anatomical characteristics intermediate between C<sub>3</sub> and C<sub>4</sub> species (5, 14) and somewhat elevated PEPC activity compared to C<sub>3</sub> species, though not nearly as high as in C<sub>4</sub> plants (2, 15, 16). RuBPC activity was reported to be lower in *P. milioides* than in C<sub>3</sub> plants by Black *et al.* (2) and Keck and Ogren (15), but Ku *et al.* (16) reported that RuBPC was similar in *P. milioides* and two C<sub>3</sub> species. More recently, Rathnam and Chollet (23) proposed that the lower sensitivity of AP to O<sub>2</sub> in *P. milioides* was due to a portion of the assimilated CO<sub>2</sub> being fixed via a C<sub>4</sub> cycle.

Two other species, *Panicum schenckii* Hack and *Panicum decipiens* Nees ex Trin., which are closely related taxonomically to *P. milioides*, have been found to exhibit O<sub>2</sub> inhibition of AP similar to *P. milioides* and intermediate to C<sub>3</sub> and C<sub>4</sub> plants (21).

An analysis of the effects of O<sub>2</sub> on AP was carried out to determine whether the reduced O<sub>2</sub> effects observed in *P. milioides* and *P. schenckii* were due to a lower CO<sub>2</sub> loss in the light or reduced sensitivity of  $g_m$ .

### MATERIALS AND METHODS

**Effect of O<sub>2</sub> on CO<sub>2</sub> Response.** Experiments were carried out with four species to determine the effects of O<sub>2</sub> on the AP response to CO<sub>2</sub> concentration. *P. maximum* Jacq., a well characterized C<sub>4</sub> grass, was used as a C<sub>4</sub> control, and tall fescue (*Festuca arundinacea* Schreb.) served as the C<sub>3</sub> control species. *P. milioides* was included, as well as *P. schenckii*, which has been found to have similar anatomical and physiological characteristics (21). These species were grown in a soil-peat mixture in a growth chamber set at 30

Photorespiration in C<sub>3</sub> species is due to the reaction of O<sub>2</sub> with RuBP<sup>2</sup> to produce P-glycolate which is then oxidized in the

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<sup>2</sup> Abbreviations: RuBP: ribulose 1,5-bisphosphate; AP: apparent photosynthesis; PEPC: phosphoenolpyruvate carboxylase;  $\Gamma$ : CO<sub>2</sub> compensation concentration;  $g_m$ : mesophyll conductance to CO<sub>2</sub>; RuBPC: ribulose-1,5-bisphosphate carboxylase;  $g$ : leaf conductance to CO<sub>2</sub>.

C during a 12-h day and 20 C at night and providing a photosynthetic photon flux density of  $1,500 \mu\text{E m}^{-2}\text{s}^{-1}$ . Plants were watered daily and fertilized with complete Hoagland nutrient solution two to three times weekly.

After the plants had been in the growth chamber for 2 or 3 weeks, AP and transpiration were measured on attached single leaves in a small Plexiglas chamber at a leaf temperature of 30 C and under a flux density of  $2,000 \mu\text{E m}^{-2}\text{s}^{-1}$ . The dewpoint of air entering the cuvette was constant at 5 C, and that of air exiting the chamber ranged from 15 to 20 C. An open gas exchange system was used with a flow rate of  $280 \text{ ml min}^{-1}$ . A small fan in the chamber provided adequate mixing, and the concentrations of  $\text{CO}_2$  and water vapor in the air leaving the chamber were assumed to be representative of those surrounding the leaves. Leaf temperature was monitored with a thermocouple touching the lower side of the leaf.

Measurements were made at 21 and 2%  $\text{O}_2$  and five  $\text{CO}_2$  concentrations entering the leaf chamber ranging from 0 to  $330 \mu\text{l l}^{-1}$ . The sequence of measurements was varied beginning in some experiments with low  $\text{CO}_2$  concentrations and in others at high  $\text{CO}_2$ . The response of AP was similar for both sequences. At each  $\text{CO}_2$  concentration AP was measured at 2 and 21%  $\text{O}_2$ ; in approximately one-half of the measurements 2%  $\text{O}_2$  was administered first and then 21%  $\text{O}_2$ . Measurements on five different plants were made for each species at each  $\text{CO}_2$  and  $\text{O}_2$  level.

$\text{CO}_2$  uptake and water loss were used to calculate leaf conductance ( $g_l$ ) and mesophyll conductance ( $g_m$ ) to  $\text{CO}_2$ . Leaf conductance, which includes a boundary layer and stomatal component was calculated from transpiration measurements. Mesophyll conductance also referred to as carboxylation efficiency, was estimated from the slope of the linear portion of the AP- $C_s$  relationship, where  $C_s$  is the substomatal  $\text{CO}_2$  concentration. Substomatal  $\text{CO}_2$  concentrations were calculated as

$$C_s = C_a - \frac{AP}{g_l}$$

where  $C_a$  is the  $\text{CO}_2$  concentration surrounding the leaf. Photorespiration was estimated from the extrapolation of the linear portion of the AP- $C_s$  curves to zero  $C_s$ .

**Effect of  $\text{O}_2$  at Limiting and Saturating Light Levels.** Experiments were conducted on five species to determine the effects of  $\text{O}_2$  on AP at low and saturating light levels. The species used in the  $\text{CO}_2$  response studies described above and *Panicum prionitis*, an apparent  $\text{C}_4$  species (21), were grown in a greenhouse maintained at 25–30 C during the day and about 20 C at night. The plants were grown in pots in a soil-peat mixture and were watered daily and fertilized with Hoagland nutrient solution two or three times weekly.

AP was measured on young, fully expanded leaves in a leaf chamber similar to that described previously for the  $\text{CO}_2$  studies. Photosynthetic photon flux densities were 0, 25, 47, 92, 155, and  $1,100 \mu\text{E m}^{-2}\text{s}^{-1}$  at the leaf level. The temperature of the leaf was maintained at 30 C and the  $\text{CO}_2$  concentration of air entering the chamber at  $310 \mu\text{l l}^{-1}$ . Measurements were made at 2 and 21%  $\text{O}_2$ . Water vapor inside the chamber was near saturation for all measurements so that transpiration and diffusive conductance could not be calculated in these experiments.

## RESULTS

**Effects of  $\text{O}_2$  on  $\text{CO}_2$  Response.** The response of AP to  $C_s$  was linear up to  $150\text{--}175 \mu\text{l l}^{-1}$  for tall fescue and *P. schenckii*, and nearly linear in the case of *P. milioides* (Fig. 1). The response of AP in *P. maximum* deviated from linearity between 30 and  $90 \mu\text{l l}^{-1}$  for *P. maximum* so the curvature in that range is not defined. The linear portion of the  $\text{CO}_2$  response curve for *P. maximum* was steeper than for the other species and represented a  $g_m$  of  $0.96 \text{ cm s}^{-1}$ . The estimated  $g_m$  for *P. maximum* was not

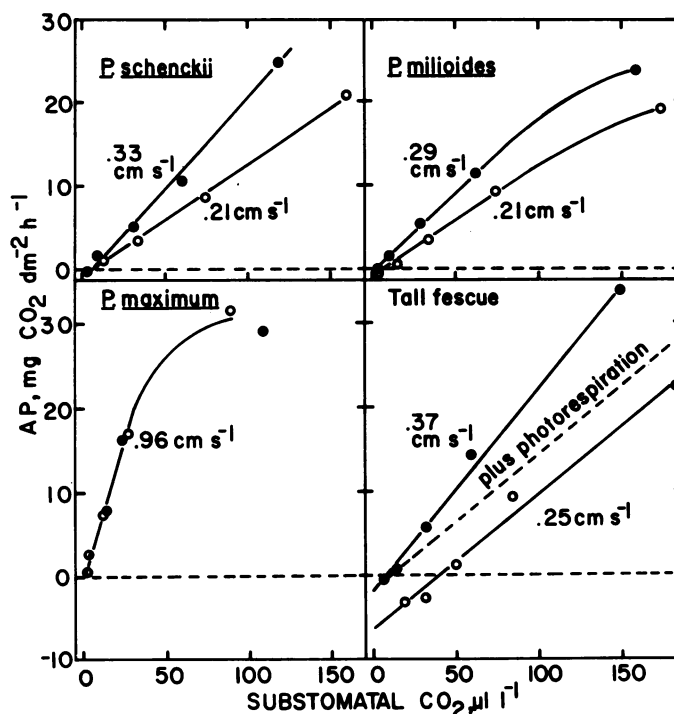


FIG. 1. Response of AP to substomatal  $\text{CO}_2$  concentrations for *P. schenckii*, *P. milioides*, tall fescue, and *P. maximum* at 2% (●) and 21%  $\text{O}_2$  (○). Indicated by each curve is the slope of the linear portion ( $g_m$ ). (---): AP plus estimated photorespiration for tall fescue. Measurements made at 30 C and  $2,000 \mu\text{E m}^{-2}\text{s}^{-1}$ .

affected by  $\text{O}_2$ . In contrast to *P. maximum*,  $g_m$  at 21%  $\text{O}_2$  was 0.25, 0.21, and  $0.21 \text{ cm s}^{-1}$  for tall fescue, *P. milioides*, and *P. schenckii*, respectively (Fig. 1). Thus, the two species with reduced photorespiration have  $g_m$  values at 21%  $\text{O}_2$  similar or slightly lower than the  $\text{C}_3$  species, tall fescue.

Photorespiration, estimated from extrapolation of the  $\text{CO}_2$  response curve to zero  $\text{CO}_2$ , was quite different in tall fescue and the two intermediate *Panicum* species. The estimated photorespiration for *P. milioides* and *P. schenckii* was only 0.95 and  $0.59 \text{ mg CO}_2 \text{ dm}^{-2}\text{h}^{-1}$ , respectively. The photorespiration rate in 21%  $\text{O}_2$  for tall fescue was estimated to be  $6.5 \text{ mg dm}^{-2}\text{h}^{-1}$ . The  $\Gamma$  value for tall fescue at 21%  $\text{O}_2$  was  $40 \mu\text{l l}^{-1}$ , and for *P. milioides* and *P. schenckii* it was estimated to be 6.9 and  $4.4 \mu\text{l l}^{-1}$ , respectively. There appeared to be little loss of  $\text{CO}_2$  in the light for *P. schenckii* and *P. milioides*, but a loss in tall fescue similar to that reported for other  $\text{C}_3$  species. The reason for the lower values for  $\Gamma$  and photorespiration values in these than earlier experiments (6, 21) is not known. Photorespiration and  $\Gamma$  for *P. maximum* were both near zero.

AP of *P. maximum* was not affected by  $\text{O}_2$  concentration (Fig. 1). The influence of  $\text{O}_2$  on AP of tall fescue was typical of that for  $\text{C}_3$  species. At  $260 \mu\text{l l}^{-1}$  of  $\text{CO}_2$  surrounding the leaf, which is approximately equivalent to the highest internal  $\text{CO}_2$  concentrations in Figure 1, the inhibition of AP at 21%  $\text{O}_2$  was 33%, which is comparable to that reported by Björkman (1) for  $\text{C}_3$  species. The  $\text{O}_2$  inhibition of AP at  $260 \mu\text{l l}^{-1}$  of  $\text{CO}_2$  in tall fescue resulted from an increased  $\text{CO}_2$  loss in the light of  $4.7 \text{ mg dm}^{-2}\text{h}^{-1}$  estimated from the zero  $\text{CO}_2$  intercepts of the lines in Figure 1, and a reduction of  $6.8 \text{ mg CO}_2 \text{ dm}^{-2}\text{h}^{-1}$  in  $\text{CO}_2$  fixed due to decreased  $g_m$  estimated from the slopes of the  $\text{CO}_2$  response curves. Reduction in  $g_m$  by 21%  $\text{O}_2$  was 33%.

The inhibition of AP by  $\text{O}_2$  in *P. milioides* and *P. schenckii* resulted entirely from a decrease in  $g_m$  at 21%  $\text{O}_2$ . The decrease in  $g_m$  was 28 and 36% for *P. milioides* and *P. schenckii*, respectively. Since  $\text{CO}_2$  loss estimated from the intercept of the AP axis and  $\Gamma$  was very small,  $\text{O}_2$  concentration did not affect these two charac-

teristics in either species.

The relationships of AP among the four species at atmospheric  $O_2$  concentration may be compared in Figure 1. At an intercellular  $CO_2$  concentration of  $90 \mu l l^{-1}$ , which was the highest concentration attained in *P. maximum* leaves, AP for this species was more than three times as high as for the other species. AP of *P. maximum* appeared to be nearly  $CO_2$  saturated at  $90 \mu l l^{-1}$ , whereas for the other species the response was linear or nearly so up to  $175 \mu l l^{-1}$  internal  $CO_2$ . The highest AP rates attained by *P. milioides* and *P. schenckii* were approximately  $20 mg CO_2 dm^{-2} h^{-1}$  as compared to  $22 mg dm^{-2} h^{-1}$  for tall fescue.

**Effect of  $O_2$  at Limiting and Saturating Light Levels.**  $O_2$  had no effect on AP of the  $C_4$  species, *P. prionitis* (Fig. 2), nor *P. maximum* (data not shown) at limiting light levels. For tall fescue, *P. schenckii*, and *P. milioides* the  $O_2$  effects were similar, the initial slopes of the light response curves being reduced by 36, 35, and 31%, respectively, at 21% compared to 2%  $O_2$ . At  $1,100 \mu E m^{-2} s^{-1}$ , AP was reduced from  $31.7 mg dm^{-2} h^{-1}$  at 2%  $O_2$  to  $22.7 mg dm^{-2} h^{-1}$  at 21%  $O_2$  for tall fescue, an inhibition of 28.4%. In contrast, AP at high light intensity in *P. schenckii* was reduced from  $31.5$  to  $24.0 mg dm^{-2} h^{-1}$  by 21%  $O_2$ , an inhibition of 23.8%, and in *P. milioides* from  $22.6$  to  $18.8 mg dm^{-2} h^{-1}$ , an inhibition of 16.8%. Therefore, inhibition of AP by  $O_2$  decreased with increasing light in all three species, but the decrease was greater for *P. milioides* and *P. schenckii*. There was no effect of  $O_2$  on AP in *P. maximum* nor *P. prionitis* at any light intensity.

## DISCUSSION

The data presented indicate that the reduced  $O_2$  response in *P. milioides* and *P. schenckii* at light saturation is due to a reduced loss of  $CO_2$  compared to tall fescue. If the decrease in  $g_m$  (smaller slope of the  $CO_2$  response curve) at 21%  $O_2$  is indicative of inhibition of RuBP carboxylation then it may be concluded that tall fescue, *P. milioides*, and *P. schenckii* have similar inhibition of

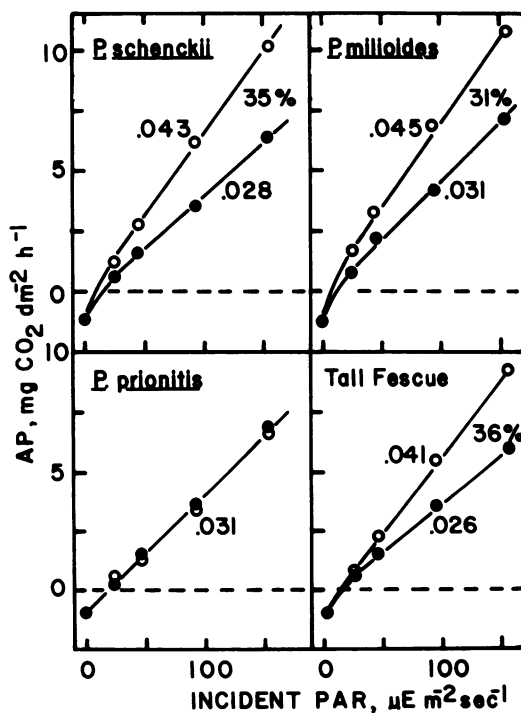


FIG. 2. Response of AP to incident PAR for *P. schenckii*, *P. milioides*, tall fescue, and *P. prionitis* at 2% (○) and 21%  $O_2$  (●). Numbers beside the lines indicate slopes in mol  $CO_2 E^{-1}$ . Percentages indicate reduction in slope by 21%  $O_2$ . Measurements made at 30 C and  $CO_2$  concentrations entering the leaf chamber of  $310 \mu l l^{-1}$ .

the carboxylase by  $O_2$ . However, since the  $CO_2$  response curves of *P. milioides* and *P. schenckii* at 21%  $O_2$  indicate very low photorespiration and  $\Gamma$ , reduced  $O_2$  had little influence on these characteristics.

Loss of  $CO_2$  estimated by extrapolation of the curves in Figure 1, to zero  $CO_2$  may not be the same as that lost at atmospheric  $CO_2$  concentrations if photorespiration is influenced by  $CO_2$  levels. Ludwig and Calvin (20) measured photorespiration in sunflower leaves as the difference in net  $CO_2$  uptake and  $^{14}CO_2$  uptake in short time intervals before assimilated  $^{14}CO_2$  evolved from the leaves. They observed no influence of  $CO_2$  concentrations on photorespiration from near  $\Gamma$  to  $300 \mu l l^{-1}$ . It is possible that photorespiration in *P. milioides* and *P. schenckii* at atmospheric  $CO_2$  levels is higher than estimated by extrapolating to zero  $CO_2$ . On the other hand, the reduced  $O_2$  inhibition at atmospheric  $CO_2$  concentrations could be accounted for by the low photorespiration rates estimated. Similar effects of  $O_2$  on  $g_m$  in *P. milioides*, *P. schenckii*, and tall fescue indicate the reduced inhibition is accounted for other than by  $O_2$  effects on carboxylation.

The differences in estimated photorespiration between tall fescue and the intermediate *Panicums* may be due to differences in refixation of respired  $CO_2$  in the light. Differential recycling may be indicated by the difference in  $O_2$  inhibition of AP in tall fescue and the intermediate *Panicums* at high, but not at low intensities. Refixation of respired  $CO_2$  may be minimal at low light but increase with light intensity and to a greater extent in *P. milioides* and *P. schenckii* than in tall fescue. Such a response to  $O_2$  and light intensity as that in the intermediate *Panicums* was postulated by Chartier (8) for a "plant with photorespiration and high recycling."

Involvement of PEPC in recycling of photorespired  $CO_2$  has been postulated for *P. milioides* because of the slightly higher PEPC activity (11, 15) and the somewhat higher percentage of  $^{14}C$  in  $C_4$  acids after short exposure to low  $CO_2$  concentrations (2) in this plant compared to  $C_3$  species. The function of PEPC, if any, in recycling of  $CO_2$  is not clear unless it operates as part of a complete  $C_4$  cycle. The low photorespiration in *P. milioides* has been explained by Rathnam and Chollet (23) as being due to operation of a  $C_4$  cycle that acts as a  $CO_2$  pump in a manner similar to that in  $C_4$  plants (12), but with somewhat lower efficiency. The contention that a  $C_4$  cycle operates in *P. milioides* was supported by differential compartmentation of certain photosynthetic enzymes in bundle sheath and mesophyll cells and increases in  $O_2$  sensitivity of photosynthesis with the use of inhibitors of PEPC.

Gas exchange data contained in this report do not reflect changes which should accompany increases in  $C_4$  cycle activity. The  $g_m$  at 21%  $O_2$  is slightly lower in *P. milioides* and *P. schenckii* than in tall fescue and is as sensitive to  $O_2$  in the *Panicum* species as in tall fescue. Concentration of  $CO_2$  in bundle sheath cells to any appreciable extent as occurs in  $C_4$  plants (12) should increase  $g_m$  and reduce its sensitivity to  $O_2$ . Similar inhibition of AP by  $O_2$  at low light intensities among the three species indicates minimal  $C_4$  activity, inasmuch as  $C_4$  plants show no  $O_2$  sensitivity at any light intensity (Fig. 2 and ref. 7).

Other published data on *P. milioides* also do not support the existence of appreciable  $C_4$  activity. Little  $^{14}C$  is incorporated in  $C_4$  acids after short periods of  $^{14}CO_2$  assimilation (2, 14) and  $^{13}C/^{12}C$  ratios determined on this species are typical of those for  $C_3$  species (6). In addition, no appreciable differential compartmentation of carboxylating or  $C_4$  acid-decarboxylating enzymes in mesophyll and bundle sheath cells was found by Ku *et al.* (16).

Two anatomical characteristics of *P. milioides* and *P. schenckii* may help account for the low photorespiration and reduced  $O_2$  sensitivity in these species. An appreciable quantity of  $CO_2$  may be released in the bundle sheath cells since they are chlorophyllous and contain numerous mitochondria and peroxisomes (5, 9). This  $CO_2$  may not be as free to diffuse to the atmosphere as that

generated in mesophyll cells and thus, apparent photorespiration may be reduced. It has also been observed that a much closer association of mitochondria, peroxisomes, and chloroplasts exists in *P. milioides* than in  $C_3$  species (9). A closer physical association of the other organelles involved in photorespiration with chloroplasts could increase the diffusive conductance between the  $CO_2$  release and fixation sites and cause greater refixation of  $CO_2$  and reduce  $CO_2$  loss.

Whatever mechanisms or characteristics of *P. milioides* and *P. schenckii* are responsible for the reduced response of AP to  $O_2$ , the reduced sensitivity appears to be due to reduced photorespiratory loss of  $CO_2$  rather than a difference in effects of  $O_2$  on carboxylation efficiency between the intermediate *Panicum* and  $C_3$  species. If such an alteration of photorespiration is possible without changing the carboxylation characteristics in  $C_3$  species, it may be easier than previously believed to reduce photorespiration through chemical or genetic means.

## LITERATURE CITED

- BRÖCKMAN O 1966. The effect of oxygen concentration on photosynthesis in higher plants. *Physiol Plant* 19: 618-633.
- BLACK CC, LD GOLDSTEIN, TB RAY, DP KESTLER, BC MAYNE 1976 The relationship of plant metabolism to internal leaf and cell morphology and to the efficiency of  $CO_2$  assimilation. In RH Burris, CC Black, eds, *CO<sub>2</sub> Metabolism and Plant Productivity*, University Park Press, Baltimore, pp 113-139
- BOWES G, WL OGREN 1972 Oxygen inhibition and other properties of soybean ribulose 1,5-diphosphate carboxylase. *J Biol Chem* 247: 2171-2176
- BOWES G, WL OGREN, RH HAGEMAN 1971 Phosphoglycolate production catalyzed by ribulose diphosphate carboxylase. *Biochem Biophys Res Commun* 45: 716-722
- BROWN RH 1976 Characteristics related to photosynthesis and photorespiration of *Panicum milioides*. In RH Burris, CC Black, eds, *CO<sub>2</sub> Metabolism and Plant Productivity*. University Park Press, Baltimore, pp 311-325.
- BROWN RH, WV BROWN 1975 Photosynthetic characteristics of *Panicum milioides*, a species with reduced photorespiration. *Crop Sci* 15: 681-685
- BULL TA 1969 Photosynthetic efficiencies and photorespiration in Calvin cycle and  $C_4$ -dicarboxylic acid plants. *Crop Sci* 9: 726-729
- CHARTIER P 1972 Net assimilation of plants as influenced by light and carbon dioxide. In AR Rees, KE Cockshull, DW Hand, RG Hurd, eds, *Crop Processes in Controlled Environments*, Ed 1 Chap III 2. Academic Press, London, pp 203-216
- DOOHAN ME 1978 Investigation of the ultrastructural aspects of the  $C_4$  syndrome. PhD thesis. Univ Wisconsin, Madison
- DOWNES RW, JD HESKETH 1968 Enhanced photosynthesis at low oxygen concentrations: differential response of temperate and tropical grasses. *Planta* 78: 79-84
- GOLDSTEIN LD, TB RAY, DP KESTLER, BC MAYNE, RH BROWN, CC BLACK 1976 Biochemical characterization of *Panicum* species which are intermediate between  $C_3$  and  $C_4$  photosynthesis plants. *Plant Sci Lett* 6: 85-90
- HATCH MD 1976 The  $C_4$  pathway of photosynthesis: mechanism and function. In RH Burris, CC Black, eds, *CO<sub>2</sub> Metabolism and Plant Productivity*, Ed 1. University Park Press, Baltimore, pp 59-81
- HEATH OVS 1969 *The Physiological Aspects of Photosynthesis*. Stanford Univ Press, Stanford, 309 p
- KANAI R, M KASHIWAGI 1975 *Panicum milioides*, a Gramineae plant having Kranz leaf anatomy without  $C_4$ -photosynthesis. *Plant Cell Physiol* 16: 669-679
- KECK RW, WL OGREN 1976 Differential oxygen response of photosynthesis in soybean and *Panicum milioides*. *Plant Physiol* 58: 552-555
- KU SB, GE EDWARDS, R KANAI 1976 Distribution of enzymes related to  $C_3$  and  $C_4$  pathway of photosynthesis between mesophyll and bundle sheath cells of *Panicum hians* and *Panicum milioides*. *Plant Cell Physiol* 17: 615-620
- KU SB, GE EDWARDS, CB TANNER 1977 Effects of light, carbon dioxide and temperature on photosynthesis, oxygen inhibition of photosynthesis, and transpiration in *Solanum tuberosum*. *Plant Physiol* 59: 868-872
- LAING WA, WL OGREN, RH 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 Physiol* 54: 678-685
- LUDLOW MM 1970 Effect of oxygen concentration on leaf photosynthesis and resistances to carbon dioxide diffusion. *Planta* 91: 285-290
- LUDWIG LJ, DT CANVIN 1971 The rate of photorespiration during photosynthesis and the relationship of the substrate of light respiration to the products of photosynthesis in sunflower leaves. *Plant Physiol* 48: 712-719.
- MORGAN JA, RH BROWN 1979 Photosynthesis in grass species differing in carbon dioxide fixation pathways. II. A search for species with intermediate gas exchange and anatomical characteristics. *Plant Physiol* 64: 257-262
- QUEBEDEAUX B, R CHOLLET 1977 Comparative growth analyses of *Panicum* species with differing rates of photorespiration. *Plant Physiol* 59: 42-44
- RATHNAM CKM, R CHOLLET 1978  $CO_2$  donation by malate and aspartate reduces photorespiration in *Panicum milioides*, a  $C_3$ - $C_4$  intermediate species. *Biochem Biophys Res Commun* 85: 801-808
- TROUGHTON JH 1971 The lack of carbon dioxide evolution in maize leaves in the light. *Planta* 100: 87-92.