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Photosynthesis in Grass Species Differing in Carbon Dioxide Fixation Pathways

III. OXYGEN RESPONSE AND ENZYME ACTIVITIES OF SPECIES IN THE *LAXA* GROUP OF *PANICUM*[1]

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ABSTRACT

Measurements of CO_2 exchange at varying O_2 concentrations in seven grass species of the *Laxa* group of *Panicum* and activities of five photosynthetic enzymes were compared to values obtained for these characters in a cool season C_3 grass, tall fescue (*Festuca arundinacea* Schreb.) and a C_4 grass, *P. maximum* Jacq. Plants were divided into three groups on the basis of the inhibition of apparent photosynthesis by 21% O_2. Rates of apparent photosynthesis in *P. prionitis* Griseb. and *P. maximum* were virtually unaffected by changes in O_2 concentration. In another group consisting of *P. hylaeicum* Mez., *P. rivulare* Trin., *P. laxum* Sw., and tall fescue apparent photosynthesis was inhibited by 28.2 to 36.0% at 21% O_2. An intermediate inhibition of 20.6 to 23.3% at 21% O_2 was exhibited by *P. milioides* Nees ex Trin., *P. schenckii* Hack., and *P. decipiens* Nees ex Trin. The CO_2 compensation concentration for *P. prionitis* and *P. maximum* was low ($\leq$6 microliters per liter CO_2 at 21% O_2) and affected little by O_2, whereas values for *P. hylaeicum*, *P. rivulare*, *P. laxum*, and tall fescue were much greater, and increased almost linearly from 2 to 48% O_2. Values for *P. milioides*, *P. schenckii*, and *P. decipiens* were intermediate to the other two groups. The effect of O_2 on total leaf conductance to CO_2 was similar to the C_3 grasses and the intermediate *Panicums*. However, estimates of photorespiration in the intermediate species were low and changed little with O_2 in comparison to estimates for the C_3 species which were higher and increased greatly with increased O_2.

Activities of phosphoenolpyruvate carboxylase were greatest in *P. maximum* and *P. prionitis* and one-fourth or less in the remaining species. Activity of ribulose bisphosphate carboxylase was 548 micromoles per mg chlorophyll per hour in tall fescue; activity in the remaining species was approximately one-fourth or less of that in tall fescue, with the exception of *P. rivulare*, in which it was 440 micromoles per milligram chlorphyll per hour. High activities of two C_4 decarboxylating enzymes, phosphoenolpyruvate carboxykinase and NADP-malic enzyme, were observed in *P. maximum* (1,988 micromoles per milligram chlorophyll per hour) and *P. prionitis* (125 micromoles per milligram chlorophyll per hour), respectively. Only minimal activities of decarboxylating enzymes were detected in the remaining species.

Panicum milioides is a species with characteristics intermediate to C_3 and C_4 photosynthetic plant types. It is intermediate with respect to O_2 inhibition of AP[2] (4, 13, 16), Γ (4, 10, 13–15, 18), leaf anatomy (4, 7, 12, 18) and effect of O_2 levels on growth (20). Keck and Ogren (13) suggested that increased affinity of RuBPC for CO_2 in *P. milioides* relative to soybean, a C_3 species, largely accounted for its reduced O_2 inhibition of AP. However, other evidence (16, and unpublished data of R. H. Brown) shows little or no difference in carboxylation efficiency between *P. milioides* and C_3 species.

Elevated activities of PEPC in *P. milioides* (13, 14, 17) may partially explain the reduced O_2 inhibition and low Γ in this species. Björkman *et al.* (1) found PEPC levels in some progeny of a cross between C_3 and C_4 species to be higher and Γ lower than in the C_3 parent, but O_2 inhibition of AP was not reduced compared to that of the C_3 species. Therefore, higher PEPC activity *per se* does not lead to reduced O_2 sensitivity of AP; compartmentalization of carboxylation reactions as in C_4 species is probably required.

Rathnam and Chollet (21) demonstrated rather high activities of PEPC in mesophyll cells of *P. milioides* and low activities in bundle sheath strands. Activities of RuBPC were high in bundle sheath strands and low in mesophyll cells. Thus, a differential compartmentation of the two carboxylases in this species was demonstrated. In addition, inhibition of PEPC by malonate or maleate increased O_2 inhibition of photosynthesis in leaf slices of *P. milioides* to the level exhibited by C_3 species (22). From these results it was proposed that the reduced inhibition of photosynthesis by O_2 in *P. milioides* was due to operation of a C_4 carbon assimilation cycle. Ku *et al.* (17) could find no differential compartmentalization of PEPC, RuBPC, or decarboxylating enzymes in mesophyll and bundle sheath cells of *P. milioides*. In addition, $^{13}C/^{12}C$ ratios (4, 5) and $^{14}CO_2$-labeling experiments (10, 12, 17) indicate little or no role for C_4 metabolism in CO_2 fixation in *P. milioides* at atmospheric CO_2 levels.

P. schenckii and *P. decipiens* have also been identified as C_3-C_4 intermediates with physiological and anatomical characteristics similar to *P. milioides* (18). *P. milioides*, *P. schenckii*, and *P. decipiens* are closely related species belonging to the Laxa group of *Panicum*. In the experiments reported in this paper we compared physiological and biochemical characteristics of the three intermediate *Panicum* species and four other species of the Laxa group of *Panicum* with a well known C_3 species, tall fescue (*Festuca arundinacea* Schreb.), and a C_4 plant, *P. maximum* Jacq.

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[2] Abbreviations: AP: apparent photosynthesis; Γ: CO_2 compensation concentration; RuBPC: ribulose 1,5-bisphosphate carboxylase; PEPC: phosphoenolpyruvate carboxylase; PR: photorespiration.

MATERIALS AND METHODS

Plant Material. Seven species in the *Laxa* group of *Panicum* were grown in pots for these experiments. They were *P. prionitis* Griseb., *P. laxum* Sw., *P. hylaeicum* Mez., *P. rivulare* Trin., *P. schenckii* Hack., *P. decipiens* Nees ex Trin., and *P. milioides* Nees ex Trin. Tall fescue (cv. "Kentucky 31") was used as a C_3 control and *P. maximum* as a C_4 control species. Three vegetative cuttings of each species were transplanted to each of three pots filled with a sandy loam soil. Plants were grown in the greenhouse under supplemental lighting from multivapor lamps which provided a photosynthetic photon flux density of 1,000 to 1,200 μE m^{-2} s^{-1}. Species were arranged at random in three blocks on the greenhouse bench. Plants were watered with half-strength Hoagland solution modified to contain $(NH_4)_2SO_4$ as the only N source. Plants were also fertilized every 7 days with NH_4NO_3 a few weeks prior to and during the gas exchange measurements. At the time measurements of gas exchange and enzyme activities were made plants had been growing for 2 to 3 months.

Gas Exchange Measurements. Apparent photosynthesis measurements were performed in an open system described by Morgan and Brown (18). Gases from pressurized cylinders containing 0.5 and 48% O_2 were mixed to provide mixtures with 2, 6, 21, or 48% O_2 and 335 ± 3 μl l^{-1} of CO_2. The gas mixture was bubbled through water at a constant temperature to raise the dew point to approximately 16 C. Leaf temperature was maintained at 25 C and monitored with a thermocouple touching the underside of the leaf. Leaves were exposed to a photosynthetic photon flux density of 1600 μE m^{-2} s^{-1} during AP measurement.

Measurements of Γ were conducted with the Mylar bag technique as previously described by Morgan and Brown (18). Determinations of Γ were made at three O_2 levels, 2.5, 21, and 44.5%. Temperature and photosynthetic photon flux density inside the Mylar bags were 27.5 C and 914 μE m^{-2} s^{-1}, respectively.

Enzyme Preparation and Assays. Whole leaf extracts were obtained by grinding approximately 1 g of tissue, transverse segments about 1 mm in width, in a mortar and pestle with acid-washed sand and the medium (5 ml total) of Gutierrez *et al.* (11). The ground material was centrifuged at 1,100*g* for 1 min. The supernatant was passed over a Sephadex G-25 M column (Pharmacia PD-10), and the eluant was used in enzyme assays.

RuBPC and PEPC were assayed at 30 C according to Willmer *et al.* (23). PEP carboxykinase was assayed at 30 C by the exchange reaction according to Dittrich *et al.* (6). NADP-malic and NAD-malic enzymes were assayed spectrophotometrically at room temperature (23). Chl was determined by the method of Wintermans and DeMots (24). Enzyme data are presented as averages from two separate experiments.

RESULTS

Effect of O_2 on AP. O_2 inhibition of AP increased in all but two species as O_2 concentrations were increased (Fig. 1). *P. maximum* and *P. prionitis* were insensitive to O_2 over the range tested. The lack of response to O_2 is typical of that reported for C_4 species (2). Tall fescue, *P. laxum, P. hylaeicum,* and *P. rivulare* were the most sensitive species. The per cent inhibition of AP by 21% O_2 for this group ranged from 28.2 for *P. hylaeicum* to 36.0 for *P. rivulare. P. milioides, P. schenckii,* and *P. decipiens* exhibited responses to O_2 intermediate to those of the other species tested. The inhibition of AP at 21% O_2 varied from 20.6 to 23.3%. The species were divided by analysis of variance into three groups: (*a*) those whose O_2 response (per cent inhibition at 21% O_2) was not significantly different from the C_3 control species (*P. laxum, P. hylaeicum,* and *P. rivulare*); (*b*) the one species not significantly different from the C_4 control (*P. prionitis*); and (*c*) those which differed significantly from both controls (*P. milioides, P. schenckii,* and *P. decipiens*). Photosynthesis in those species most sensitive to O_2 appeared to decrease in a curvilinear fashion with increases in O_2 at low levels, whereas those with intermediate sensitivity showed a nearly linear decrease over the 2 to 48% O_2 range.

Effect of O_2 on Γ. The O_2 response of Γ of the eight *Panicum* species and tall fescue is displayed in Figure 2. This graph reveals a pattern among species similar to that found with the O_2 responses of apparent photosynthesis. *P. maximum* and *P. prionitis* had relatively low values which were affected little by changes in O_2, although Γ of both species tended to increase at high O_2 levels. *P. laxum, P. hylaeicum, P. rivulare,* and tall fescue had higher values which increased greatly as O_2 was increased. The relative responses of these four species to O_2 were similar.

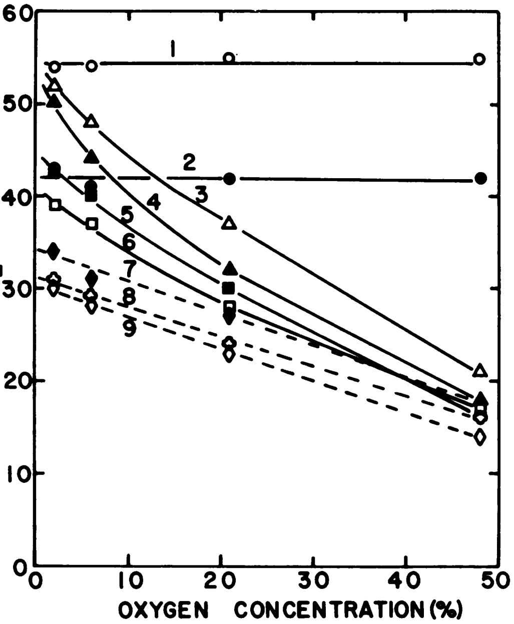

FIG. 1. AP of *Panicum* species and tall fescue at four O_2 concentrations. 1: *P. maximum*; 2: *P. prionitis*; 3: *P. laxum*; 4: *P. rivulare*; 5: tall fescue; 6: *P. hylaeicum*; 7: *P. schenckii*; 8: *P. milioides*; 9: *P. decipiens*.

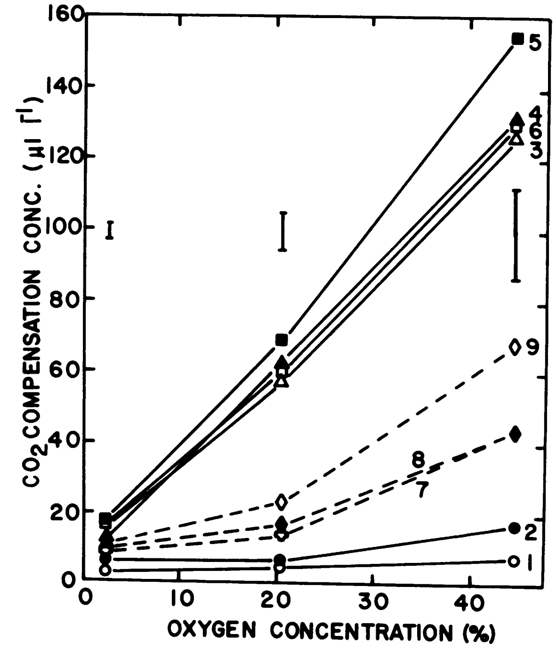

FIG. 2. O_2 response curves of the CO_2 compensation concentration of *Panicum* species and tall fescue. Identity of species are the same as in Figure 1. Vertical bars are the least significant differences among species at the 0.05 level of probability.

Table I. *Activities of Five Photosynthetic Enzymes in Eight Panicum Species and in Tall Fescue*

Species	PEPC[a]	RuBPC	RuBPC/PEPC	PEPCK	NADP-ME	NAD-ME
			μmol/mg Chl·h			
P. maximum	363	117	0.32	1,988	6	21
P. prionitis	1,509	64	0.04	ND[b]	126	21
P. decipiens	66	120	1.82	ND	18	16
P. milioides	88	144	1.63	ND	24	26
P. schenckii	92	137	1.49	ND	15	18
Tall fescue	45	548	12.2	ND	10	16
P. hylaeicum	46	142	3.09	ND	12	10
P. laxum	56	144	2.57	ND	12	12
P. rivulare	68	440	6.47	ND	11	14

[a] PEPC: phosphoenolpyruvate carboxylase; RuBPC: ribulose 1,5-bisphosphate carboxylase; PEPCK: phosphoenolpyruvate carboxykinase; NADP-ME: NADP-malic enzyme; NAD-ME: NAD-malic enzyme.

[b] Not detectable.

The values of Γ for *P. decipiens, P. milioides,* and *P. schenckii* are intermediate to those observed in the previous two groups of plants, and this intermediacy becomes especially evident at the highest O_2 concentrations used. These intermediate Γ values are all significantly different at the 0.05 probability level from those of tall fescue and *P. maximum* at all O_2 concentrations except 21% O_2 where Γ for *P. schenckii* was not significantly different from that of *P. maximum* (Fig. 2). The slope of the curve relating Γ to O_2 in the intermediate species was decidedly biphasic and less steep than the slope observed in tall fescue and the other C_3 *Panicum* species (Fig. 2). The slopes for the C_3 *Panicum* species and tall fescue deviated only slightly from linearity.

Enzyme Activities. Activity of PEPC, the primary carboxylating enzyme in C_4 plants, was greatest in *P. maximum* and *P. prionitis* (Table I). Considerably lower activity of PEPC was detected in the remaining species. *P. milioides* and *P. schenckii* displayed the greatest activity of PEPC among the O_2-sensitive species whereas *P. decipiens* had activity similar to that of *P. rivulare.* RuBPC activity in tall fescue was 548 μmol mg Chl^{-1} h^{-1}. With the exception of *P. rivulare,* which had an activity of 440 μmol mg Chl^{-1} h^{-1}, the remaining grasses generally exhibited approximately one-fourth the activity of RuBPC detected in tall fescue.

The ratio of RuBPC/PEPC activity was highest in tall fescue and the other C_3 *Panicums. P. milioides, P. schenckii,* and *P. decipiens* displayed the smallest ratio of RuBPC/PEPC activity among the O_2-sensitive *Panicums* due to their possession of somewhat elevated activity of PEPC. These ratios were much greater than those of the C_4 species.

High activities of decarboxylating enzymes were present only in *P. maximum* and *P. prionitis. P. maximum* had high activity of PEP carboxykinase activity in agreement with earlier reports of it being a PEP carboxykinase-type C_4 plant (9). *P. prionitis* exhibited high activity of NADP-malic enzyme activity, indicating that it is an NADP-malic enzyme-type C_4 plant. None of the other species had decarboxylase activities approaching those found in the C_4 species. Activities of both NAD- and NADP-malic enzymes were slightly higher in *P. milioides,* however, than in those species whose O_2 responses were typical of C_3 species.

DISCUSSION

The gas exchange and enzyme activity data presented in this paper indicate clear-cut differences in CO_2 metabolism among species assigned to the *Laxa* group of *Panicum. P. prionitis,* the only species studied in the *Laxa* group whose AP was insensitive to O_2, was found to be an NADP-malic enzyme-type C_4 species. Anatomical characteristics (18) and $^{13}C/^{12}C$ ratios (5) also indicate that it possesses the C_4 cycle of CO_2 fixation. Three *Panicum* species responded to O_2 in a manner similar to tall fescue and exhibited Γ values and enzyme activities rather typical of C_3 species, although RuBPC activity in *P. hylaeicum* and *P. laxum* was less than one-half that in tall fescue. The *Panicum* species which exhibited a reduced O_2 response compared to most C_3 plants also had lower Γ values which were less sensitive to O_2 concentrations. The lower Γ and reduced response of AP to O_2 in *P. schenckii* and *P. decipiens* were similar to that observed in these experiments and reported earlier for *P. milioides* (4, 10, 13–15, 18, 20).

In earlier studies of *P. milioides* its intermediate characteristics were related to activities of enzymes involved in photosynthesis (10, 14). The ratio of activities of RuBP oxygenase/PEPC in C_3, C_4, and intermediate species was related linearly to Γ in those studies. The RuBPC/PEPC ratio was also related to Γ, but in a curvilinear pattern with Γ being highest in those species with high ratios. Activity of RuBP oxygenase was not determined in our study, but the RuBPC/PEPC ratio was not closely related to Γ in these species. The ratio for the intermediate species ranged from 1.49 in *P. schenckii* to 1.82 in *P. decipiens* (Table I). These values are similar to those reported earlier for *P. milioides* (17). A ratio of 12.2 was obtained for tall fescue, a value typical of those reported for cool season C_3 grasses (3, 17). The lack of relationship between the ratio RuBPC/PEPC and Γ was due to the lower ratio in the C_3 *Panicum* species (2.57–6.47) which had Γ values similar to tall fescue. The low RuBPC/PEPC ratios in the C_3 *Panicums* in this study may be typical of *Panicum* species with the C_3 pathway. Black *et al.* (3) reported a value of 4.18 for *P. communtatum* and Ku *et al.* (17) obtained a ratio of 6.4 for *P. bisulcatum.* In both cases cool season grasses had ratios more than twice as high as the C_3 *Panicums.*

The relative insensitivity of Γ in *P. milioides, P. schenckii,* and *P. decipiens* to low O_2 levels is similar to the decreased sensitivity observed by Keck and Ogren (13) in *P. milioides* and may be due to participation of PEPC in CO_2 fixation in these species at low CO_2 concentrations. Kestler *et al.* (14) found that 16% of the ^{14}C assimilated by *P. milioides* was in malate plus aspartate when CO_2 concentration was near Γ. The slope of Γ-O_2 relationship for the intermediate species in our study was also less than those of the C_3 species at high O_2 levels. Keck and Ogren (13) attributed the lower sensitivity of Γ in *P. milioides* at O_2 levels above 10% to a smaller $K_m(CO_2)$ of RuBPC in *P. milioides* than in soybean and recycling of CO_2 by PEPC. The difference in $K_m(CO_2)$ for RuPBC in *P. milioides* and soybean was not great, however, and $K_i(O_2)$ of the enzyme was virtually the same.

The lower response of Γ to O_2 in *P. milioides, P. schenckii,* and *P. decipiens* gives a relatively poor indication of O_2 effects on photorespiration, since Γ reflects a balance between CO_2 efflux and influx but not rates of processes involved. If the data in Figures 1 and 2 are used to estimate photorespiration and leaf conductance to CO_2, then effects of O_2 on these two parameters can be visualized. Total conductance to $CO_2(g_t)$ was defined as,

$$g_t = \frac{AP}{C_a - \Gamma}$$

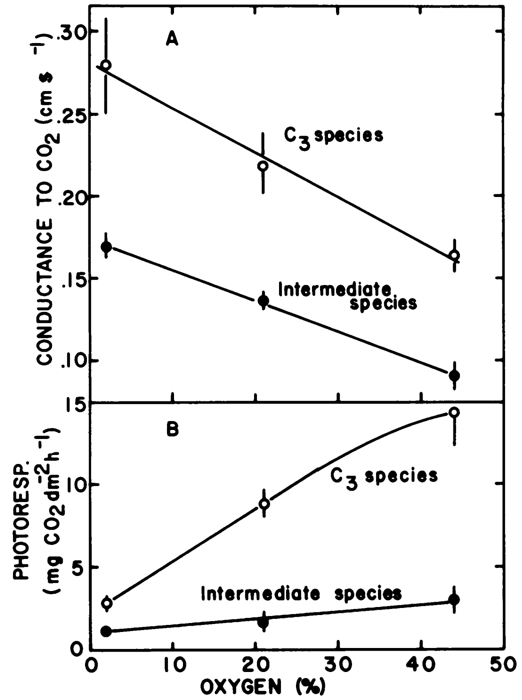

FIG. 3. Estimates of total leaf conductance (k_t) to CO_2 and photorespiration (PR) for C_3 (tall fescue, *P. laxum*, *P. hylaeicum*, and *P. rivulare*) and intermediate (*P. milioides*, *P. schenckii*, and *P. decipiens*) species at three oxygen centrations. Estimates of AP rates at 44.5% O_2 were interpolated from the data presented in Figure 1 to obtain values of PR and g_t at 44.5% O_2. Vertical bars represent ± SD of the means.

where C_a = external CO_2 concentration. Photorespiration was estimated as the intercept of the AP-C_a relationship at $C_a = 0$, thus PR = $g_t\Gamma$. Limitations to the estimates obtained in this way are that: (*a*) AP and Γ were not determined under exactly the same conditions; (*b*) some of the photorespired CO_2 is refixed before escaping the leaf and is thus undetected; and (*c*) the CO_2 response curve of AP may not be linear between Γ and $C_a = 0$. Because of the second limitation, and perhaps the third, PR is underestimated. Nevertheless, the relationships are worth considering because they indicate the nature of the reduced O_2 response in the intermediate *Panicum* species.

Average values of g_t and PR for the intermediate and C_3 species are presented in Figure 3. Average PR values for the C_3 species increased from 2.9 mg CO_2 dm^{-2} h^{-1} at 2% O_2 to 14.4 mg CO_2 dm^{-2} h^{-1} at 44% O_2 (Fig. 3B), an O_2 effect on PR similar to that reported for other C_3 species (8). In the intermediate species, however, estimated PR was low and responded very little to O_2. In contrast to O_2 effects on PR, the slopes of the CO_2 response curves (g_t) were affected in a similar way in the C_3 and intermediate species as shown by the similar slopes in Figure 3A. Although the g_t values in Figure 3A include conductance of the air-leaf boundary layer and stomata, these have been shown to be unaffected by O_2 (19), so the effect of O_2 is mainly on mesophyll conductance. The O_2 response of mesophyll conductance has been attributed mainly to its effect on carboxylation (13). If a portion of the CO_2 assimilated by the intermediate *Panicums* is fixed by a C_4 cycle as proposed by Rathnam and Chollet (21, 22) for *P. milioides*, a decrease in O_2 sensitivity of carboxylation efficiency and PR would probably result. It appears, however, that the reduced response of AP to O_2 in *P. milioides*, *P. schenckii*, and *P. decipiens* is due mainly to a low and unresponsive PR rather than reduced inhibition of carboxylation of RuBP. A similar conclusion is drawn by Brown (unpublished data) from a study of O_2 effects on the response of AP to intercellular CO_2 concentration in *P. milioides* and *P. schenckii*.

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