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Steady-State Photosynthesis in Alfalfa Leaflets

EFFECTS OF CARBON DIOXIDE CONCENTRATION[1]

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STEVEN G. PLATT,[2] ZVI PLAUT,[3] AND JAMES A. BASSHAM
Laboratory of Chemical Biodynamics, Lawrence Berkeley Laboratory, University of California, Berkeley, California 94720

ABSTRACT

When the CO_2 concentration to which *Medicago sativa* L. var. El Unico leaflets were exposed was increased from half-saturation to saturation (doubled rate of photosynthesis), glycolate and glycine production apparently decreased due to inhibition of a portion of the glycolate pathway. Serine and glycerate production was not inhibited. We conclude that serine and glycerate were made from 3-phosphoglycerate and not from glycolate and that the conversion of glycine to serine may not be the major source of photorespiratory CO_2 in alfalfa. In investigations of glycolate and photorespiratory metabolism, separate labeling data should be obtained for glycine and serine as those two amino acids may be produced from different precursors and respond differently to environmental perturbations. The increased photosynthetic rate (at saturating CO_2) resulted in greater labeling of both soluble and insoluble products. Sucrose labeling increased sharply, but there was no major shift of tracer carbon flow into sucrose relative to other metabolites. The flow of carbon from the reductive pentose phosphate cycle into the production of tricarboxylic acid cycle intermediates and amino acids increased. Only small absolute increases occurred in steady-state pool sizes of metabolites of the reductive pentose phosphate cycle at elevated CO_2, providing further evidence that the cycle is well regulated.

In recent years there has been increased interest in the growth of plants in atmospheres with elevated CO_2 levels, which cause increased rates of production (26, 27) and increased N_2 fixation in legumes (8). We have described an apparatus and a set of experimental techniques that allow us to obtain data on the concentrations of numerous labeled metabolites during photosynthesis with $^{14}CO_2$ by whole alfalfa leaflets (15, 16). With this method, the flow of labeled C during steady-state and perturbed photosynthesis (1) in whole leaflets can be investigated to a degree that was not previously possible. Given the advantages of growing alfalfa at elevated CO_2 levels and the potential use of alfalfa leaves as a source of protein for direct human consumption (5), we have now investigated the effect of CO_2 concentration on alfalfa photosynthetic metabolism using $^{14}CO_2$ as a tracer.

Most previous investigators of the effects of $^{14}CO_2$ concentration on photosynthetic leaf metabolism in higher plants did not examine changes in labeling occurring as a function of time during perturbed steady-state photosynthesis with $^{14}CO_2$. Rather, leaf material was exposed to fixed $^{14}CO_2$ concentrations for fixed periods of time (13, 19). Mahon *et al.* (12) did remove samples as a function of time, however, $^{14}CO_2$ exposure time was insufficient to label PGA[4] completely. Some investigators concerned themselves primarily with metabolites of the glycolate pathway (12, 19) rather than with the flow of carbon to all early metabolites under conditions of differing CO_2 concentration.

Snyder and Tolbert (19) recently presented data suggesting that high levels of CO_2 may not suppress glycolate pathway metabolite production and photorespiration (both taken to be indicated by glycine plus serine production). We, however, present data indicating that glycolate and glycine production in alfalfa is inhibited by saturating levels of CO_2, while serine production is not. The apparently different origins of glycine and serine under our conditions, and the need for separate labeling data on those two metabolites are discussed.

MATERIALS AND METHODS

Plant Material. Alfalfa (*Medicago sativa* L. var. El Unico) seeds were planted in 12 cm of vermiculite. The plants were grown at 3,000 ft-c and 15 C with a 9-hr light period and a 15-hr dark period. Plants were fertilized with modified Hoagland solution, and leaflets were selected and excised as described earlier (15).

Steady-State Photosynthesis Apparatus. The apparatus used to obtain and follow steady-state photosynthesis by excised whole alfalfa leaflets was described earlier (15). Its components include a closed gas recirculation system, $^{14}CO_2$ and $^{12}CO_2$ supply systems, a leaflet exposure device, and two light banks. $^{12}CO_2$, $^{14}CO_2$, and O_2 content in the gas stream is continuously recorded. Light intensity (sum of the intensity supplied to the upper and lower surfaces of the leaflets) was 3,600 ft-c. The air temperature within the leaflet exposure chamber was measured with a thermocouple.

Photosynthetic Rates and CO_2 Compensation Point. Several preliminary experiments were conducted using sets of 15 to 60 whole excised alfalfa leaflets, the steady-state leaf exposure device, and $^{12}CO_2$ in order to determine alfalfa photosynthetic rate (μmol CO_2/hr·mg Chl) and its CO_2 compensation point under various conditions. CO_2 and O_2 concentrations were varied as desired through manipulation of gas reservoirs (15), and through slow addition of $^{12}CO_2$, O_2, and N_2 to the circulating gas

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[2] To whom requests for reprints should be addressed. Present address: Western Regional Research Center, A.R.S., U.S.D.A., Berkeley, Calif. 94710.

[3] Present address: Agricultural Research Organization, Bet-Dagan, Israel.

[4] Abbreviations: C_3 plants: plants which initially fix CO_2 primarily by the photosynthetic carbon reduction or C_3 cycle; F6P: fructose 6-phosphate; PEPA: phosphoenolpyruvate; PGA: 3-phosphoglyceric acid; UDPG: uridine diphosphoglucose; RPP: reductive pentose phosphate; TCA: tricarboxylic acid.

stream. Rates were calculated from the slope of the $^{12}CO_2$ recorder trace (CO_2 concentration as a function of time), system gas volume, and leaflet Chl content (2). The rate under a given set of conditions was determined after preliminary photosynthesis under those conditions for approximately 10 min. Rates are reported at the average CO_2 concentration prevailing during the measurement period (CO_2 concentration range during those periods was not greater than ±8% of the average concentration). The CO_2 compensation point at 20% O_2 was determined in a closed system starting with an initial CO_2 concentration above compensation in one case and below compensation in a second determination. The two determinations were averaged. The compensation point at 5% O_2 was determined by allowing photosynthesis to occur until the CO_2 concentration in the closed system was reduced to the compensation point value.

Perturbed Steady-State Photosynthetic $^{14}CO_2$ Fixation. Two similar experiments, A and B, were conducted. In each, 60 alfalfa leaflets were exposed to $^{14}CO_2$ in air using the steady-state photosynthesis apparatus. In both experiments, leaflets were first exposed to $^{12}CO_2$ for a period of time previously shown to be sufficient to bring about a steady rate of photosynthesis (15). In experiment A, that period was followed by three successive periods of photosynthesis with $^{14}CO_2$; half-saturating, then saturating, then half-saturating. In experiment B, the final period of photosynthesis with half-saturating $^{14}CO_2$ was omitted. The exact $^{14}CO_2$ concentrations used are shown under "Results." $^{14}CO_2$ concentrations refer to the total amount of CO_2 present during the periods of exposure to tracer. A concentration of X% $^{14}CO_2$ means X% total CO_2 was present. Experiment A was conducted at 16 C ± 1 C, 3,600 ft-c, 21% O_2, and with $^{14}CO_2$ of specific radioactivity 25.8 μCi/μmol. Experiment B was conducted at 18 C ± 1 C, 3,600 ft-c, 20% O_2, and with $^{14}CO_2$ of specific radioactivity 22.3 μCi/μmol.

Fifteen samples (each containing four leaflets) were removed in each experiment as a function of time of exposure to $^{14}CO_2$. Each sample was immediately frozen and ground in liquid N_2, and then ground with 80% ethanol (v/v) in a dry ice-acetone bath. The leaflet powder was extracted with 13 ml 80% ethanol (dark, 20 C) and the Chl content was determined (2). The leaflet powder was then successively extracted with 4 ml 20% ethanol (25 C) and twice with 2 ml water (85 C ± 10 C). The extracts of each sample were combined. The pellet from each sample was collected on filter paper in a Büchner funnel, washed with several drops of formic acid, and dried in a vacuum dessicator over silica gel and KOH. The dried pellets were combusted (Packard automatic combustion apparatus) to give data on $^{14}CO_2$ fixation into insoluble materials. Sample extracts were analyzed by liquid scintillation for fixation into soluble metabolites (15).

$^{14}CO_2$ fixation into individual soluble metabolites was analyzed by two-dimensional paper chromatography. Four chromatograms were developed for each sample. Most metabolites were determined from chromatograms developed for 24 hr in each direction, and 48 hr in each direction using, with one modification, the solvent system of Pedersen *et al.* (14). The pH of the phenol-water-acetic acid-EDTA solvent used in the 24-hr development was adjusted to pH 4.2. Quantitative glycolate isolation and glycine and serine isolation were accomplished on two sets of chromatograms (16). Radioactive areas were located, major labeled metabolites identified, and radioactivity in each compound determined as described earlier (14, 15). Fixation results were expressed on the basis of μg atoms ^{14}C/mg Chl fixed into each metabolite and into total, soluble, and insoluble products. The μg atoms of ^{14}C given under "Results" were calculated by dividing the radioactive contents of the product in μCi by the specific radioactivity of the entering $^{14}CO_2$.

RESULTS

Photosynthetic Rates and CO_2 Compensation Point. The dependence of the alfalfa leaflet's net photosynthetic rate upon CO_2 concentration (23% O_2, 18 C, 3,600 ft-c) was as follows. At low levels of CO_2 the rate of photosynthesis increased with increasing CO_2 and saturation was reached at approximately 0.06% CO_2. The CO_2 concentration at half-saturation (when the photosynthetic rate was half of its maximal value) was 0.023%.

The rate of photosynthesis of alfalfa leaflets was also found to be strongly dependent on the atmospheric O_2 content (Fig. 1, 0.035% CO_2, 23 C, 3,600 ft-c). A photosynthetic rate increase of 50% was observed upon lowering the O_2 concentration from 21 to 2%. In experiments with two additional sets of leaflets, the photosynthetic rate at 0.025% CO_2 and 18 C increased by an average of 41% on lowering the O_2 concentration from 20 to 2%.

We determined that the compensation point (18 C) for our leaflets in the presence of 20% O_2 was 0.0049% CO_2. The compensation point value was O_2-sensitive and decreased to below 0.0010% CO_2 in the presence of 5% O_2.

Perturbed Steady-State $^{14}CO_2$ Fixation. The rate of photosynthesis was 72 μmol $^{14}CO_2$/hr·mg Chl during the first period of experiment A (Fig. 2). Similar data were obtained in experiment B. The over-all rate of photosynthesis doubled in both experiments when the $^{14}CO_2$ concentration was raised. The increase was reflected in the rates of labeling of both soluble and insoluble products with approximately 40% of the total increase accounted for by an increased labeling of solubles. During the final period of experiment A the photosynthetic rate decreased to about the same value as during the first period of low $^{14}CO_2$ concentration (Fig. 2).

Elevated $^{14}CO_2$ concentration brought about an immediate increase in the rates of labeling of alanine (Fig. 3), malate, citrate, aspartate, and glutamate (Fig. 4) during experiment A and experiment B (data not shown).

In experiment A, PGA (Fig. 5) and the sugar mono- and diphosphates (labeling curves similar in shape to that shown for PGA) reached label saturation during the initial period of photosynthesis with low concentration $^{14}CO_2$, and approximately doubled in steady-state pool size when the $^{14}CO_2$ concentration was raised. PEPA (Fig. 4) increased by a greater percentage. The total labeling increase observed for the RPP cycle metabolites was 0.9 μg atoms ^{14}C/mg Chl, which is equivalent to less than 1 min of the additional ^{14}C incorporation occurring at saturating CO_2 (1.3 μg atoms ^{14}C/min·mg Chl). During experiment B, the steady-state pool sizes of PGA and the other identified RPP cycle metabolites (sugar mono- and diphosphates except F6P) were virtually unchanged when the $^{14}CO_2$ concentration was raised (data shown only for PGA, Fig. 6). Absolute F6P labeling increased by a small amount (from 0.06 to 0.09 μg atoms ^{14}C/mg Chl).

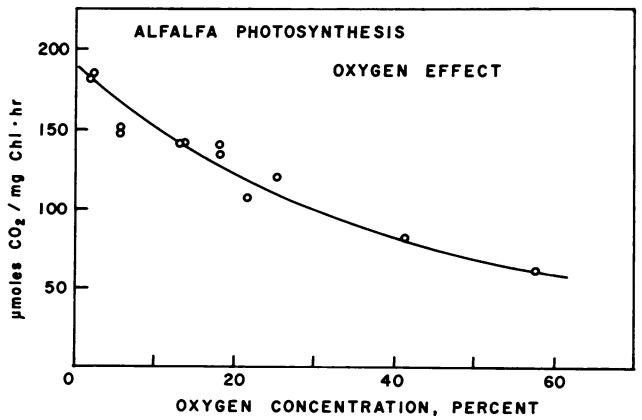

FIG. 1. Alfalfa leaflet photosynthetic rate in relation to O_2 concentration at 0.035% CO_2, 23 C, and 3,600 ft-c.

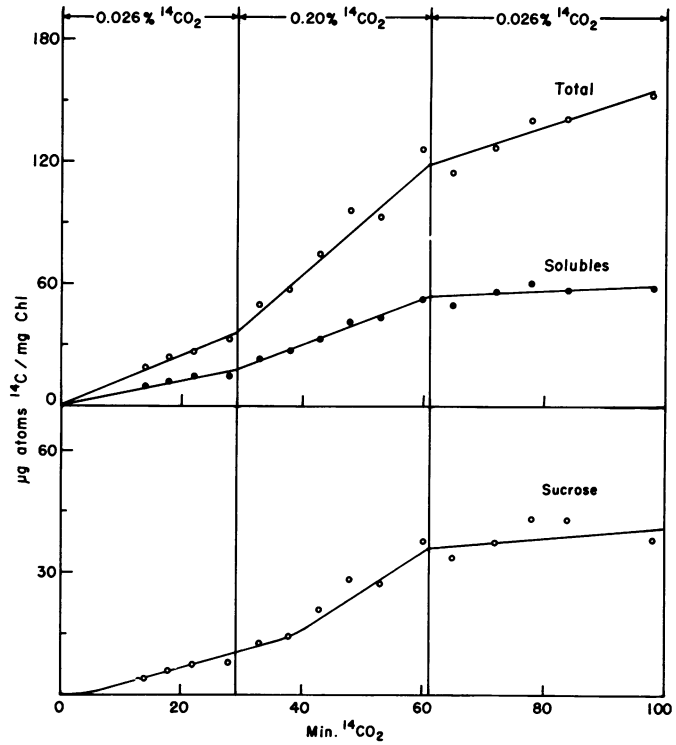

FIG. 2. Total photosynthetic ^{14}C incorporation, ^{14}C incorporation into soluble products, and ^{14}C incorporation into sucrose by alfalfa leaflets exposed to $^{14}CO_2$ (25.8 μCi/μmol) in air at 3,600 ft-c and 16 C ± 1 C (experiment A).

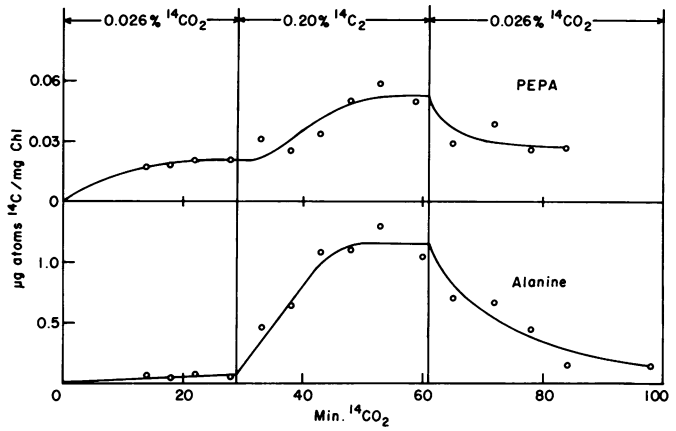

FIG. 3. Labeling of PEPA and alanine in alfalfa leaflets photosynthesizing with $^{14}CO_2$ under the conditions described in Figure 2 (experiment A).

Labeling curves for glycerate and serine in experiment A were similar to that for PGA, however, labeling curves for glycine and glycolate were different (Fig. 5). Steady-state pool sizes of PGA, glycerate, and serine increased when the $^{14}CO_2$ concentration was raised, and declined when the $^{14}CO_2$ concentration was returned to its initial value. Glycolate and glycine labeling declined when the $^{14}CO_2$ concentration was raised and increased when the $^{14}CO_2$ concentration was readjusted to half-saturating.

In experiment B, as in A, the labeling curves obtained for PGA, glycerate, and serine were strikingly similar to each other and different from those obtained for glycine and glycolate (Fig. 6). The steady-state concentrations of recently fixed carbon found in the PGA, glycerate, and serine pools did not change when the $^{14}CO_2$ level was increased. Glycolate and glycine labeling, however, dropped rapidly when the $^{14}CO_2$ concentration was increased, indicating that the pool sizes of photosynthetically active glycolate and glycine had decreased.

The production of labeled glycine, glycerate, and serine during the initial period of photosynthesis with half-saturating $^{14}CO_2$ was substantial and similar in both experiments. After 14 min of photosynthesis with $^{14}CO_2$ during experiment A, 8% of the soluble ^{14}C was present in glycine, 7% in serine, and 8% in glycerate.

Elevated $^{14}CO_2$ concentration resulted in higher UDPG and F6P steady-state levels in both experiments (data not shown). Sucrose was the major soluble product formed, and its rate of labeling increased at elevated levels of $^{14}CO_2$ (Fig. 2). Sucrose labeling accounted for 35% of the total photosynthetic rate during the first period of experiment A and 29% of that rate during the first period of experiment B. The absolute labeling rate of sucrose increased greatly under the condition of high $^{14}CO_2$. However, its labeling as a per cent of the total fixation rate increased to only 37% in experiment A and 40% in experiment B.

DISCUSSION

CO_2 concentrations used in the labeling experiments were chosen on the basis of data obtained for the dependence of photosynthetic rate upon CO_2 concentration. The CO_2 compensation point of El Unico alfalfa, 0.0049% CO_2 at 18 C and 20% O_2, is in accord with a previous determination that alfalfa is a high compensation point species (10). The variation of photosynthetic rate with O_2 concentration, the high compensation point of the leaflets at air level O_2, and the O_2 dependence of that compensation point indicate that substantial photorespiration and O_2 inhibition of photosynthesis occur in alfalfa at 18 C (4, 6, 7, 27).

The data from both ^{14}C tracer experiments indicate the precise regulation of the RPP cycle and of the carbon flow from it.

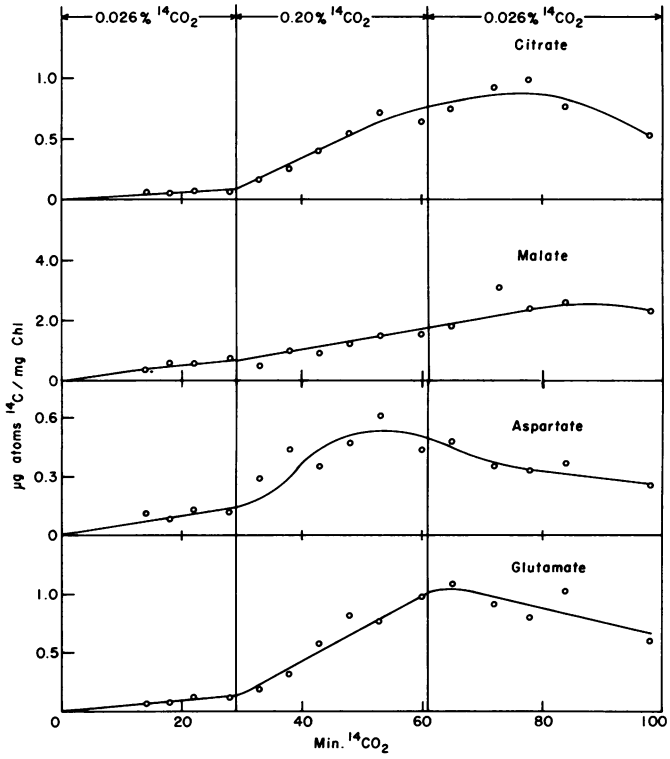

FIG. 4. Labeling of citrate, malate, aspartate, and glutamate in alfalfa leaflets photosynthesizing with $^{14}CO_2$ under the conditions described in Figure 2 (experiment A).

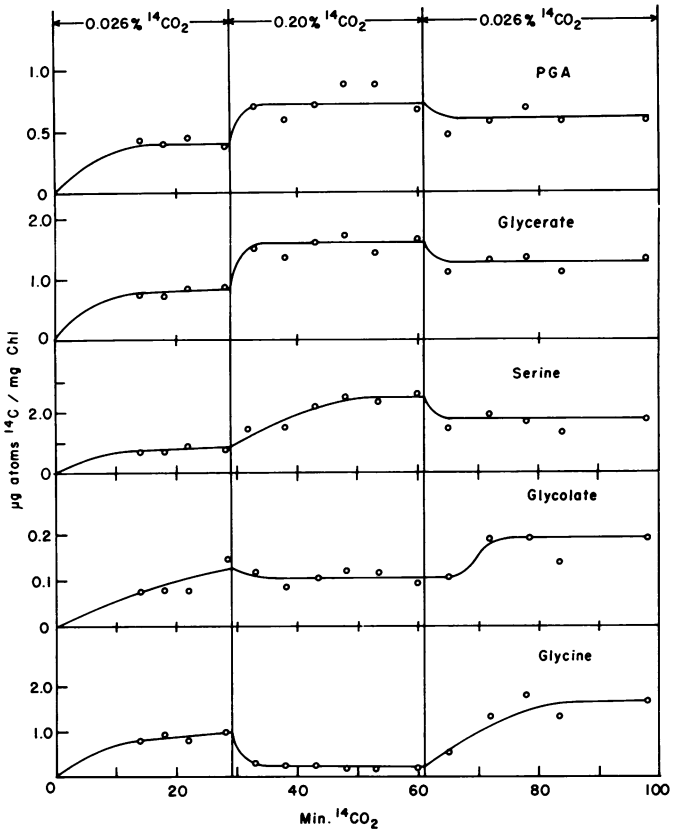

FIG. 5. Labeling of several metabolites in alfalfa leaflets photosynthesizing with $^{14}CO_2$ under the conditions described in Figure 2 (experiment A).

Absolute steady-state pool sizes of the RPP cycle metabolites PGA and the sugar mono- and diphosphates were essentially unchanged during experiment B and increased in experiment A by only a small amount (relative to the additional $^{14}CO_2$ incorporation occurring) at saturating $^{14}CO_2$. This occurred even though $^{14}CO_2$ was clearly limiting and the photosynthetic rate doubled. Carbon withdrawal from the RPP cycle for use in leaf metabolism increased almost as rapidly as did $^{14}CO_2$ influx.

There was not a major shift in the proportion of carbon flow into sucrose at elevated $^{14}CO_2$. While the absolute labeling rate of sucrose greatly increased, its labeling as a percentage of the total fixation rate increased by little in one experiment and only moderately in the other. Sharp increases in relative sucrose labeling at elevated $^{14}CO_2$ observed in some previous nonkinetic and shorter term experiments with other plant species (13, 19) may be partly due to differences in extents of saturation of sucrose precursors at high and low CO_2.

The increased rates of labeling of malate, citrate, and some amino acids (Figs. 3 and 4) with high CO_2 suggest that there was an increased anapleurotic carbon flow into the TCA cycle. This could be due to stimulation of the carboxylation of PEPA and perhaps pyruvate due to elevated CO_2. The increased rate of labeling of alanine suggests an accelerated conversion of PEPA to pyruvate.

In summary, the over-all picture presented by the data of the labeling experiments is one of increases in tracer carbon flow to and through pools of numerous soluble metabolites including sucrose, producing generally increased rates of production of soluble and insoluble products at saturating $^{14}CO_2$. This is in accord with the increased productivity of many crop plants at elevated levels of CO_2, and supports the idea that alfalfa crop productivity could be enhanced through atmospheric manipulation.

Formation of glycolate, glycine, and serine in C_3 plants has been often attributed to the glycolate pathway sequence glycolate →→ glycine → serine →→ glycerate which is sometimes equated with the occurrence of photorespiration (17, 20-22). However, an alternative path for synthesis of glycine and serine has been proposed which does not depend upon glycolate synthesis and any concomitant photorespiration (18). That alternative path consists of the sequence, PGA → glycerate →→ serine → glycine, that is initiated by 3-P-glycerate phosphatase, an enzyme present in many plants including alfalfa (18). Evidence has already been obtained for production of glycerate from PGA during photosynthesis in several species of C_3 plants other than alfalfa (9, 17), although serine in those experiments appeared to be synthesized predominantly from glycolate.

In our experiments, an elevated concentration of $^{14}CO_2$ resulted in decreased levels of label in glycine and glycolate (Figs. 5 and 6), presumably due to decreased glycolate formation and decreased tracer carbon flow to glycine. In marked contrast, serine and glycerate steady-state levels during both experiments reflected the size of the PGA pool (increasing or remaining constant as did PGA concentration) and not the label in glycine and glycolate (Figs. 5 and 6). These results indicate that glycine is made from glycolate, whereas the predominant production of glycerate and serine is from PGA. Label in serine and glycerate either increased or remained constant at elevated $^{14}CO_2$ so that ^{14}C flow to those metabolites was apparently not inhibited.

It might be argued that in going from low CO_2 pressure to high CO_2, the pathway to serine changed completely so that serine was formed from glycolate under low CO_2 pressure and from PGA under high CO_2 pressure. While this is possible, we would

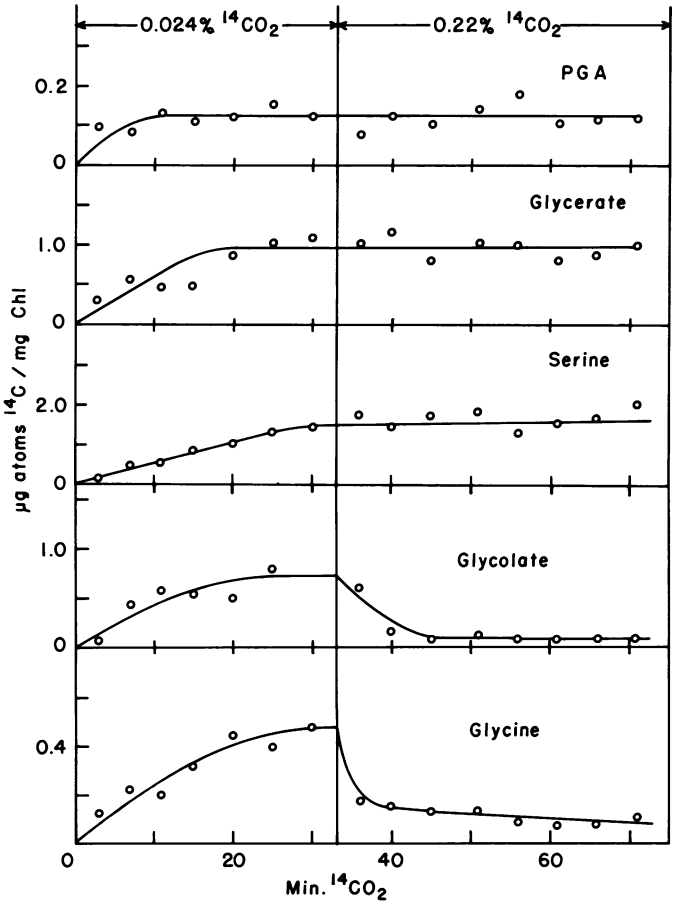

FIG. 6. Labeling of several metabolites in alfalfa leaflets photosynthesizing with $^{14}CO_2$ (22.3 μCi/μmol) in air at 3,600 ft-c and 18 C ± 1 C (experiment B).

not then have expected the serine level to follow the PGA level so closely in both tracer experiments. Our results cast some doubt on the notion that the conversion of glycine to serine is the major source of photorespiratory CO_2 in alfalfa. The predominant serine production from PGA in alfalfa, and our evidence for the occurrence of substantial photorespiration at least under low $^{14}CO_2$, indicate that alfalfa photorespiratory CO_2 release may occur mainly by mechanisms of glycolate oxidation that do not involve serine formation (28).

Some previously published evidence indicates serine production from PGA during photosynthesis by other higher plant C_3 species under certain conditions (24, 25). Data on soybean are contradictory, suggesting in one case that serine arises from glycolate (17), and in another from P-glycerate (23). The substantial levels of glycerate and serine labeling which we observed in alfalfa are comparable to levels of those metabolites observed in other C_3 species (11, 17).

Glycine- and serine-labeling data have often been used in drawing conclusions about the extent of operation of glycolate pathway metabolism and photorespiration (3, 11, 13, 19). Aside from the controversy (28) surrounding identification of the glycine to serine transformation as the main source of photorespiratory CO_2, conclusions about photorespiration, drawn on the basis of data on those two amino acids, can be of limited value given our observation that their labeling may respond quite differently to environmental perturbation. Information on only the sum of glycine and serine can be especially misleading as it may conceal different responses. Separate data on glycolate, glycine, and serine should be obtained. Serine labeling should not be taken to be indicative of glycolate metabolism unless that amino acid has been shown to arise from glycolate and not from glycerate under all conditions studied.

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