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Effect of Oxygen Concentration on ^{14}C-Photoassimilate Transport from Leaves of *Salvia splendens* L.[1]

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ABSTRACT

Partitioning and transport of recently fixed photosynthate was examined following $^{14}CO_2$ pulse-labeling of intact, attached leaves of *Salvia splendens* L. maintained in an atmosphere of 300 microliters per liter CO_2 and 20, 210, or 500 milliliters per liter O_2. Under conditions of increasing O_2 (210, 500 milliliters per liter), a smaller percentage of the recently fixed ^{14}C in the leaf was allocated to starch, whereas a greater percentage of the fixed ^{14}C appeared in amino acids, particularly serine. The increase in ^{14}C in amino acids was reflected in material exported from source leaves. A higher percentage of ^{14}C in serine, glycine, and glutamate was recovered in petiole extracts when source leaves were maintained under elevated O_2 levels. Although pool sizes of these amino acids were increased in both the leaves and petioles with increasing photorespiratory activity, no significant changes in either ^{14}C distribution or concentration of transport sugars (*i.e.* stachyose, sucrose, verbascose) were observed. The data indicate that, in addition to being recycled intracellularly into Calvin cycle intermediates, amino acids produced during photorespiration may also serve as transport metabolites, allowing the mobilization of both carbon and nitrogen from the leaf under conditions of limited photosynthesis.

Although considerable interest exists in intracellular recycling of both C and N during photorespiration (24, 26), little importance is attached to the possible role of the key photorespiratory intermediates as intercellular metabolites. For example, amino acids such as serine and glutamate, which are generated during the recycling of photorespiratory C and N, are also ubiquitous components of phloem exudates (30). This observation challenges the view that key photorespiratory intermediates are conservatively cycled within specific organelles or even within the cells where they are synthesized.

The effects of varying O_2 (3, 8, 16, 24) and CO_2 (24, 25, 28) levels on metabolism in source leaves are well documented. During photorespiration, the distribution of ^{14}C in starch in leaf tissues declines, concomitant with an increased incorporation of newly fixed C into glycine and serine (28, 29). Rates of movement of ^{14}C-labeled (21, 28) as well as ^{11}C- and ^{13}N-labeled (6) photoassimilates from source leaves under varying photorespiratory conditions have been reported previously. This paper identifies the metabolites actually exported from source leaves of *Salvia splendens* at varying O_2 levels.

MATERIALS AND METHODS

Plant Material. Twelve-week-old plants of *Salvia splendens* L. cv St. John's Fire (Stokes Seeds, St. Catherines, Ontario, Canada) were used for all experiments. Plants were grown from seed in a soil:peat:perlite mix (1:1:1, v/v) in a greenhouse under natural lighting with day temperatures of 25 to 30°C and night temperatures of 18 to 23°C. The plants were supplied once weekly with commercial 20:20:20 fertilizer.

Chemicals. $NaH^{14}CO_3$ (55.5 mCi mmol^{-1}) was obtained from New England Nuclear). Dansyl chloride (*N,N*-dimethyl-1-napthylamine-5-sulfonic acid chloride), authentic dansyl amino acids, and amyloglucosidase (from *Rhizopus*, 10,000 units g^{-1}) were purchased from Sigma Chemical Co. Porapak Q resin (80–100 mesh) was purchased from Chromatographic Specialties Ltd., Brockville, Ontario, Canada.

Photosynthesis Measurements. Intact, attached, fully expanded leaves were used for all experiments. An open gas-exchange system similar to that described by Ludwig and Canvin (14) was used for measurement of photosynthetic rates. The leaf was sealed into a Perspex leaf cuvette (6.5 ml internal volume [14]), and a humidified gas stream containing predetermined O_2 (supplied from commercially prepared cylinders) and CO_2 (generated by Wosthoff gas mixing pumps; H. Wosthoff, D463 Bochum, FRG) levels was passed over the leaf at a flow rate of 0.5 l min^{-1}. Light, provided by three 75-w incandescent lights and filtered through a 0.5% $CuSO_4$ solution, was supplied at an intensity of 540 μE m^{-1} s^{-1} (PAR, 400–700 nm) at the level of the cuvette surface. Photosynthetic rates were obtained using a ADC-225-MK3 IR gas analyzer (Analytical Development Co. Ltd., Hoddeson, U.K.) operated in the differential mode. Leaf temperature and chamber temperature were measured using YSI 1000 ohm precision themistors (Electro Sonic Inc., Willowdale, Ontario, Canada). Humidity and transpiration measurements were obtained with a EG & G model 911 Dew-All Digital Humidity Analyzer (EG & G Environmental Equipment, Waltham, MA).

$^{14}CO_2$ Pulse-Labeling. An intact leaf was allowed to photosynthesize in an atmosphere containing 300 μl l^{-1} CO_2 and 210 ml l^{-1} O_2 for 30 min to establish a steady rate of photosynthesis. The O_2 partial pressure of the gas mixture was then switched to 20, 210, or 500 ml l^{-1} and photosynthesis was allowed to continue for a further 30 min. The gas stream was then diverted from the leaf cuvette, and 10 μCi of $^{14}CO_2$, generated in a 10-ml syringe by the addition of 5 N H_2SO_4, was injected into the cuvette by inserting the syringe needle between the rubber seals holding the leaf in the cuvette. After a 1-min labeling period, the gas flow over the leaf was reestablished. After a 15-min chase period with unlabeled CO_2, the leaf and petiole were excised and extracted separately in boiling 80% ethanol. Chl content of the leaf tissues were determined using the method of Arnon (1).

^{14}C-Metabolite Analysis. Soluble ^{14}C-labeled products from leaves and petioles were removed by three further extractions in

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80% ethanol at 70°C. The extracts were pooled, reduced in volume to about 1 ml, passed through coupled 1-ml columns of Dowex 50 (H^+) and Dowex 1 (formate$^-$) and fractionated into neutral, basic, and weakly and strongly acidic components as described by Atkins and Canvin (2). Neutral compounds were separated by TLC on Eastman cellulose sheets in *n*-propanol:ethyl acetate:water (7:1:2, v/v), weakly acidic compounds in ethanol:NH_4OH:water (17:1:2, v/v) and basic compounds on Eastman silica gel sheets in *n*-butanol:acetone:dicyclohexylamine:water (5:5:1:1, v/v). Radioactive metabolites were detected by autoradiography on Kodak X-OMAT X-ray film and cut out from the plates for quantitation of ^{14}C by liquid scintillation counting in a xylene:0.5% PPO scintillation mixture.

Radioactivity in starch was determined by treating the extracted residues from leaves and petioles with 50 units of amyloglucosidase (19) in 5 ml of Na-acetate buffer (pH 4.5) for 4 h at 45°C and counting aliquots of the supernatant in Toluene:methyoxyethanol (5:4,v/v) containing 0.7% PPO. TLC and autoradiography showed that over 99% of the ^{14}C in the supernatant was [^{14}C]glucose, indicating complete digestion of the starch.

Amino Acid and Sugar Quantitation. Samples of the basic fractions corresponding to one-tenth of the total were converted to their dansyl derivatives (15) by reaction with 0.4 ml Na-bicarbonate buffer (pH 9.8) and 0.5 ml dansyl chloride (3.5 mg ml^{-1}) for 1.5 h at 37°C. The reaction mixtures were then made to 4.0 ml with 0.1 N HCl and applied to 1-ml columns of Porapak Q resin (15). Dansyl hydroxide was eluted with 8 ml of 5% acetic acid and dansyl amino acids with 10 ml 80% (aq) acetone. The acetone fractions were taken to dryness and resuspended in 0.1 ml of ethanol/triethylamine (99:1, v/v), and 0.02-ml aliquots were spotted on Eastman silica gel sheets. Dansyl amino acids were identified by cochromatography with authentic dansyl derivatives in chloroform:*tert*-amyl alcohol:HCOOH (70:30:3, v/v). This solvent system allowed separation of the dansyl derivatives of the major amino acids found in the tissue extracts, with the exception of aspartate and glutamine, which occasionally ran as a single spot. Quantitative analysis of each amino acid was obtained by scanning the TLC plates (Turner model lll fluorometer equipped with a 7–60 primary filter and 2A plus 65A secondary filters; G.K. Turner & Associates, Palo Alto, CA) and comparing peak area measurements to those of known quantities of authentic dansyl amino acids.

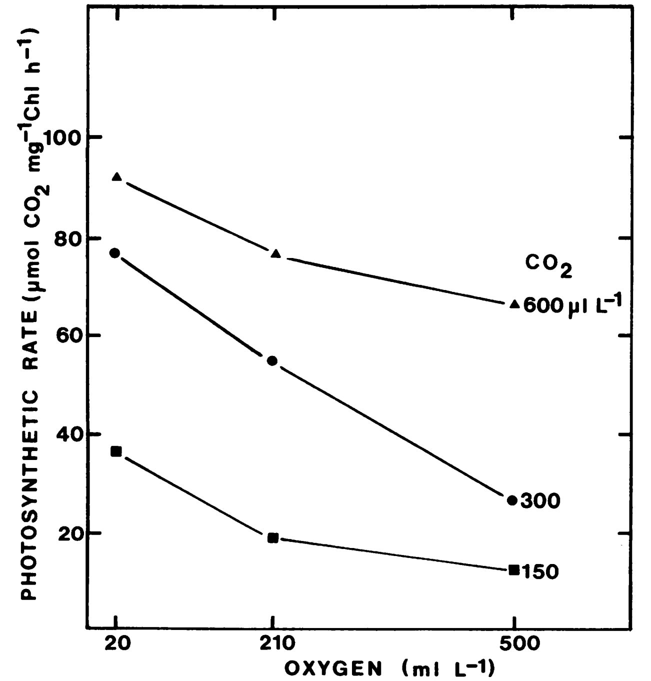

FIG. 1. The effect of varying O_2 and CO_2 levels on net photosynthetic rate of attached, intact leaves of *S. splendens*. Data represent the means of three measurements obtained from different leaves maintained at each O_2 and CO_2 level.

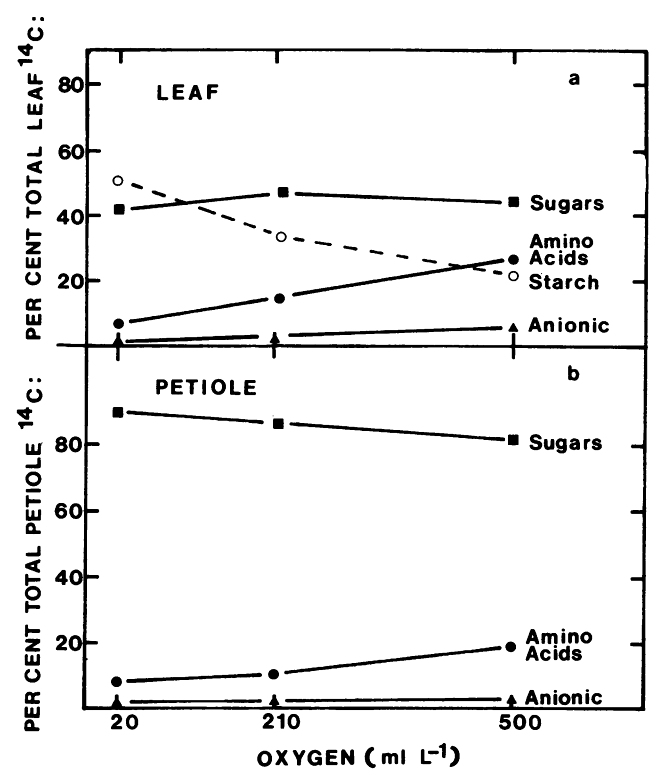

FIG. 2. The effect of O_2 level on distribution of ^{14}C in products extracted from leaves and petioles of *S. splendens* following pulse-labeling with $^{14}CO_2$. Leaves were allowed to photosynthesize in an open gas stream containing 300 μl l^{-1} CO_2 and 210 ml l^{-1} O_2 for 30 min, then the O_2 partial pressure was changed as indicated. After a further 30-min photosynthetic period at the new O_2 level, leaves were pulse-fed $^{14}CO_2$ for 1 min as described in "Materials and Methods." After a 15-min chase with $^{12}CO_2$ at the indicated O_2 level, leaves and petioles were killed and extracted for metabolite analysis. Data represent the means of triplicate experiments for each O_2 level. Total ^{14}C recovered: 20 ml l^{-1} O_2, 7.09 ± 0.31 dpm × 10^6 (leaf), 4.57 ± 0.25 dpm × 10^4 (petiole); 210 ml l^{-1} O_2, 7.40 ± 1.67 dpm × 10^6 (leaf), 8.29 ± 2.93 dpm × 10^4 (petiole); 500 ml l^{-1} O_2, 3.78 ± 0.27 dpm × 10^6 (leaf), 6.70 ± 0.72 dpm × 10^4 (petiole).

Quantitation of sugars containing fructose residues (*i.e.* verbascose, stachyose, sucrose, and fructose) in extracts was determined using resorcinol (9).

RESULTS

The net photosynthetic rates of attached leaves of *Salvia splendens* L. exposed to varying levels of O_2 or CO_2 are shown in Figure 1. The pattern is typical of C_3 plants where net photosynthesis is reduced by lower CO_2 levels or higher O_2 levels (*i.e.* the Warburg effect). At 300 μl l^{-1} CO_2, for example, an increase in O_2 partial pressure from 20 ml l^{-1} to 210 or 500 ml l^{-1} resulted in a decrease in net photosynthesis rate of approximately 30% and 60%, respectively.

A change in the O_2 environment around the leaf also resulted in a marked change in the allocation of ^{14}C among various metabolites following a pulse of $^{14}CO_2$ (Fig. 2a). The distribution of ^{14}C in the transport sugars commonly found in members of the Lamiaceae (*i.e.* stachyose, sucrose, verbascose [11]) was not

Table I. *The Effect of Increasing O_2 Partial Pressure on Distribution of ^{14}C in the Neutral Fractions from Leaves and Petioles of S. splendens L.*

Experimental conditions were as described in Figure 1 and "Materials and Methods." Data represent the means of triplicate experiments for each O_2 level (± SE)

	Percentage of Neutral Fraction ^{14}C at Following Oxygen Partial Pressure (ml l^{-1})		
	20	210	500
		%	
Leaf			
Verbascose	3.4 ± 0.7	7.3 ± 1.6	6.7 ± 1.4
Stachyose	38.6 ± 1.3	38.3 ± 1.8	38.6 ± 1.7
Galactinol	17.3 ± 0.7	18.6 ± 0.7	17.5 ± 1.1
Raffinose	3.9 ± 0.4	6.8 ± 0.4	5.8 ± 0.5
Sucrose	24.8 ± 0.3	27.3 ± 2.7	24.9 ± 1.6
Petiole			
Verbascose	12.8 ± 2.0	14.7 ± 4.1	16.2 ± 1.1
Stachyose	57.3 ± 4.8	55.7 ± 2.5	54.2 ± 2.0
Galactinol	ND[a]	ND	ND
Raffinose	6.5 ± 0.8	8.7 ± 0.6	9.5 ± 0.6
Sucrose	18.2 ± 3.8	18.6 ± 2.2	18.4 ± 2.1

[a] Not detected.

Table II. *The Effect of Increasing O_2 Partial Pressure on Pool Sizes of Sugars and Amino Acids in Source Leaves and Petioles of S. splendens L.*

Experimental procedure was as described in Figure 1 and "Materials and Methods." Data represent the means of triplicate measurements obtained from different leaves at each O_2 level (± SE).

	Oxygen Partial Pressure (ml l^{-1})		
	20	210	500
Leaf			
		μmol mg^{-1} Chl	
Sugars	2.85 ± 0.76	3.36 ± 0.60	3.36 ± 0.62
Amino acids		*nmol mg^{-1} Chl*	
Serine	35.2 ± 1.3	71.2 ± 6.7	101.3 ± 28.1
Glycine	6.3 ± 0.4	30.9 ± 1.5	59.2 ± 14.2
Gutamate	144.6 ± 19.8	283.8 ± 38.8	641.9 ± 52.7
Glutamine	43.8 ± 12.3	64.0 ± 9.2	120.7 ± 17.9
Aspartate	22.0 ± 3.5	46.8 ± 6.5	65.4 ± 4.9
Asparagine	16.5 ± 2.3	21.6 ± 5.1	21.4 ± 0.7
Alanine	90.2 ± 6.5	103.4 ± 17.7	196.5 ± 74.4
Threonine	10.1 ± 1.3	14.4 ± 1.9	15.1 ± 1.7
Petiole			
		nmol $petiole^{-1}$	
Sugars	475 ± 4	552 ± 56	583 ± 43
Amino acids			
Serine	37.3 ± 4.4	50.5 ± 1.3	60.2 ± 3.7
Glycine	7.6 ± 0.5	13.2 ± 1.4	14.7 ± 0.7
Glutamate	17.8 ± 0.4	36.4 ± 5.3	46.4 ± 3.0
Glutamine	19.6 ± 0.5	33.8 ± 4.1	46.6 ± 2.1
Aspartate	39.5 ± 7.8	46.1 ± 6.8	75.6 ± 3.5
Asparagine	11.7 ± 2.3	12.0 ± 1.7	8.3 ± 0.4
Alanine	14.1 ± 0.8	24.7 ± 1.9	36.1 ± 3.7
Threonine	11.1 ± 2.1	12.3 ± 1.9	14.9 ± 0.9

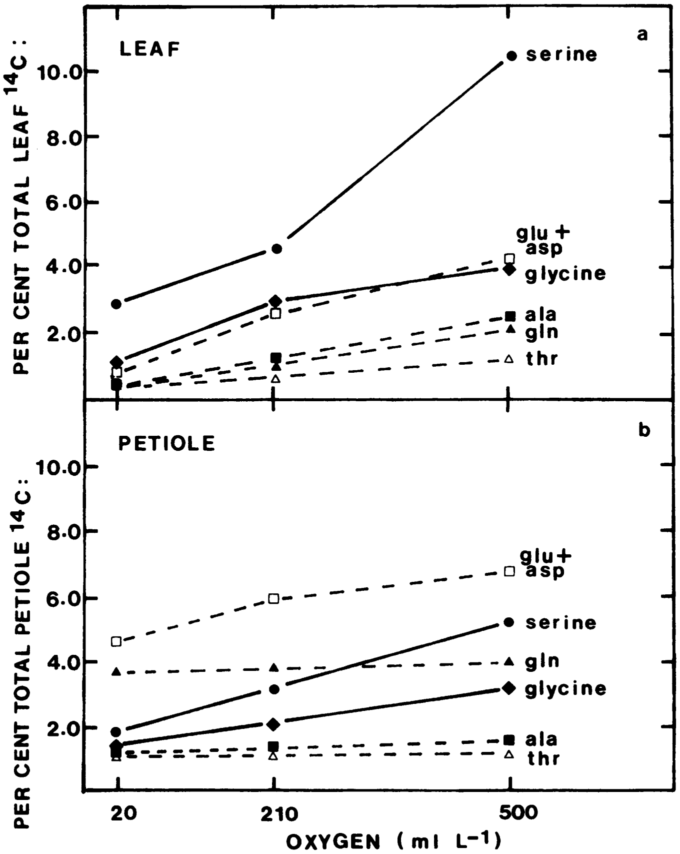

FIG. 3. The effect of O_2 level on distribution of ^{14}C in amino acids in leaves and petioles of *S. splendens*. Experimental conditions were as described in Figure 1 and "Materials and Methods." Data represent the means of triplicate experiments for each O_2 level. ala, alanine; asp, aspartate; gln, glutamine; glu, glutamate; thr, threonine.

appreciably altered by O_2 level in either the leaf tissues (Fig. 2a; Table I) or in the petioles (Fig. 2b; Table I). However, a smaller percentage of ^{14}C in the leaf tissue was incorporated into starch at high O_2 levels, which corresponded with an increased incorporation into amino acids (Fig. 2a). The percentage of ^{14}C in amino acids in the petiole (Fig. 2b) also increased as the O_2 level around the source leaf was raised.

Analysis of the amino acid fraction showed that, in the leaf tissue (Fig. 3a), the distribution of label in all amino acids increased with increasing O_2. Partitioning of ^{14}C into serine was markedly enhanced. In the petiole (Fig. 3b), ^{14}C distribution in serine and glycine was also markedly increased at higher O_2 levels while that in glutamine, alanine, and threonine did not change.

Further analysis (Table II) showed that the actual pool sizes of amino acids were increasing as the O_2 level around the leaf was raised. In leaf tissues, all major amino acids, with the exception of asparagine and threonine, showed increased pool sizes under high O_2 partial pressures. Levels of glycine, serine, glutamate, and glutamine in particular rose, indicative of a significant flux of both photorespiratory C and N in the leaves. In the petiole, a parallel rise in the pool sizes of these amino acids was also apparent (Table II).

DISCUSSION

Early studies on the metabolism of photorespiratory intermediates (10, 17, 24, 27) indicated that PGA and sucrose are formed by the internal (*i.e.* intracellular) recycling of carbon via the glycolate pathway (Fig. 4). The scheme in Figure 4 also takes into account the possibility of an additional intercellular com-

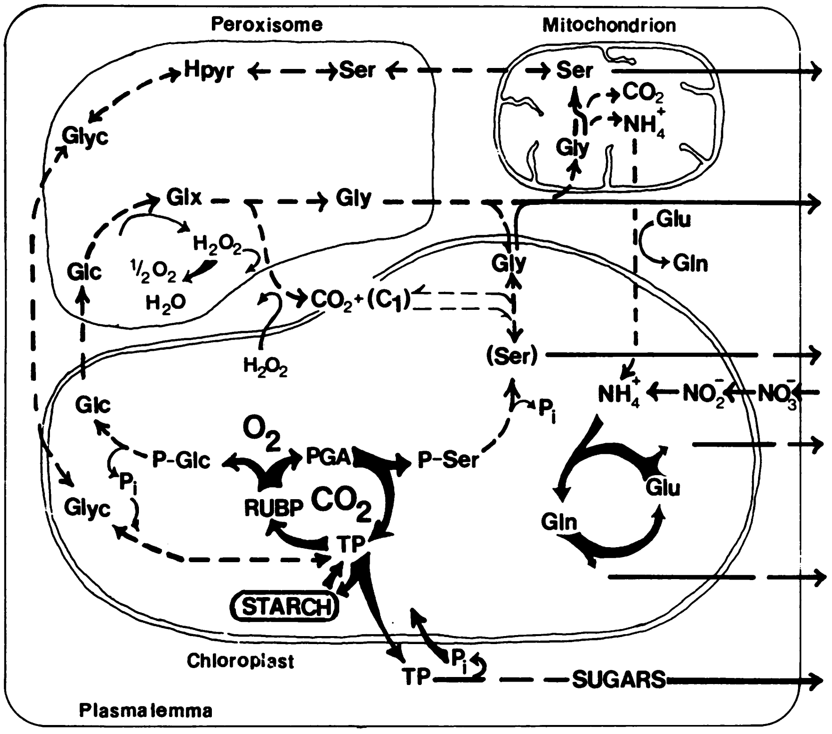

FIG. 4. Possible routes for synthesis of sugars and amino acids exported from a typical C_3 leaf cell during photorespiration. Glc, Glycolate; Gln, glutamine; Glu, glutamate; Glx, glyoxylate; Gly, glycine; Glyc, glycerate; Hpyr, hydroxypyruvate; P-ser, phosphoserine; Ser, serine; TP, triose phosphate.

ponent, namely the export of sugars formed from glycolate as well as the export of glycine, serine, glutamate, and glutamine. Although it is argued that the photorespiratory nitrogen cycle represents the major flux of N within the leaf (26), less is known about the biochemical sources of amino acids destined for transport from source leaf tissues (6, 7, 22). Little photorespiration evidently occurs in sink leaves (20); therefore, photorespiratory activity in source leaves may provide key metabolites needed for development and maintenance of growing sinks.

The relatively unchanged pool sizes of transport sugars in both leaves and petioles of *Salvia* (Table II) indicate that photorespiratory activity may serve to maintain constant sugar levels as suggested previously (28, 29). Because the recycling of carbon from glycolate to sugars requires both NADPH and ATP, it has been suggested that photorespiratory carbon cycling provides a means of dissipating excess light energy (18). Recent studies (23), however, question the view that illumination is accompanied by a general increase in the ATP/ADP quotient outside the chloroplast and specifically not in the cytosol.

During photorespiration, the major gases generated appear to be NH_3 and CO_2. It has been suggested (18) that considerable recycling of the CO_2 via the Calvin cycle occurs under conditions when stomates are closed (*e.g.* water stress). Refixation of photorespiratory CO_2 may affect energy dissipation as mentioned above (18) and may also alter the metabolism of other gases such as ethylene (5), which is also a product of amino acid breakdown. There is some debate whether photorespiratory serine synthesis requires NH_3 release as several intercellular mechanisms (Fig. 4) may account for the synthesis of this amino acid (13, 22). However, there is good evidence that most of the NH_3 generated during glycine decarboxylation is refixed (12) and not released from the tissue (4). The reassimilation of photorespiratory NH_3 would also utilize reducing equivalents (6, 26).

Interestingly, assimilates labeled in source leaves following feeding of exogenous $^{13}NH_3$ are readily translocated at rates similar to ^{11}C-labeled photoassimilates (6). The data currently available indicate that the amino acids glutamate, glutamine, and serine are most heavily labeled following exposure of leaf tissue to $^{13}NH_3$ (7). Further experiments are in progress to determine whether the ^{13}N-products exported under varying O_2 levels are the same as those labeled from $^{14}CO_2$ (Fig. 3; Table II) in the present study.

LITERATURE CITED

1. ARNON DI 1949 Copper enzymes in isolated chloroplasts; polyphenol oxidase in *Beta vulgaris*. Plant Physiol 24: 1-15
2. ATKINS CA, DT CANVIN 1971 Photosynthesis and CO_2 evolution by leaf discs: gas exchange, extraction and ion-exchange fractionation of ^{14}C-labelled products. Can J Bot 49: 1225-1234
3. COUDRET A, F FERRON, JP GAUDILLERE 1981 Photosynthates formation in wheat under different partial oxygen pressures and temperatures. Photosynthetica 15: 21-27
4. FARQUHAR GD, PM FIRTH, R WETSELAAR, B WEIR 1980 On the gaseous exchange of ammonia between leaves and the environment: determination of the ammonia compensation point. Plant Physiol 66: 710-714
5. GRODZINSKI B 1984 Enhancement of ethylene release from leaf tissue during glycolate decarboxylation. A possible role for photorespiration. Plant Physiol 74: 871-876
6. GRODZINSKI B, S JAHNKE, R THOMPSON 1984 Translocation profiles of ^{11}C and ^{13}N-labelled metabolites after assimilation of $^{11}CO_2$ and ^{13}N-labelled ammonia gas by leaves of *Helianthus annuus* and *Lupinus albus*. J Exp Bot 35: 678-690
7. HANSON AD, RE TULLY 1979 Amino acids translocated from turgid and water-stressed barley leaves. II. Studies with ^{13}N and ^{14}C. Plant Physiol 64: 467-471
8. HITZ WD, CR STEWART 1980 Oxygen and carbon dioxide effects on the pool size of some photosynthetic and photorespiratory intermediates in soybean (*Glycine max* L. Merr.). Plant Physiol 65: 442-446
9. HUBER SC, DW ISRAEL 1982 Biochemical basis for partitioning of photosynthetically fixed carbon between starch and sucrose in soybean (*Glycine max* Merr.). Plant Physiol 69: 691-696
10. JIMINEZ E, RL BALDWIN, NE TOLBERT, WA WOOD 1962 Distribution of C^{14} in sucrose from glycolate-C^{14} and serine-3-C^{14} metabolism. Arch Biochem Biophys 98: 172-175
11. KANDLER O 1967 Biosynthesis of poly- and oligosaccharides during photosynthesis in green plants. *In* A San Pietro, FA Greer, TJ Army, eds, Harvesting the Sun. Academic Press, NY, pp 131-152
12. KEYS AJ, IF BIRD, MJ CORNELIUS, PJ LEA, RM WALLSGROVE, BJ MIFLIN 1978 Photorespiratory nitrogen cycle. Nature 275: 741-743
13. LAWYER AL, KL CORNWELL, PO LARSEN, JA BASSHAM 1981 Effects of carbon dioxide and oxygen on the regulation of photosynthetic carbon metabolism by ammonia in spinach mesophyll cells. Plant Physiol 68: 1231-1236
14. LUDWIG LJ, DT CANVIN 1971 An open gas-exchange system for the simultaneous measurement of the CO_2 and $^{14}CO_2$ fluxes from leaves. Can J Bot 49:

1299–1313

15. Macnicol PK 1978 Determination of specific radioactivity of plant amino acids using dansylation. Anal Biochem 85: 71–78
16. Mahon JD, H Fock, DT Canvin 1974 Changes in specific radioactivities of sunflower leaf metabolites during photosynthesis in $^{14}CO_2$ and $^{12}CO_2$ at normal and low oxygen. Planta 120: 125–134
17. Miflin BJ, AFH Marker, CP Whittingham 1966 The metabolism of glycine and glycollate by pea leaves in relation to photosynthesis. Biochim Biophys Acta 120: 266–273
18. Powles SB, CB Osmond 1978 Inhibition of the capacity and efficiency of photosynthesis in bean leaflets illuminated in a CO_2-free atmosphere at low oxygen: a possible role for photorespiration. Aust J Plant Physiol 5: 619–629
19. Rauser WE 1978 Early effects of phytotoxic burdens of cadmium, cobalt, nickel and zinc in white beans. Can J Bot 56: 1744–1749
20. Salin ML, PH Homann 1977 Changes of photorespiratory activity with leaf age. Plant Physiol 48: 193–196
21. Servaites JC, DR Geiger 1974 Effects of light intensity and oxygen on photosynthesis and translocation in sugar beet. Plant Physiol 54: 575–578
22. Shingles R, L Woodrow, B Grodzinski 1984 Effects of glycolate pathway intermediates on glycine decarboxylation and serine synthesis in pea (*Pisum sativum* L.). Plant Physiol 74: 705–710
23. Stitt M, RM Lilley, HW Heldt 1982 Adenine nucleotide levels in the cytosol, chloroplasts and mitochondria of wheat leaf protoplasts. Plant Physiol 70: 971–977
24. Tolbert NE 1983 The oxidative photosynthetic carbon cycle. *In* DD Randall, DG Blevins, R Larson, eds, Current Topics in Plant Biochemistry and Physiology, Vol 1. University of Columbia, Columbia, MO, pp 63–77
25. Waidyanatha UP, AJ Keys, CP Whittingham 1975 Effects of carbon dioxide on metabolism by the glycollate pathway in leaves. J Exp Bot 26: 15–26
26. Wallsgrove RM, AJ Keys, PJ Lea, BJ Miflin 1983 Photosynthesis, photorespiration and nitrogen metabolism. Plant Cell Environ 6: 301–309
27. Wang D, ER Waygood 1962 Carbon metabolism of C^{14}-labeled amino acids in wheat leaves. I. A pathway of glyoxylate-serine metabolism. Plant Physiol 37: 826–832
28. Wardlaw IF 1983 Assimilate movement in *Lolium* and *Sorghum* leaves. III. Carbon dioxide concentration effects on the metabolism and translocation of photosynthate. Aust J Plant Physiol 9: 705–713
29. Yamauchi M, Y Yamada 1980 Effect of CO_2 concentration on photorespiration, sucrose synthesis and carbon transport in C_3 and C_4 plants. Soil Sci Plant Nutr 26: 191–204
30. Ziegler H 1974 Nature of transported substances. *In* MH Zimmermann, JA Milburn, eds, Transport in Plants, Vol I, Phloem Transport. Springer-Verlag, Heidelberg, pp 59–100