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Photosynthesis and Photorespiration in *Typha latifolia*[1]

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ABSTRACT

Photosynthetic rates of *Typha latifolia*, the broad-leaved cattail, are the equivalent of rates reported in tropical grasses and other plants which assimilate carbon by the phosphopyruvate carboxylase reaction, but photosynthesis in *T. latifolia* proceeds by a typical Calvin cycle. Glycolate oxidase, the photorespiratory enzyme, is present in high concentration in this species, but only minor quantities of the assimilated carbon pass through the photorespiratory pathway. However, continued operation of the pathway is apparently essential in the maintenance of assimilatory capacity. Glycolate oxidase function is not closely coupled to stomatal operation in *T. latifolia*.

For a number of years following the description of the ribulose-1,5-diP carboxylase reaction (3), it was believed that this represented a universal pathway of carbon dioxide fixation in green plants. The more recently described pathway coupled to P-pyruvate carboxylase (20, 14), however, has proved to be widely distributed also (15, 17). Surveys of assimilatory capacity have generally indicated a substantially greater rate of net assimilation in plants with the latter pathway. Since plants carboxylating ribulose-1,5-diP also possess an active photorespiratory pathway coupled to glycolate oxidase (8, 9, 15, 17, 28), the CO_2 loss associated with these reactions may generate the lower assimilatory efficiency.

Among the most efficient dry matter producers known are cattails, members of the aquatic genus, *Typha* (30). A brief report of the effect of oxygen upon the assimilatory efficiency of *Typha angustifolia* (12) suggests that this high efficiency may be associated with the ribulose-1,5-diP pathway. Studies of glycolate oxidase level have also demonstrated a high photorespiratory capability in *Typha latifolia* (21). The experiments reported here were designed to: (*a*) determine photosynthetic rates of *Typha* directly by infrared gas analysis, (*b*) establish the nature of the carboxylation reaction, and (*c*) estimate the proportion of the carbon assimilated which passes through the glycolate oxidase reaction.

MATERIALS AND METHODS

Plants of the broad-leaved cattail, *T. latifolia*, were grown in growth chambers or a greenhouse in Baccto potting soil supplemented with complete nutrient solution. Materials for most of the experiments were grown at 17-hr photoperiods and a 12 hr/12 hr thermoperiod of 30 C/25 C. Material for some experiments was grown in the greenhouse at Syracuse, New York, with natural photoperiod and temperatures of around 30 C during the day and 20 C during the night. Photosynthetic rates of detached leaves with the base submerged in distilled water were measured with the Beckman model 215A infrared gas analyzer. Transpiration was measured electrohygrometrically (19). Ribulose-1,5-diP carboxylase was assayed according to Björkman (5). Leaves were homogenized at 1 C in 0.04 M tris-chloride (pH 7.8), 0.01 M $MgCl_2$, 0.25 M ethylenediamimetetraacetic acid, and 1.0 mM reduced glutathione. The clear yellow supernatant of a 37,000*g* × 10 min centrifugation was used as the enzyme source. One gram of leaf was added to each milliliter of homogenizing medium. The reaction was initiated by adding 0.3 ml of the homogenizing medium with 1.55 μmoles of ribulose-1,5-diP and 15 μmoles of $NaH^{14}CO_3$ (10^5 cpm) to 1.3 ml of the enzyme preparation. At intervals, 0.4-ml samples were removed and acidified with 0.1 ml of 6 N acetic acid. Controls consisted of a zero time sample that was acidified immediately upon mixing the reaction components, and a reaction mixture lacking ribulose-1,5-diP which was acidified at the end of the experimental period. The same enzyme preparation procedure was used for phosphopyruvate carboxylase except that dithioerythritol was sometimes substituted for reduced glutathione to provide an alternative test for sulfhydryl protection. The assay system for this enzyme, after Slack and Hatch (25), contained 1.55 μmoles of phosphopyruvate and 15 μmoles of sodium glutamate in substitution for the ribulose-1,5-diP used above. Controls were the same. For the assay of glycolate oxidase activity, leaves were homogenized in 0.067 M phosphate buffer (pH 7.8) and filtered through four layers of 60 mesh cheesecloth. This homogenate was used directly in a polarographic assay (10) with the Clark electrode. The reaction was initiated by adding 10 μmoles of sodium glycolate in 0.2 ml of the phosphate buffer to 2.8 ml of the enzyme preparation. Controls were samples to which no glycolate was added. Addition of the enzyme cofactor, flavin mononucleotide, was not found to be stimulatory, and this was omitted from the assay system. Reagents were from Sigma.

For $^{14}CO_2$ assimilation experiments, leaves were preilluminated in 2×10^6 ergs cm^{-2} sec^{-1} of light with their base in distilled water or a glycolate oxidase inhibitor, 0.01 M α-hydroxypyridinemethanesulfonic acid (Aldrich), for 30 min prior to release of $^{14}CO_2$ by the acidification of a bicarbonate solution. Carbon dioxide concentration was 370 μl $liter^{-1}$ after addition of bicarbonate, to eliminate artifacts arising from high CO_2 concentrations. Following 10 min of photosynthesis with water or 20 min with the inhibitor, the leaves were killed with boiling 80% ethanol. In the controls, 1.8 μc of $^{14}CO_2$ were used. In the experiments with inhibitor, 2.02 μc of $^{14}CO_2$ were used. The different time periods and specific radioactivities of $^{14}CO_2$ were used to assure that approximately the same amount of radioactivity would be recovered from chromatograms of both treatments without overloading with plant extracts. Total cpm recovered from chromatograms per g of leaf extracted were 43,200 ± 21,600 (0.95 confidence interval) for the water controls and 53,600 ± 8,300 for experiments in inhibitor. For the short time experiments, leaf

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disks were floated on distilled water in an Erlenmeyer flask above which was a funnel containing hot ethanol that could be released by pinch clamp immediately upon acidification of the bicarbonate. The shortest time periods at which measurable counts were recovered was 2 sec. Carbon dioxide concentrations of 900 μl liter^{-1} were utilized in the short time period experiments.

Glycolate-1-^{14}C (Nuclear-Chicago) was fed through the bases of excised leaves submerged in distilled water or the glycolate oxidase inhibitor. Following a 30-min equilibration period in the dark or light in the absence of labeled glycolate, leaves were transferred to a solution of 2.3 μc of glycolate-1-^{14}C (4.59 μc/μmole). Radioactive glycolate was fed for 1 hr with two distilled water chases of approximately 5 ml, as transpiration depleted the solution.

For all identifications, compounds were separated by paper chromatography, identified by radioautography as verified with known standards (14), and eluted from the paper for counting with a Nuclear-Chicago model 186 decade scaler in conjunction with a D47 gas flow detector with an efficiency of 21%. The separation techniques did not resolve glucose and sucrose, and so these compounds are reported together. Neither was of particular interest except as "end products" of glycolate metabolism.

RESULTS

Direct measurement of the carbon dioxide assimilation rates of *T. latifolia* leaves documented directly the great assimilation efficiency of this plant (Table I). These rates are generally comparable to those reported for many of the species assimilating carbon by the dicarboxylic acid pathway (11). This is in qualitative agreement with productivity surveys which indicate that uncultivated cattail marshes often are as productive as intensively cultivated tropical agriculture based on sugar cane and maize (30).

Assays for ribulose-1,5-diP and phosphopyruvate carboxylases utilizing acid-stable counts recovered from incubation mixtures with $NaH^{14}CO_3$ indicated that the principal carbon-incorporating enzyme in *T. latifolia* is ribulose-1,5-diP carboxylase (Fig. 1). Activity was never detectable in extracts where the pyruvate was provided as an acceptor. With ribulose-1,5-diP as an acceptor, there was a linear increase in the acid-stable counts for at least a 20-min period. Although we used standard assay procedures for both enzymes, and the phosphopyruvate carboxylase is not known to be particularly labile in other systems, the possibility always exists that the enzyme is inactivated by the procedure. To preclude this possibility, short time period incorporation experiments were performed with leaf disks to determine the functional CO_2 incorporation pathway *in vivo*. The familiar extrapolation to zero time curves for these experiments indicated that the ribulose-1,5-diP pathway is indeed the primary assimilatory pathway in *T. latifolia* (Fig. 2). At 2 sec exposure to $^{14}CO_2$, almost 90% of the counts recovered are in glycerate 3-P and sugar phosphates. Detectable counts do not appear in malate until 20 sec, and, even by this time, radioactivity is at a very low level in the acid. It can be argued that the CO_2 concentration (900 μl liter^{-1} in air) required by this experiment up to the 20-sec time period "forces" the ribulose-1,5-diP carboxylase reaction, but, when considered together with the activity assays, this experiment indicates that it is unlikely that phosphopyruvate carboxylase occurs in *Typha*.

Feeding of glycolate-1-^{14}C was designed to determine the fate of carbon passing through the photorespiratory pathway and to estimate the effectiveness of a glycolate oxidase inhibitor in arresting the pathway prior to inhibitor utilization in photosynthetic CO_2 incorporation experiments. Since a certain proportion of the glycolate is decarboxylated (27), feeding glycolate labeled

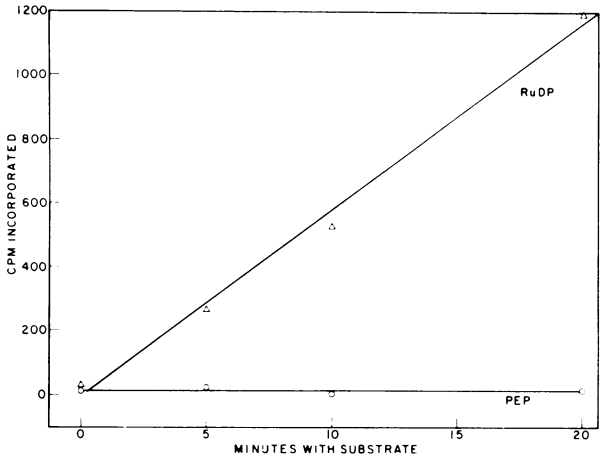

FIG. 1. Incorporation of radioactivity from $NaH^{14}CO_3$ into the acid-stable fraction of a cell-free system from *T. latifolia* leaves. The reaction was in 0.04 M tris-chloride (pH 7.8), 0.01 M $MgCl_2$, 0.025 M ethylenediaminetetraacetic acid, 1.0 mM reduced glutathione, and contained 15 μmoles of $NaH^{14}CO_3$ (10^5 cpm) with 1.55 μmoles of ribulose-1,5-diP (RuDP) or phosphopyruvate (PEP). The assay with phosphopyruvate also contained 15 μmoles of sodium glutamate. Temperature was 21 C. Samples (0.4 ml) were removed at intervals and acidified with 0.1 ml of 6N acetic acid. Radioactivity was determined with a planchet counter of 21% efficiency.

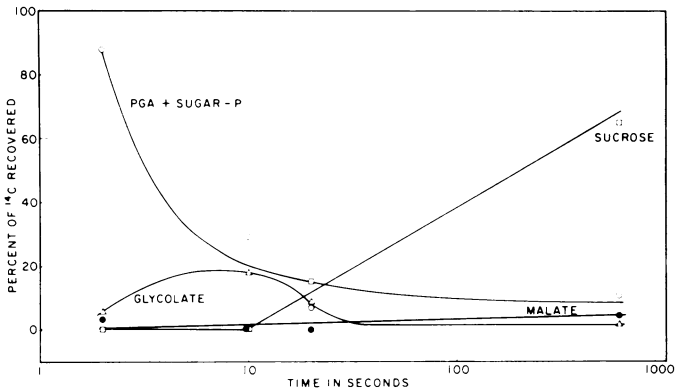

FIG. 2. Relation between time between $^{14}CO_2$ exposure and leaf killing, and the proportion of radioactivity recovered from various metabolic intermediates. $^{14}CO_2$ was liberated into air by acidification of a $NaH^{14}CO_3$ solution, and leaves were killed with boiling 80% ethanol. Light was 2×10^6 ergs cm^{-2} sec^{-1}, and temperature was 30 C. The ethanolic extraction product was chromatographed two-dimensionally in butan-1-ol-propionic acid-water (142:71:100) and redistilled phenol saturated with water. Compounds were localized by radioautography. Radioactivity of eluted samples was determined by planchet counting.

Table I. *Assimilation Rates of Typha latifolia Leaves*

Assimilation rates of detached leaves with the base submerged in distilled water were measured by infrared gas analysis at 25 C, 340 μl of CO_2 per liter, and a light intensity of 2×10^6 ergs cm^{-2} sec^{-1}.

Experiment	Assimilation Rates	
	mg CO_2 g^{-1} hr^{-1}	*mg CO_2 dm^{-2} hr^{-1}*
1	16.3	62.2
2	14.5	43.5
3	18.0	68.7
4	18.1	67.9

in the C_1 position alllowed us to detect reassimilation of this moiety. The inhibitor proved to be quite effective at the concentrations regularly employed (31), with less than 10% of the fed glycolate metabolized further in a 1-hr period (Table II). In the feeding experiments, significant label from glycolate was recovered in only five compounds, and by far the bulk of the glycolate was converted into glucose or sucrose, or both, at the end of an hour. The effect of light upon the fate of the label was interesting. The label remaining in glycolate was four times greater when the compound was fed in the dark compared with the light feeding levels, suggesting that either: (*a*) glycolic acid metabolism is facilitated by light, or (*b*) uptake was ATP-limited so that a portion of the glycolate was not reaching cell organelles active in its metabolism. Since glycolate metabolism is largely restricted to glyoxysomes (18), an ATP-dependent transport process could limit the movement of fed glycolate to these organelles. However, since there is little reason to believe that glycolate transport is energy-dependent, it seems more likely that glycolate oxidation is light-influenced. A likely mechanism is through the effect of light upon the oxygen concentration of the cell, although direct effects through novel forms of glycolate oxidase (2) cannot be ruled out. Also interesting is the light-dependent appearance of label in malate. Our failure to detect phosphopyruvate carboxylase activity in *Typha* suggests that an as yet undescribed energy-dependent pathway leads from glycolate to malate. The products of glycolate-1-^{14}C feeding to leaves reported here are essentially similar to earlier studies (7, 16, 23, 24), although significant label in malate has not been reported consistently in other feeding studies. The marked difference between the total counts incorporated in inhibited and uninhibited leaves suggests that the greater assimilatory efficiency of *Typha* does not arise out of a conservation of CO_2 produced in the photorespiratory process. The stoichiometry of ^{14}C loss in *T. latifolia* without glycolate oxidase inhibition is what would be predicted from previous studies (27) on other plants.

The effect of a glycolic acid oxidase inhibitor upon the distribution of photosynthetically incorporated $^{14}CO_2$ was determined by one-way comparison with Student's *t*, which indicated that there were significant reductions in percentage of the radioactivity occurring in sugar phosphates, glycerate, serine, glycine, and malate, and a significant increase in the proportion of the label occurring in glycolate upon inhibition (Table III). Although the feeding experiments indicated substantial effectiveness of the inhibitor, the accumulation of glycolate during photosynthesis of *T. latifolia* leaves in the presence of the inhibitor is much lower than the values reported previously for other plants (32). The increase in the glycolate fraction over the 20-min period in the presence of the inhibitor was only 7.64% which, divided by the proportion of the fed glycolate uncoverted under inhibition in the feeding experiments, yields a value of 8.4% for the total photosynthetically fixed carbon moving through the glycolate pathway. The increased label in glycolate upon inhibition is reflected in compensatory decreases in serine, glycine, and malate, which showed an aggregate decrease of 6.78% in the inhibitor experiments. The general insignificance of the glycolate pathway in carbon metabolism of *T. latifolia* is indicated by the indistinguishable quantities formed of the final products of photosynthesis, glucose and sucrose, whether the inhibitor was present or absent. The lower level of sugar phosphates present upon inhibition probably reflects pool size modifications arising from photosynthetic rate differences in inhibited and uninhibited leaves.

Since the experiments with inhibitors indicated that the glycolate oxidase reaction was of minor importance in over-all carbon metabolism, we assayed a number of *T. latifolia* plants to determine general level of glycolate oxidase. So that the values could be directly compared with assimilatory capacity, the glycolate oxidase activity in μl of O_2 g^{-1} hr^{-1} was converted to mg of CO_2 g^{-1} hr^{-1} based on the stoichiometry of the reaction with 1 mole of O_2 set equal to 4 mole equivalents of CO_2 as glycolate. The equivalency, reported elsewhere for numerous assay systems, was verified for ours by allowing complete depletion of known quantities of glycolate. Mean activity of seven plants was 9.483 ± 1.817 (95% confidence interval) mg CO_2 equivalents as glycolate

Table II. *Recovery of ^{14}C in the Products of Glycolate-1-^{14}C Feeding to Typha latifolia Leaves under Different Treatments*

Excised leaves were fed 0.0023 mc of glycolate-1-^{14}C in 0.01 M α-hydroxypyridinemethanesulfonic acid solution or in distilled water. Leaves were either in complete darkness or in light of 2×10^6 ergs cm^{-2} sec^{-1}, as indicated. Temperature was 25 C. Data are mean values from three to five experiments. Feeding was for 1 hr.

Compound	Treatments		
	Glycolate fed in distilled water		Glycolate fed in α-hydroxypyridinemethanesulfonic acid, light
	Light	Dark	
	cpm/g fresh wt		
Glycolate	19,500	83,900	642,000
Glycine	13,700	16,300	5,410
Serine	11,400	1,400	17,500
Malate	33,100	3,400	0
Glucose + sucrose	264,000	244,000	42,300
Total	342,000	349,000	704,000

Table III. *Recovery of ^{14}C in the Products of Photosynthesis in the Presence of $^{14}CO_2$*

Photosynthesis of detached leaves proceeded with the leaf base in distilled water or 0.01 M α-hydroxypyridinemethanesulfonic acid for 30 min prior to release of $^{14}CO_2$ by acidification of a bicarbonate solution. Photosynthesis continued for 10 min in distilled water or 20 min in the inhibitor prior to killing in boiling 80% ethanol. Air contained 1.8 μc of $^{14}CO_2$ in distilled water experiments and 2.02 μc of $^{14}CO_2$ in inhibitor experiments. Light was 2×10^6 ergs cm^{-2} sec^{-1} and CO_2 was 370 μl $liter^{-1}$ of air upon $^{14}CO_2$ release. Temperature was 29 C. Total radioactivity recovered from chromatograms per g of leaf extracted was 43,200 ± 21,600 (0.95 confidence interval) for the water controls, and 53,600 ± 8,300 for experiments in inhibitor. Data are mean percentage of counts in each compound with the 95% confidence interval by Student's *t*.

Compound	Treatment	
	Distilled water	α-Hydroxypyridinemethanesulfonic acid
	%	%
Glucose + sucrose	55.4 ± 9.7	69.3 ± 23.5
Glycerate-3-P + sugar phosphates[1]	14.8 ± 5.8	7.1 ± 1.7
Glycine[1]	7.35 ± 2.42	3.98 ± 0.87
Malate[1]	6.05 ± 2.12	3.98 ± 0.84
Glycerate[1]	5.17 ± 1.26	1.45 ± 0.54
Serine[1]	4.96 ± 0.43	3.62 ± 0.86
Glycolate[1]	1.34 ± 1.01	8.92 ± 2.53
Aspartate	1.22 ± 0.48	0.66 ± 0.45
Alanine	0.71 ± 0.42	0.90 ± 0.15

[1] Inhibition of glycolate oxidase had a significant effect, at the 95% level, upon the percentage of the incorporated carbon in the compound.

g^{-1} hr^{-1}. This indicates that the photorespiratory capacity recoverable as glycolate oxidase is many times the level that would be predicted from the inhibitor experiments and is sufficient to process a significant proportion of the carbon fixed.

It is well known that inhibition of glycolate oxidase causes stomatal closure (33), and this is the explanation generally advanced for the decreased photosynthetic rate upon incubation of leaves in glycolate oxidase inhibitor solution. In our $^{14}CO_2$ incorporation experiments, rates were consistently reduced about 70% by the inhibitor. Diffusion theory predicts that if the action of an experimentally introduced molecule is principally upon the stomatal mechanism, the magnitude of the transpiration decline should exceed the magnitude of the photosynthesis decline (34). In addition, if the inhibitor affects carbon incorporation rate through effecting stomatal closure, there should be a simultaneous decrease in transpiration rate and assimilation rate upon inhibition. In experiments where photosynthetic and transpiration rates were simultaneously measured, however, the carbon assimilation rate consistently showed a very rapid and pronounced response to the inhibitor while the transpiration rate never showed a dramatic change and the first evidence of an effect consistently lagged 6 to 8 min behind the assimilation effect (Table IV). The photosynthetic rate typically showed a depressed level within 3 min of inhibitor introduction, while transpiration rate lagged 6 min behind and never showed the dramatic decline found in photosynthetic rate. It can be argued that *Typha* has substantial epidermal transpiration which is masking the stomatal effect, but this explanation does not explain the substantial time lag observed. Attempts at direct measurement of stomatal aperture through the use of collodion impressions and epidermal strips were ineffective through a prevalence of artifactual effects. Similarly, porometer techniques could not be utilized because of the intractable shape of the *Typha* leaf. Repeated experiments with the inhibitor, however, resulted in transpiration reductions of 35%, far lower than the photosynthetic inhibition.

TABLE IV. *Effect of a Glycolate Oxidase Inhibitor upon Photosynthesis and Transpiration of T. latifolia Leaves*

An excised leaf with its base in distilled water was allowed to come to steady state photosynthesis and transpiration as monitored by infrared gas analysis and electrohygrometry, respectively. At t = 5 min, the leaf was transferred to a 0.01 M solution of α-hydroxypyridinemethanesulfonic acid. Light, CO_2 concentration, and temperature were as described for Table I. Photosynthetic rate was 18.1 mg CO_2 g^{-1} hr^{-1} and transpiration rate was 2.04 g H_2O g^{-1} hr^{-1} at the initial steady state.

Time	Assimilation	Transpiration
min	%	%
0	100	100
5	100	100
7.5	92	100
10	65	100
12	31	100
14	23	97
16	39	89
18	19	86
20	19	82
22	12	79
24	12	72
26	12	70
30	8	68
40	12	66

DISCUSSION

These studies of the photosynthetic and photorespiratory metabolism of *T. latifolia* indicate that this species has the most efficient CO_2 assimilation system known to be coupled to the carboxylation of ribulose-1,5-diP. The much lower level of glycolate metabolism in comparison with other Calvin cycle plants (28, 32) suggests that this efficiency may arise out of carbon conservation through minimal photorespiration. Why this conservation should be coupled with glycolate oxidase levels sufficient to process much of the carbon fixed remains enigmatic, unless we assume that the enzyme operates very far from optimal conditions *in vivo*. Reassimilation of CO_2 is not a likely explanation of the CO_2 conservation when the feeding experiments are considered. These experiments indicated that about the same proportion of glycolate carbon is lost in *Typha* as has been reported for other plants. Another possibility is that the supply of glycolate is closely regulated in *Typha*. A mechanism for such regulation is not obvious although it may be related to the couple between the O_2 requirement for glycolate formation (29) and the O_2 requirement for glycolate oxidation.

The glycolate feeding experiments indicate that malate is a product of glycolate metabolism in the light. This product might arise out of a condensation of glyoxylate and acetyl-CoA (6), although there is no evidence to indicate that the necessary reactions occur in leaves.

Like all inhibitor studies, the ones reported here are not unambiguous. The lack of simultaneity between the decline of carbon assimilation and the decline of transpiration in leaves treated with the glycolate oxidase inhibitor suggests: (*a*) the inhibitor has a pronounced direct effect upon the operation of the photosynthetic apparatus, or (*b*) glycolic acid oxidation and photosynthesis are closely coupled. If, as Tanner and Beevers indicated (26), α-hydroxypyridinemethanesulfonic acid is a general inhibitor, these experiments indicate a pronounced effect upon one of the primary photosynthetic systems. If, as Zelitch has indicated (31), this compound is a relatively specific inhibitor of glycolate oxidase, we must conclude that the oxidation of glycolate is essential to continued assimilatory capacity in *Typha*. A close coupling between glycolic acid oxidation and photosynthesis in *Typha* may operate through an NADPH shuttle coupled to glyoxylate reduction (22), which would allow photophosphorylation to proceed (1) in spite of a lack of stoichiometry between the ATP and NADPH requirements of the cell.

Vandor and Tolbert (29) have reported that glycolate synthesis from fructose-1,6-diP proceeds in the dark in the presence of NADPH and O_2. Therefore, both the synthesis and the further conversion of glycolate are oxygen-sensitive steps. The low level of carbon moving through glycolate oxidase in *Typha*, but the pronounced sensitivity of carbon assimilation to glycolate oxidase inhibition, suggests to us that the most important function of the glycolate pathway is metabolic regulation. The most conspicuous property of the metabolic sequence involving glycolate is the large of number of reactions that require products, or substrates, of the photosynthetic reactions. One of the serious problems that the photosynthetic apparatus confronts is the production of O_2 proximal to unstable electron transients in the photosynthetic electron transport sequence. Although it is likely that these transients are isolated from the oxygen production site through the membrane organization system, it still remains important to maintain chloroplast O_2 concentration low. The tight spatial appression of glyoxysome and chloroplast membranes observed in electron micrographs (13) suggests that the glycolate oxidase reaction's fundamental function may be depletion of molecular oxygen produced by the photosynthetic apparatus.

The glycolate "pathway" is a cycle operating in parallel with the Calvin cycle since it shares common substrates with that cycle. The large number of feedback points in the coupled cycles

make them a pronounced example of a regulatory network. The partitioning of the reactions among organelles has already been considered elsewhere (18), but it is important to recognize that spatial separation of alternative control functions provides time lags which will serve to damp perturbations caused by external transients. If, as our studies indicate, there is a pathway from glyoxylate to malate in leaves, the glycolate pathway represents a couple among the light reactions, the Calvin cycle, "fatty acid" metabolism, and amino acid metabolism, in addition to the obvious couple with pyridine and adenine nucleotide-dependent reactions. Experimental resolution of networks is exceedingly difficult because of the difficulty of designing unambiguous experiments. Multiple alternative branch points capable of removing compounds from either the Calvin cycle or the glycolate cycle provide scant opportunity for designing unambiguous experiments in the absence of completely specific inhibitors.

Our work with *T. latifolia* does indicate, however, that (*a*) Calvin cycle photosynthesis is not obligatorily inefficient, (*b*) the efficiency of the Calvin cycle photosynthesis in *Typha* may arise out of stringent control of the movement of photosynthetic products through glycolate oxidase, (*c*) there is a close couple between photorespiratory and assimilatory capabilities, and (*d*) neither of these processes is closely coupled to stomatal aperature regulation.

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