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A SURVEY OF THE RATES AND PRODUCTS OF SHORT-TERM PHOTOSYNTHESIS IN PLANTS OF 9 PHYLA

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A SURVEY OF THE RATES AND PRODUCTS OF SHORT-TERM PHOTOSYNTHESIS IN PLANTS OF 9 PHYLA*

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SUMMARY

1. Short-term photosynthetic experiments using $C^{14}O_2$ and paper chromatography were performed with 27 different plants representing nine phyla: Schizophyta (Schizophyceae), Euglenophyta, Chlorophyta, Charophyta, Chrysophyta, Rhodophyta, Bryophyta, Pteridophyta, and Spermatophyta.

2. There is a remarkable uniformity in the types of ethanol-soluble compounds which became radioactive in the entire group of plants used. The amounts of the different compounds varied considerably percentage-wise among the various plants as would be expected because of their inherent metabolic differences and the variations in their physiological states induced by experimental conditions.

3. Sucrose became radioactive in very different amounts in two major groupings of plants: a) those containing only photosynthetic tissue and b) those containing non-photosynthetic tissue as well. The amount of radioactive sucrose in the former group was much lower than that in the latter.

4. An unidentified compound became radioactive in appreciable amounts in two of the blue-green algae, but was radioactive in very small amounts or not visible at all on the chromatograms of all other plants.

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INTRODUCTION

In consideration of the great differences in general physiology among plants the question arises whether there is a uniformity in the reactions involved in the fixation of carbon during the early steps of photosynthesis or whether there may also be differences in these basic reactions. To investigate this question and to determine whether any differences, should they occur, might be correlated with phylogenetic relationships, a survey of representatives of major plant groups was made with respect to the kinds and relative amounts of the compounds into which carbon was incorporated during short-term photosynthesis. The general methods employed in the study were tracer technique using C^{14} for labeling compounds and paper chromatography for separating and identifying them.

EXPERIMENTAL METHODS

Photosynthesis experiments were performed with the following plants: Phormidium, Synechococcus and two species of Nostoc (blue greens), Chlorella, Scenedesmus, Haematococcus, Spirogyra and Chlorococcum (green algae), Nitella, Vaucheria (a yellow-green alga), Euglena, Porphyridium (a red alga), Fontinalis and Funaria (mosses), Conicephalum (a liverwort), Ceratopteris and Polystichum (ferns), yew, juniper, squash, soybean, Kalanchoë, tomato, ivy, avocado and barley.

With the exceptions of Haemotococcus, Spirogyra, Nitella, yew, juniper and ivy, all of which were used directly from their places of growth, the plant materials used in these experiments were grown in the laboratory. The algae were grown under conditions shown in Table I and in media described in Table II. The mosses, liverwort, and ferns were grown in dishes of either pond water or V medium on a fluorescent light shelf. The squash, soybean, Kalanchoë, tomato and avocado were grown in a fluorescent light chamber.

Because of the differences in form between the algae and the other plants, two general methods of carrying out the CO_2 fixation experiments were employed. The algae were centrifuged from their nutrient media, washed once with distilled water and centrifuged again. 75 cc. of a 1% suspension of algae in distilled water (based on packed cell volume) was poured into a flat chamber (Figure 1). This chamber was illuminated between two incandescent lamps providing light intensities shown in Table III for a 15-or 20-minute period to permit the algae to adjust to the light conditions. The suspension was kept at about room temperature during this period by placing the chamber in a water-cooled bath. Throughout this period and the rest of the experiment, heat from the lamps was reduced by means of water-cooled infrared heat filters placed between the lamps and the illumination chamber. Following the adjustment period 200 λ of sodium bicarbonate solution containing 400 μc. C^{14} per ml. was injected into the vessel, which was stoppered immediately and shaken continuously in the light beam for 5 minutes. At this time the contents were dumped into 300 cc. of boiling absolute ethanol, thus making an 80% ethanol solution. This mixture was then brought to a boil again and immediately cooled in a cold water bath.

The total amount of activity fixed by the algae was determined by drying an aliquot of the ethanol suspension on an aluminum plate and counting the radioactivity with a wide-mouth Geiger Müller counter. The amount of activity fixed in 80%-ethanol soluble compounds was determined by centrifuging the ethanol suspension and similarly plating and counting an aliquot of the supernatant. The distribution of activity in the various compounds in the 80%-ethanol extract was determined by two-dimensional chromatography of a concentrate of the extract on Whatman No. 1 paper. Phenol-water was used as the first solvent and a butanol-propionic acid-water mixture as the second solvent. Radioautograms of the resulting chromatograms were made with "No-Screen" X-ray film in order to find the location of the radioactive compounds. These

compounds were identified by the relation of their positions to known compounds and to each other and, in cases of doubt, by co-chromatography with a known compound.[1] The activity in each spot on the chromatograms was counted and tabulated in terms of percentage of the total activity on the chromatogram.

The CO_2 fixation experiments with the higher plants were carried out in a gas-tight chamber with parallel glass sides (Figure 2). The thalli, leaves or larger portions of plants used for the experiments were transferred to small tubes of water in this chamber as quickly as possible after being removed from the rest of the plant. Thalli or leaves which appeared likely to wilt during the experiments were sprayed with water prior to the adjustment period. The chamber was illuminated in the same way as it was for the algae with the varying light intensities shown in Table III. The chamber was closed and air drawn through it during the adjustment period which varied from 5 to 15 minutes. Following this time the chamber was partially evacuated and radioactive CO_2 was introduced in the amounts shown in Table III. After 5-minutes' exposure to radioactive CO_2 (10 minutes in the case of the liverwort) the plant parts were removed either directly into boiling 80% ethanol in the case of both ferns, Funaria, squash, soybean, tomato, and barley or first into liquid nitrogen where they were ground and then into boiling 80% ethanol in the case of Fontinalis, liverwort, yew, juniper, Kalanchoë, ivy and avocado. The total activity, the activity in the 80%-soluble portion and its distribution in the various compounds was determined in the same way for these suspensions as it was for the corresponding suspensions of algae.

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(1) A. A. Benson, J. A. Bassham, M. Calvin, T. C. Goodale, V. A. Haas and W. Stepka, J. Am. Chem. Soc., 72, 1710 (1950).

RESULTS

The rates of CO_2 fixation of the 19 plants tested varied greatly as might be expected with such a wide diversity of plant types, ages of the material, etc. The rates ranged from 0.3 μ mol. CO_2 fixed/gram of wet plant material in 5 minutes in the case of the liverwort to 14.5 μ mol./g./5 min. in the case of Fontinalis. (See Table III.) There was also a wide variation in the percentage of the fixed activity which was extractable with 80% ethanol. For those plants in which experimental methods permitted this value to be obtained, this figure varied from 17.7% for Kalanchoë to 88.8% for yew.

Although there are wide variations in the rates at which the different plants fixed CO_2 and incorporated it into insoluble materials, there was a remarkable similarity in the kinds of soluble compounds formed. However, their percentage-wise distribution showed great variation. The detailed results are reported in Table III and some representative chromatograms from which the data were obtained are shown in Figure 3.

DISCUSSION

Several striking points stand out in the results of this survey of the photosynthetic pattern of a variety of plants. One of these is the remarkable uniformity with which the various phosphates and amino acids are found to become radioactive in this type of experiment. Hexose monophosphates appeared radioactive on chromatograms of all 19 plants while pentose- and triose-phosphates and phosphoglyceric acid were found in all but one. The uridine diphosphate glucose and UDP galactose spot was on all but 3 papers, and ribulose diphosphate, phosphoglycolic acid, and phospho-enol-pyruvate were easily visible on the majority of chromatograms. Of the amino acids, serine and alanine became radioactive in all the experiments, aspartic and glutamic acids in seventeen and glycine in sixteen. It is quite probable that compounds which

appeared radioactive in all but a few of the experiments as described actually were radioactive in every one but to such a low degree that the activity was not detectable by the procedures used in these experiments. The general uniformity in the compounds which became radioactive in these varied plants indicates that the same basic pattern of reactions occurred in the incorporation of CO_2 into cell constituents in all of the plants tested. And since nearly all major plant phyla are represented in the experiment it seems safe to assume that this set of reactions is the one which is responsible for all photosynthetic CO_2 fixation and early metabolism.

Despite the uniformity in the occurrence of these compounds, there is a great variation in the percentage-wise distribution of radioactivity among the various plants. Individual variations cannot yet be interpreted since they certainly must be expected in a survey of this type for a number of reasons, residing partly in the experimental procedures and partly in the organisms themselves. Conditions under which the experiments were performed were patterned after those previously found to be suitable for Scenedesmus and soybean and were certainly not optimum for all, if for any, of the organisms tested. In some of the organisms these conditions almost certainly induced quite abnormal physiological states. In addition to the variation caused by environmental factors, there are variations caused by differences in the inherent metabolic rates of different organisms and differences in age of the material used, etc.

However, there are two compounds which are found to be radioactive in widely different amounts in different groups of plants. These two cases exceed by far the variations which may be attributed to the factors mentioned. One of these compounds is sucrose, the distribution of which seems to divide the plants into two distinct major groups, one in which it contains less than

10% of the soluble radioactivity and the other in which it contains more than 35% of the soluble radioactivity (Figure 3A,B). An inspection of the plants which constitute these two groups suggests that this difference is associated with a structural feature of the plants, namely the absence or presence of living non-photosynthetic tissue. The more rapid synthesis of sucrose in those plants containing non-photosynthetic tissues can be rationalized in terms of the selective advantage which lies in the production of a disaccharide rather than a monosaccharide as the soluble energy source for such tissues. Because of the glycosidic link in sucrose, hexose from it may be brought into the metabolic stream without prior activation by ATP such as a monosaccharide would require. Thus the transport of sucrose carries 2-5 Kcals more energy than the equivalent carbohydrate as a monosaccharide. Evidence to support this hypothesis that the amount of disaccharide formed is related to the presence or absence of non-photosynthetic tissue in the plant rather than to its phylogenetic relationships is found in the experiments of Bean with Iridophycus, a multicellular red alga containing non-photosynthetic tissue.[2] In his experiments, which were carried out in a manner comparable to that used in this laboratory, ~50% of the activity on the chromatogram was found in the disaccharide, floridoside (α-d-galacto-pyranosyl-2-glycerol).

In order to test how deep-seated the relationship between the presence or absence of non-photosynthetic tissue and the rate of sucrose production might be, experiments were done with two plants (a moss and a fern) which during one phase of their life cycle contain no non-photosynthetic tissue but which do develop it in another phase. Presumably they might be expected to produce sucrose less rapidly during the former phase than during the latter one.

(2) Ross Bean, Thesis, University of California, 1954.

In a comparison of the results of these experiments with plants in the two phases of development, it must be kept in mind that the moss protonemata and fern prothalli used were not of the same species as the mature moss and fern tested. However, the fact that the forms containing only photosynthetic tissue produced 23 and 24% sucrose (in moss protonemata and fern prothalli, respectively) and that the forms containing non-photosynthetic tissue produce 48 and 37% (in the mature moss and fern) could indicate that the potential for a higher rate of sucrose production is physiologically controlled in forms without colorless cells and does not come into full operation until non-photosynthetic tissue is developed.

The second compound which becomes radioactive in different amounts in different groups of plants is one of unknown identity which accounts for 7 and 21% of the activity of Synechococcus and Nostoc and is found (in small amounts, 1% or less) in only nine other plants (Fig. 3C,D). This compound runs slightly farther than alanine in the phenol direction and a somewhat shorter distance in the butanol-propionic acid direction. It is weakly ninhydrin positive and does not appear to be α,ϵ, diaminopimelic acid.[4] Upon heating in 1 N H^+ at 100° C. for 1 hour at least three new substances are formed.

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(4) Elizabeth Work and D. L. Dewey, J. Gen. Microbiol., 9, 394 (1953).

Table I

CULTURING CONDITIONS FOR ALGAE

Algae	Culture vessel	Aeration	Agitation	Medium	Light
Phormidium	250 ml. Erlenmeyer	no special provision	occasional swirling by hand	V	fluorescent
Nostoc muscorum	2500 ml. culture flask	air bubbled through	"	FG	"
Nostoc sp.	250 ml. Erlenmeyer	no special provision	"	soil and water	"
Synechococcus cedrorum	2500 ml. culture flask	air drawn over	constant shaking	FG + 0.1% Na glutamate	incandescent
Chlorococcum sp.	2500 ml. culture flask	"	"	V	fluorescent
Chlorella	"	"	"	"	"
Scenedesmus	"	"	"	"	"
Euglena	"	no special provision	occasional swirling by hand	E	"
Vaucheria	250 Erlenmeyer	"	"	V	"
Porphyridium	2500 ml. culture flask	air drawn over	constant shaking	S and B	incandescent

Table II

CONTENTS OF MEDIA USED FOR ALGAE

	V	PG	E	S and B
cation-free water	1 l.	1 l.	1 l.	500 cc.
sea water				500 cc.
1 M KNO_3	5 cc.	11.7 cc.		5 cc.
1 M K_2HPO_4	0.5 cc.	5.7 cc.	3 cc.	0.6 cc.
1 M KH_2PO_4	0.5 cc			
1 M $MgSO_4 \cdot 7H_2O$	2 cc.	1 cc.	2 cc.	0.2 cc.
0.1 M $Ca(NO_3)_2$	0.25 cc.	1 cc.		
1 M NH_4NO_3			6 cc.	
1 M NH_4Cl		1 cc.		
$NaAc \cdot 3H_2O$			5 g.	
Difco tryptone			5 g.	
trace elements solution*	1 cc.	1 cc.		
iron and EDTA solution**	1 cc.	1 cc.	1 cc.	1 cc.
adjusted to pH	~6.8	~8.5	~7.0	~8.5

(*) 1 cc. trace elements contains 1.43 mg. H_3BO_3, 1.05 mg. $MnSO_4 \cdot H_2O$, 0.05 mg. $ZnCl_2$, 0.04 mg. $CuSO_4 \cdot 5H_2O$, 0.01 mg. $H_2MoO_4 \cdot H_2O$.

(**) The iron and EDTA solution was prepared according to the method described by Jacobsen.[3] The concentration of $FeSO_4 \cdot 7H_2O$ in media with 1 cc. of this solution per liter is 0.0009 M.

(3) Louis Jacobsen, Plant Physiol., 26(2), 411 (1951).

Table III

RADIOACTIVE CO_2 FIXED IN 5-MINUTE PHOTOSYNTHESIS EXPERIMENTS

	Phormidium	Nostoc muscorum	Nostoc sp.	Synechococcus	Haematococcus	Chlorococcum
Condition of experiment						
Age of plant material	20 days	20 days		4 days		48 hrs.
Light intensity (footcandles on each side of lollipop)	2700	6500	2700	-	2700	-
CO_2 given (μc)	100	80	100	80	40	-
Specific activity of CO_2 (mc/mMol $BaCO_3$)	16.1	16.1	-	16.1	16.1	-
Activity fixed						
Total counts fixed in 5 min./cc. packed algae or g. wet wt. leaves (10^6 c/m)	-	3.0	-	2.0	-	-
Counts fixed in 80% ethanol-soluble compounds (10^6 c/m)	2.8	2.5	0.8	0.6	1.3	-
% of fixed activity in solubles	-	83.3	-	28.8	-	-
Distribution of activity in 80% ethanol-soluble compounds (% of total on chromatogram)						
Phosphates						
Ribulose diphosphate	-	5.5	2.0?	20.8	-	15.1
Uridine diphosphate glucose and UDP galactose	t	7.5	4.7	8.3	1.4	4.8
Hexose monophosphates	28.6	6.7	23.8	20.8	10.8	16.7
Phosphoglyceric acid	21.8	2.5	35.7	16.8	0.7	10.2
Phosphoglycolic acid	8.9	0.1	3.1	2.1	-	0.7
Phospho-enol-pyruvic acid	0.9	t		2.8	0.4	1.5
Pentose- and triose-phosphates	-	14.6	3.4	3.1	2.2	3.3
Unknowns in phosphate region	3.0	7.7	2.7	9.6	2.5	-

Table III-2

	Chlorella	Scenedesmus	Spirogyra	Nitella	Euglena	Vaucheria
Condition of experiment						
Age of plant material	3 days	24 hrs.			6 days	
Light intensity (footcandles on each side of lollipop)	30,000	7500	2700	2700	7500	2700
CO_2 given (μc)	150	80	100	100	80	100
Specific activity of CO_2 (mc/mMol $BaCO_3$)	8.0	16.1	16.1	16.1	16.1	16.1
Activity fixed						
Total counts fixed in 5 min./cc. packed algae or g. wet wt. leaves (10^6 c/m)	26.4	15.5	-	-	2.7	-
Counts fixed in 80% ethanol-soluble compounds (10^6 c/m)	-	10.0	6.4	4.0	1.5	10.4
% of fixed activity in solubles	-	64.1	-	-	54.7	-
Distribution of activity in 80% ethanol-soluble compounds (% of total on chromatogram)						
Phosphates						
Ribulose diphosphate	2.8	2.5	1.4	5.0	3.3	5.3
Uridine diphosphate glucose and UDP galactose	7.6	17.4	12.3	6.2	16.7	5.5
Hexose monophosphates	12.1		25.9	40.8	43.4	18.6
Phosphoglyceric acid	25.0	4.5	7.5	24.0	10.4	36.4
Phosphoglycolic acid	t	0.4	t	t	t	t
Phospho-enol-pyruvic acid	1.9	0.6	0.9	2.0	0.4	2.2
Pentose- and triose-phosphates	t	1.1	1.8	4.1	3.3	1.3
Unknowns in phosphate region	-	1.8	0.9	0.5	1.7	8.7

Table III-3

	Porphyridium	Funaria (protonemata)	Fontinalis (mature gametophyte)	Liverwort* (mature gametophyte)	Ceratopteris (mature sporphyte)	Polystichum (prothalli)
Condition of experiment						
Age of plant material	19 days	20 days				20 days
Light intensity (footcandles on each side of lollipop)	7500	2700	2000	900	600	2700
CO_2 given (μc)	80	100	253	500	227	100
Specific activity of CO_2 (mc/mMol $BaCO_3$)	16.1	16.1	9.1	9.1	9.1	16.1
Activity fixed						
Total counts fixed in 5 min./cc. packed algae or g. wet wt. leaves (10^6 c/m)	1.9	-	42.0	0.9	-	-
Counts fixed in 80% ethanol-soluble compounds (10^6 c/m)	0.5	17.8	28.0	0.7	0.8	1.6
% of fixed activity in solubles	24.3	-	66.5	77.8	-	-
Distribution of activity in 80% ethanol-soluble compounds (% of total on chromatogram)						
Phosphates						
Ribulose diphosphate	14.9	t	t	5.2	?	-
Uridine diphosphate glucose and UDP galactose	3.9	5.7	0.8	?	6.3	8.8
Hexose monophosphates	12.7	11.7	9.4	21.0	26.2	17.0
Phosphoglyceric acid	5.2	11.6	2.2	2.9	5.7	9.7
Phosphoglycolic acid	t	-	-	t	?	0.6
Phospho-enol-pyruvic acid	t	1.1	0.2	0.4	0.5	0.2
Pentose- and triose-phosphates	3.0	0.5	t	t	0.5	1.4
Unknowns in phosphate region	2.1	0.9	-	1.1	-	0.4

Table III-4

	Yew	Juniper	Squash	Soybean	Kalanchoë
Condition of experiment					
Age of Plant Material	previous year's growth	spring growth	4 weeks	5 weeks	16 weeks short day
Light intensity (footcandles on each side of lollipop)	50,000	5000	2000	3000	13,000
CO_2 given (μc)	245	244	190	236	326
Specific activity of CO_2 (mc/mMol $BaCO_3$)	9.1	9.1	9.1	9.1	9.1
Activity fixed					
Total counts fixed in 5 min./cc. packed algae or g. wet wt. leaves (10^6 c/m)	1.6	-	-	-	1.7
Counts fixed in 80% ethanol-soluble compounds (10^6 c/m)	1.4	2.5	15.2	37.0	0.3
% of fixed activity in solubles	88.8	-	-	-	17.7
Distribution of activity in 80% ethanol-soluble compounds (% of total on chromatogram)					
Phosphates					
Ribulose diphosphate	-	0.6	?	0.1	-
Uridine diphosphate glucose and UDP galactose	-	4.8	8.0	1.3	5.2
Hexose monophosphates	4.2	6.6	38.3	12.5	29.2
Phosphoglyceric acid	4.2	2.2	11.9	2.1	0.4
Phosphoglycolic acid	-	t	t	-	-
Phospho-enol-pyruvic acid	0.9	t	0.4	0.2	-
Pentose- and triose-phosphates	?	1.2	0.2	1.3	1.8
Unknowns in phosphate region	5.4	-	1.4	0.2	0.8

Table III-5

Condition of experiment	Tomato	Ivy	Avocado	Barley
Age of Plant Material	young leaves of 3 mos. plant	previous year's growth	young leaves of seedling	seedling
Light intensity (footcandles on each side of lollipop)	13,000	13,000	5000	5000
CO_2 given (μc)	196	349	263	276
Specific activity of CO_2 (mc/mMol $BaCO_3$)	9.1	9.1	9.1	9.1
Activity fixed				
Total counts fixed in 5 min./cc. packed algae or g. wet wt. leaves (10^6 c/m)	-	3.1	-	-
Counts fixed in 80% ethanol-soluble compounds (10^6 c/m)	10.8	2.6	10.1	11.5
% of fixed activity in solubles	-	83.9	-	-
Distribution of activity in 80% ethanol-soluble compounds (% of total on chromatogram)				
Phosphates				
Ribulose diphosphate	t	-	3.3	1.4
Uridine diphosphate glucose and UDP galactose	0.6	0.8	2.3	-
Hexose monophosphates	3.2	4.1	13.8	7.8
Phosphoglyceric acid	0.2	-	5.0	0.9
Phosphoglycolic acid	t	?	0.2	-
Phospho-enol-pyruvic acid	t	?	-	?
Pentose- and triose-phosphates	0.6	4.6	1.5	0.3
Unknowns in phosphate region	0.2	0.9	0.3	-

Table III-6

	Phormidium	Nostoc muscorum	Nostoc sp.	Synechococcus	Haematococcus	Chlorococcum	Chlorella	Scenedesmus	Spirogyra
Sugars									
Raffinose	-	-	-	-	?	-	-	-	-
Maltose	-	-	-	-	t	-	-	-	0.8
Sucrose	3.8	3.8	6.0	-	-	9.2	3.8	1.6	9.9
Glucose	2.3	2.5	-	-	-	-	1.1	-	-
Mannose, mannoheptulose galactose, sedoheptulose	-	0.8	-	-	-	-	-	-	-
Fructose	-	1.6?	?	-	1.1?	-	0.4	-	-
Ribulose	-	3.0	t	-	-	-	-	-	-
Amino acids									
Aspartic acid	12.0	11.7	11.0	4.9	5.0	6.0	5.5	19.2	2.3
Glutamic acid	9.6	0.4	3.8	0.3	7.9	0.3	0.6	2.1	8.9
Serine	t	1.0	t	1.5	2.5	6.7	7.1	6.9	1.7
Glycine	t	0.8	t	-	1.2	1.4	3.5	1.9	2.7
Threonine	-	-	-	-	t	-	-	1.7	-
Alanine	1.4	1.9	1.5	1.2	2.1	19.1	4.5	4.0	18.3
Misc. below alanine	-	-	-	-	19.6	-	-	-	-
Miscellaneous									
Unknowns beyond alanine	-	-	-	-	-	-	-	9.3	-
Dextrins?	-	-	-	-	-	-	-	-	-
Unknown below alanine	2.6	20.9	0.9	6.7	t	-	-	0.2	0.5
Totals									
In phosphate region	65.2	44.6	75.4	84.3	18.0	52.3	49.4	28.3	50.7
Sugars	6.1	11.7	6.0	-	1.1	9.2	5.3	1.6	10.7
Amino acids	23.0	15.8	16.3	7.9	18.7	33.5	21.2	35.8	33.9
Mono- and dicarboxylic acids**	2.8	?	4.5	2.1	43.0	3.8	21.0	22.1	3.8

Table III-7

	Nitella	Euglena	Vaucheria	Porphyridium	Funaria (protonemata)	Fontinalis (mature gametophyte)	Liverwort* (mature gametophyte)	Ceratopteris (mature sporophyte)	Polystichum (prothalli)
Sugars									
Raffinose	-	-	-	-	-	5.2	-	-	-
Maltose	-	-	-	-	1.0	5.9	0.4	-	t
Sucrose	2.3	-	3.0	1.7	22.8	47.7	45.0	35.6	24.2
Glucose	-	0.5	-	-	-	-	-	2.1	-
Mannose, mannoheptulose, galactose, sedoheptulose	-	-	-	-	-	-	-	0.5	-
Fructose	-	0.4	-	-	-	-	0.4	5.8	-
Ribulose	-	-	-	-	-	-	-	-	-
Amino acids									
Aspartic acid	0.4	1.4	4.6	3.1	2.1	3.3	1.7	0.5	7.2
Glutamic acid	0.4	0.5	0.3	4.4	2.3	3.0	0.8	0.3	1.0?
Serine	1.1	2.5	4.1	7.9	6.5	1.6	0.8	0.5	2.9
Glycine	8.1	6.2	2.7	17.5	10.0	2.3	1.7	0.3	1.3
Threonine	-	-	-	-	-	-	-	-	-
Alanine	2.5	0.6	2.8	10.5	21.2	12.2	16.0	10.5	10.0
Misc. below alanine	-	-	-	3.0	-	-	-	-	-
Miscellaneous									
Unknowns beyond alanine	-	-	-	6.0	-	-	-	-	-
Dextrins?	-	3.0	-	-	-	-	-	-	-
Unknown below alanine	-	0.4	-	1.3	0.6	-	0.4	-	-
Totals									
In phosphate region	82.6	80.1	78.0	41.0	31.5	12.6	31.2	39.2	38.1
Sugars	2.3	0.9	3.0	1.7	23.8	58.8	45.8	44.0	24.2
Amino acids	12.5	11.2	14.5	46.4	42.1	22.4	21.0	12.1	22.4
Mono- and dicarboxylic acids**	1.1	3.8	4.0	2.0	5.3	6.6	4.2	2.7	15.0

Table III-8

	Yew	Juniper	Squash	Soybean	Kalanchoë	Tomato	Ivy	Avocado	Barley
Sugars									
Raffinose	-	-	2.9	-	-	-	-	-	-
Maltose	-	0.9	2.6	0.7	0.8	1.0	0.8	1.0	0.8
Sucrose	48.0	41.1	16.5	59.0	39.7	65.5	73.9	45.3	59.8
Glucose	-	7.6	0.9	0.3	-	-	-	-	-
Mannose, mannoheptulose, galactose, sedoheptulose	1.8 SH	2.8	0.4	-	-	-	-	15.8	-
Fructose	-	1.8	0.4	1.0	-	0.8	-	0.9	0.5
Ribulose	-	1.1	-	-	-	-	-	0.3	-
Amino acids									
Aspartic acid	t	1.0	t	0.5	-	1.4	0.4	-	2.2
Glutamic acid	t	t	t	0.1	-	0.6	0.1	-	0.6
Serine	1.2	6.3	2.2	6.3	2.1	4.4	1.5	2.3	4.3
Glycine	?	-	0.3	-	11.1	2.0	1.7	t	2.4
Threonine	-	-	-	-	0.8	-	-	-	0.3
Alanine	27.9	5.5	10.1	3.7	1.0	11.1	9.4	1.7	14.6
Misc. below alanine	-	-	-	-	-	-	-	-	-
Miscellaneous									
Unknowns beyond alanine	-	-	-	-	-	-	-	-	-
Dextrins?	-	3.2	-	-	-	-	-	-	-
Unknown below alanine	-	-	-	-	-	-	-	-	-
Totals									
In phosphate region	9.3	15.4	69.2	17.7	37.4	4.8	10.4	26.4	10.4
Sugars	49.8	50.7	22.7	61.0	40.5	67.3	74.7	63.3	61.1
Amino acids	29.1	17.4	12.6	10.6	15.0	19.5	13.1	4.0	24.4
Mono- and dicarboxylic acids**	6.6	13.9	3.7	8.1	3.5	6.1	0.2	3.9	3.2

t Indicates radioactive spot on film, but activity too low to count accurately
? Indicates radioactive spot which may be compound listed but spots not distinct enough for certainty
* 10-minute experiment
** Activity in individual acids was not determined because spots were streaked

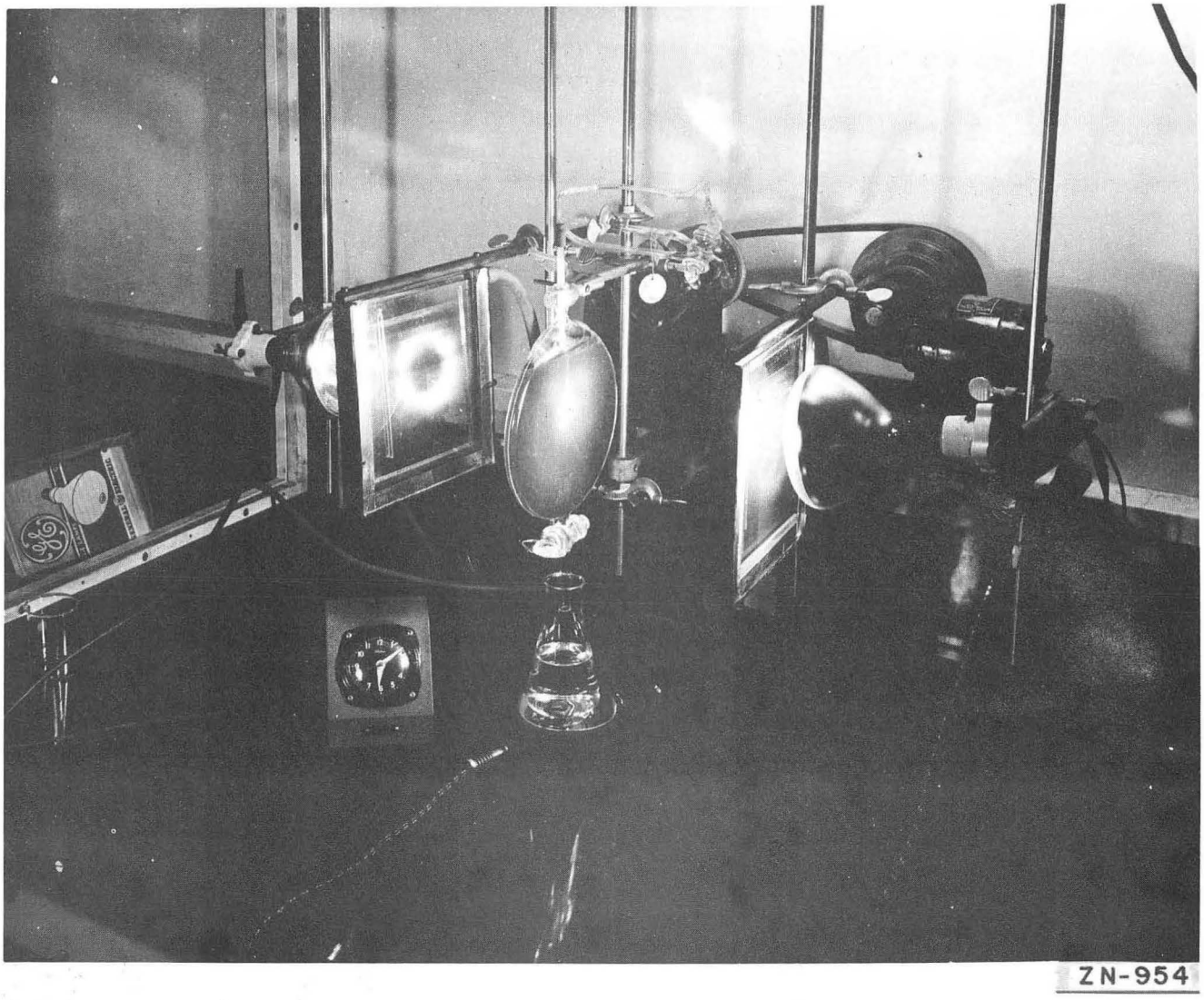

Fig. 1 - Apparatus for algae experiments.

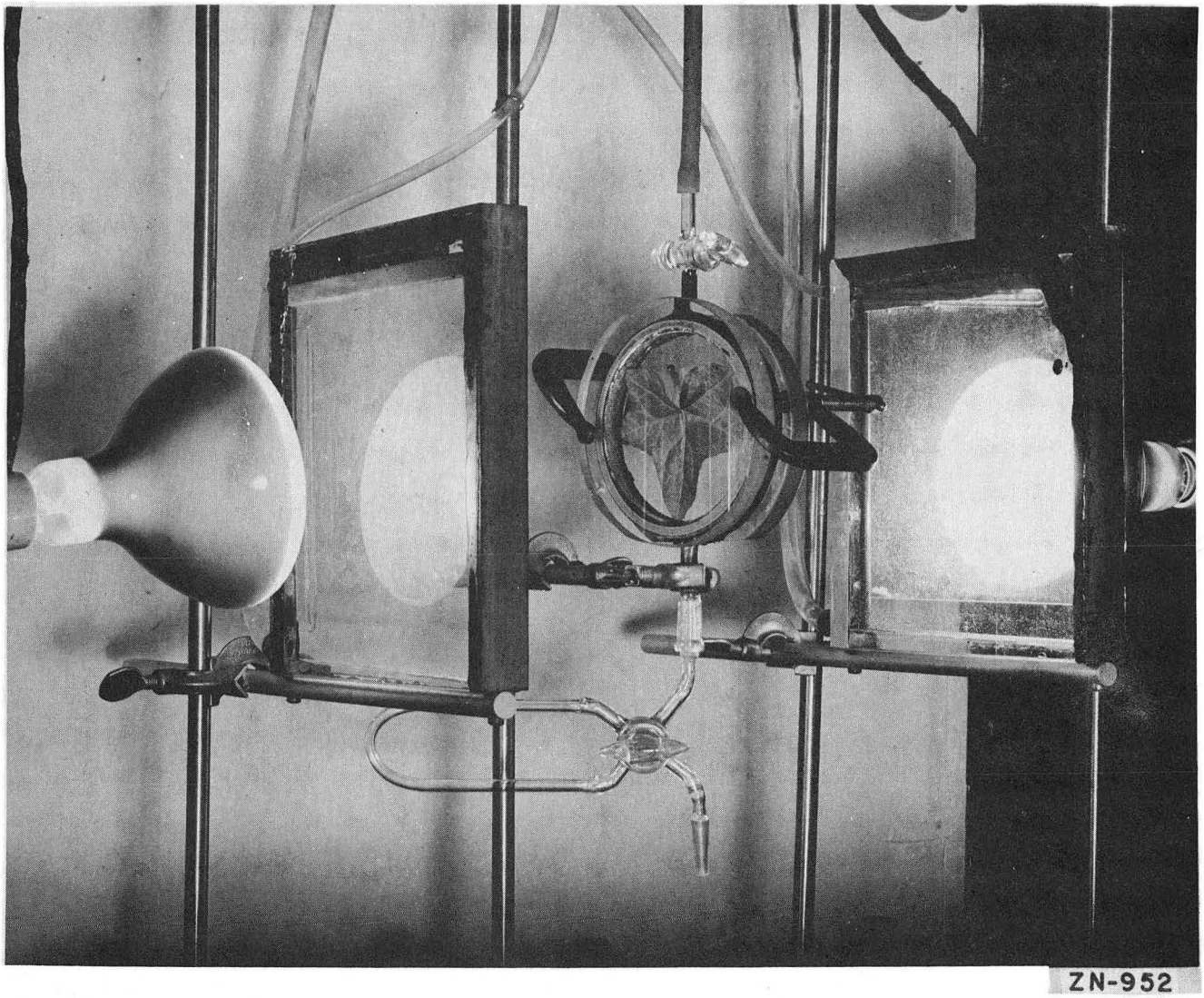

Fig. 2 - Apparatus for leaf experiments.

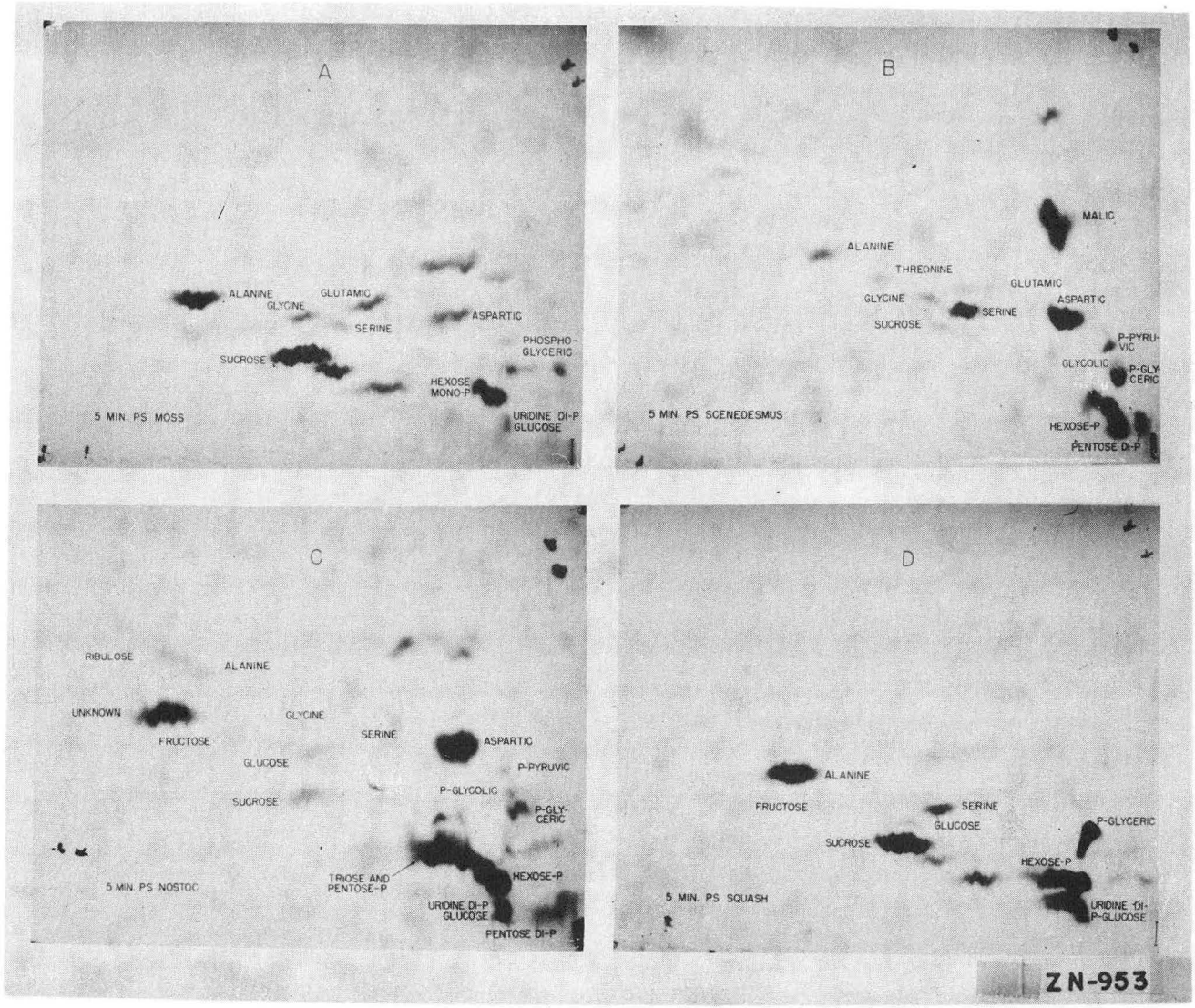

Fig. 3 - Representative chromatograms from which data in Table III were obtained.

A. 5 min. photosynthesis Fontinalis showing high concentration of sucrose.

B. 5 min. photosynthesis Scenedesmus showing low concentration of sucrose.

C. 5 min. photosynthesis Nostoc muscorum showing high concentration of unknown compound below and slightly to the left of alanine.

D. 5 min. photosynthesis squash showing absence of unknown compound below alanine.