Influence of Some Catalyst Poisons on Phototactic Movements of Chloroplasts

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1. INTRODUCTION

All investigations on the influence of chemical factors on phototactic chloroplast movements were hitherto highly fragmentary and referred mainly to narcotics (Eleving 1886, Linsbauer and Abramowicz 1910), some gases such as O_2 , CO_2 etc. (Demoor 1895, Lewis 1898, Senn 1908) or substances affecting the hydrature of the cells (Küster 1906, Senn 1908). Some rare investigations were also concerned with other substances, mostly inorganic salts (Senn 1908) but the choice of these substances was clearly accidental.

It seems, therefore, that an investigation may be revelant on the connection between phototactic movements and the effect of substances either inhibiting selectively only one of the metabolic processes or affecting in a definite way the physico-chemical properties of the protoplasm. Recently numerous similar investigations on protoplasmatic movements have been undertaken (Olson and du Buy 1940, Seifriz and Uraguchi 1941, Sweeney 1941, 1944, Sweeney and Thimann 1938, 1942, Allen and Price 1950) and because of this comparison of the results obtained with chloroplast behaviour may be very valuable.

In the course of a major research on the mechanism of phototactic chloroplast movements undertaken at the Laboratory of Plant Physiology of the Jagellonian University it was decided to investigate the effect of chemical substances on chloroplast movements. In the present paper a report is made on the first stage of this investigation, namely, on the effect of some enzymatic inhibitors attacking chiefly the enzymes responsible for respiration and photosynthesis.

2. METHOD

For experiments *Lemna trisulca* L. leaves of surface area 4—7 mm² were used.

The experimental method consisted in testing the effect of various inhibitor concentrations on photosynthesis and respiration and then obser-

ving the effect on phototactic movements of selected inhibitor concentrations affecting either photosynthesis and respiration of one of these processes only. For photosynthetic and respiration measurements the technique described in an earlier paper (Zurzycki 1955) was used. After the respiration and photosynthesis rates of a leaf chosen for experiments had been measured in various light intensities, the leaf was taken out of the respirometer chamber and placed in the inhibitory solution in darkness. After 1 — 2 hours the leaf was again removed together with a drop of the inhibitory solution and the measurements were repeated. For each inhibitor concentration this procedure was repeated 3 — 5 times. The graphs 1 — 3 illustrate the response to various inhibitor concentrations of the respiration and photosynthesis rates in various light intensities. Each of the points plotted on the graphs indicates the mean photosynthesis or respiration rate expressed as the percentage of the controls.

To assess the response of phototactic chloroplast movements in the selected inhibitor concentrations the chloroplast arrangements after 3 hours of illumination were correlated to light intensity and the rate of chloroplast movements was measured (Zurzycka and Zurzycki 1953).

The 3 substances used as inhibitors were: hydroxylamine hydrochloride $\text{NH}_4\text{OH} \cdot \text{HCl}$ (m. w. 69), sodium azide NaN_3 (m. w. 65) and berberine sulphate $\text{C}_{20}\text{H}_{17}\text{NO}_4 \cdot \text{H}_2\text{SO}_4 \cdot \text{H}_2\text{O}$ (m. w. 451). As the permeability of this least compound is highly dependent on the pH (Strugger 1939) the acidity of the solution was set at the pH level — 7.5 by adding KOH.

3. RESULTS

3.1. Influence of inhibitors on photosynthesis and respiration

Hydroxylamine concentrations of less than 10^{-5} M/l have no noticeable influence on photosynthesis. A slight inhibition becomes manifest at concentrations of $5 \cdot 10^{-5}$ M/l. As the concentration of this poison raises photosynthesis is more and more inhibited, when the concentration reaches $5 \cdot 10^{-3}$ M/l the photosynthesis rate is only 2—6% of the control, at the concentration of $5 \cdot 10^{-2}$ M/l photosynthesis can no longer be detected. Photosynthesis inhibition is independent of light intensity solely in weaker light intensities — up to 3000 lux — and in stronger light there is a relative drop in the inhibition. This is clearly visible in the case of the $5 \cdot 10^{-3}$ M/l concentration. This last result contradicts Weller and Frank (1941) who report that in *Chlorella* a given hydroxylamine concentration produces always the same percentage drop in the rate of photosynthesis independently of light intensity. None of the hydroxylamine concentrations used affected in any way the respiration rate. This confirms

the results obtained by Shibata (1933) and Nakamura (1938) who found that this poison inhibits only assimilation and has no effect on respiration.

Fig. 1. The effect of hydroxylamine hydrochloride on photosynthesis and respiration in *Lemna trisulca*.

Fig. 2. The effect of sodium azide on photosynthesis and respiration in *Lemna trisulca*.

Sodium azide concentrations of 10^{-5} M/l and less have no influence on respiration and photosynthesis. When the concentration is 10^{-4} M/l a slight, just exceeding error limits, stimulation both of photosynthesis and respiration becomes apparent. Beyond this concentration photosynthesis rate drops sharply, much more so than in the case of hydroxylamine, and the drop is always independent of light intensity — as for instance in the concentrations of 10^{-3} and 10^{-2} M/l. Photosynthesis is finally interrupted when the concentration is 10^{-1} . Respiration is reduced by approximately 40% when the concentration reaches 10^{-3} M/l and beyond this inhibition does not increase. A similar effect of NaN_3 on respiration was assessed by Keilin (1936) in yeast and by Marsh and Goddard (1939) in carrot slides.

Fig. 3. The effect of berberine sulphate on photosynthesis and respiration in *Lemna trisulca*.

The character of the changes in photosynthesis and respiration produced by berberine sulphate are somewhat different. The concentration of 10^{-4} M/l has a small inhibitory effect on photosynthesis and as the concentration increases inhibition also augments, though, very slowly. No sudden intensification of inhibition is to be observed here as is the case with hydroxylamine and even more with sodium azide. When concentration is 10^{-1} M/l photosynthesis rate is still more than 10% higher than in the controls. On the other hand, respiration rate is very markedly reduced beginning from the 10^{-5} M/l concentration and this inhibition rises together with the concentration increase, at 10^{-1} M/l respiration

rate is approximately 15% of the corresponding value in the controls. Berberine sulphate has been used as a selective inhibitor of respiration (Schmitz 1951, Krieg 1954) but hitherto its effect on photosynthesis has not been investigated.

3.2. The influence of inhibitors on the chloroplast arrangements and phototactic movements

For investigating the influence of the inhibitors on chloroplast arrangements and phototactic movements of chloroplasts the inhibitory solutions were chosen as follows from the results described in the precedent paragraph:

Concentration	Photosynthesis rate	Respiration rate
Hydroxylamine $5 \cdot 10^{-3}$ m/l	7%	100%
„ $5 \cdot 10^{-2}$ „	0%	100%
Sodium azide 10^{-3} „	65%	approx. 70%
„ 10^{-1} „	0%	„ 70%
Berberine sulphate 10^{-2} „	60%	„ 50%

The experimental procedure was here similar to that used in experiments on gaseous metabolism, the *Lemna trisulca* leaves are placed for 1 — 2 hours in the proper poison solution in light conditions adjusted so as not to disturb the required initial chloroplast arrangement. After the leaves have been long enough in the inhibitor the light intensity is changed and observations are made of 1) the relation between the chloroplast arrangements and light intensity and 2) the course of the various phototactic reactions.

3.2.1. The influence of inhibitors on the relation between chloroplast arrangements and light intensity

Using the method described in an earlier paper (Zurzycki and Zurzycka 1953) the curve for chloroplast arrangements within light intensities ranging from 0 to 15000 lux is plotted. In this series of experiments the initial chloroplast arrangement is epistrophe. The curves are plotted for leaves placed in fresh water and $5 \cdot 10^{-2}$ M/l solutions of hydroxylamine and 10^{-1} M/l sodium azide. The results from these experiments are given in Table 1. From the tabulated data, where each entry is the computed mean value from at least 4 repetitions, it appears that within the range of light intensities applied neither of the two inhibitors influences the percentage of epistrophe chloroplasts characteristic for the given light

Table 1

Dependence of chloroplast arrangements on light intensity. Time of exposition 3 hours.
The numbers indicate the % of chloroplasts in horizontal position

Light intensity	15000	10000	5500	900	120	0
Control	10,1	15,1	33,9	72,0	100,6	20,8
Hydroxylamine 5,10 ⁻² M.	10,7	17,6	30,6	73,0	97,9	42,2
Sodium azide 10 ⁻¹ M.	10,8	15,0	35,1	69,1	95,4	55,9

intensity. However, there is some divergence in the change of chloroplasts to apostrophe (VI-th position in Table I for light intensity — 0). But, as apostrophe in *Lemna trisulca* depends on numerous biological factors such as the age of the cell, the starch content, and such like all difficult to estimate quantitatively, and because the irregularity in the mean values is relatively small, it does not seem justifiable to consider the irregularity to be a specific effect caused by the poisons.

3.2.2. The influence of the inhibitors on the course of the various phototactic reactions

For experiments on the influence of the inhibitors on the course of phototactic reactions the following 6 kinds of reactions have been chosen: epistrophe — parastrophe, epistrophe — apostrophe, parastrophe — epistrophe, parastrophe — apostrophe, apostrophe — epistrophe and apostrophe — parastrophe. The inhibitors used are hydroxylamine in concentrations of 5 · 10⁻² and 5 · 10⁻³ M/l, sodium azide in concentrations of 10⁻¹ and 10⁻³ M/l and berberine sulphate in concentration of 10⁻² M/l. The reactions enumerated above may be divided into two groups in respect to their response to the inhibitors used.

In the first group are the reactions epistrophe — parastrophe and epistrophe — apostrophe. The three poisons used influence neither the character nor the rate of these reactions and the reactions develop in the same way as in the control (Table 2).

The other group covers the reactions: parastrophe — epistrophe, parastrophe — apostrophe and apostrophe — epistrophe; in all these reactions the inhibitory effect of the poisons is clearly marked.

5 · 10⁻² M/l hydroxylamine concentrations block completely the three reactions. When the concentration of this inhibitor is 5 · 10⁻³ M/l the inhibition is somewhat less. For instance in the parastrophe — epistrophe reaction the final reduction percentage of the reaction calculated in respect to the controls is in hydroxylamine concentrations of 5 · 10⁻² and 5 · 10⁻³ M/l 68% and 100% respectively.

Table 2

Phototactic movements plotted against time. The numbers indicate the % of chloroplasts in horizontal position

Time min.	0	5	10	15	20	25	30	40	60	80	100	120	180
Epistrophe — parastrophe (120 — 15000 lux)													
Control	100	66,5	51,0	42,3	38,7	31,8	28,0	20,9	16,7	6,8	5,6	3,4	12,9
Hydroxylamine 5.10 ⁻³ M	100	66,3	53,2	45,7	37,6	29,2	26,3	19,4	14,7	12,4	10,8	10,4	10,1
Hydroxylamine 5.10 ⁻² M	100	78,5	54,4	40,4	33,6	29,4	26,3	18,8	20,2	16,4	12,0	12,6	10,7
Sodium azide 10 ⁻³ M	100	72,6	48,1	38,8	30,1	29,1	20,8	14,6	11,4	10,2	7,7	7,0	8,9
Sodium azide 10 ⁻¹ M	100	62,6	46,3	32,6	25,8	25,2	25,3	21,1	18,3	15,3	15,9	12,8	10,8
Epistrophe — apostrophe (120 — 0 lux)													
Control	100				75,0			57,7	47,7	37,9	28,9	28,4	20,8
Hydroxylamine 5.10 ⁻³ M	100				79,7			62,3	44,5	38,3	31,8	29,7	23,1
Hydroxylamine 5.10 ⁻² M	100				71,3			50,8	43,8	33,0	27,9	27,0	31,7
Sodium azide 10 ⁻³ M	100				53,8			45,5	43,9	39,3	34,7	28,9	26,4
Sodium azide 10 ⁻¹ M	100				80,6			72,7	63,5	59,0	61,1	56,5	55,9
Apostrophe — parastrophe (0—15000 lux)													
Control	6,5				9,2			9,2	10,5		7,8	10,5	10,5
Hydroxylamine 5.10 ⁻³ M	23,4				7,1			4,1	3,0		6,1	4,1	4,1
Hydroxylamine 5.10 ⁻² M	12,9				10,3			10,3	11,2			13,7	13,7
Sodium azide 10 ⁻³ M	17,0		19,0		15,0		18,0	16,0	16,0		12,0	13,4	13,4
Sodium azide 10 ⁻¹ M	5,9		5,1		4,3		4,3	4,3	3,4		5,1	5,9	5,9

The inhibition of the three reactions in sodium azide solutions of 10⁻¹ and 10⁻³ M/l is very much like (Table 3). The response to berberine sulphate is essentially the same as to the other two poisons but the response to berberine sulphate cannot be compared directly with the response to the other inhibitors. The colour of berberine sulphate solutions at concentration of 10⁻³ M/l is distinctly yellow which causes a drop

in the intensity of light when it reaches the cells. For this reason the inhibitor has not been used in experiments on the influence of poisons on the relation between chloroplast arrangements and light intensity.

Table 3

Phototactic movements plotted against time. The numbers indicated the % of chloroplasts in horizontal position

Time min	0	5	10	15	20	25	30	40	60	80	100	120	180
Parastrophe — epistrophe (15000 — 120 lux)													
Control	6,9	20,3	42,9	63,6	70,4		75,5	86,6	93,3	97,7	89,6	93,5	90,8
Hydroxylamine 5.10 ⁻³ M	2,3		6,3		12,7		18,4		27,4	24,6	30,5	26,9	29,5
5.10 ⁻² M	7,2		12,6		6,9		9,0	9,6	9,6	10,3	8,7	10,1	7,9
Sodium azide 10 ⁻³ M	3,1		29,8		44,6		56,9	60,9	59,1	52,2	53,2	49,4	48,5
" 10 ⁻¹ M	5,4		8,2		12,2		19,6	18,1	19,5	16,9	14,7	13,7	14,1
Apostrophe — epistrophe (0 — 120 lux)													
Control	16,8		39,6		54,3		63,9	77,2	84,1	88,1	90,1	90,4	89,3
Hydroxylamine 5.10 ⁻³ M	16,8		20,9		22,5		30,9	33,9	33,2	43,8	50,5	49,4	38,4
" 5.10 ⁻² M	12,0		13,2		15,0		17,2	17,1	28,0	26,5	23,4	21,2	17,7
Sodium azide 10 ⁻³ M	7,5		13,9		46,3		53,8	56,4	62,9	68,3	74,2	61,2	64,5
" 10 ⁻¹ M	8,5		10,2		11,5		11,1	9,8	11,0	13,0	11,6	14,5	11,2
Parastrophe — apostrophe (15000 — 0 lux)													
Control	6,9		28,7		57,8		72,1	55,6	42,6	33,0	33,0	27,8	24,3
Hydroxylamine 5.10 ⁻³ M	6,4		9,1		13,8		18,3	21,1	18,7		12,8	10,0	10,0
" 5.10 ⁻² M	1,9		2,9		2,9		3,9	3,9	2,9	2,9	3,9	3,9	3,9
Sodium azide 10 ⁻³ M	9,1		13,4		37,0		60,6	55,0	51,6			51,6	51,6
" 10 ⁻¹ M	3,3		5,0		6,7		8,3	5,0	5,0	5,0	6,7	4,1	5,6

4. DISCUSSION

When the response of various living organisms to the inhibitors here used is compared it appears that *Lemna* is relatively more resistant. In *Chlorella* for instance, already a 10⁻⁴ M/l concentration of hydroxylamine reduces the photosynthesis rate by 40 — 95% (Nakamura 1938, Waller and Frank 1941) while in *Lemna* the same effect is not produced till the concentration is some tens of times stronger. The slime mould *Physarum* is approximately 100 times more susceptible to sodium azide inhibition than *Lemna* (Allen and Price 1950); on the other hand Marsh and Goddard (1939) report a strong and persistent drop in the respiration rate of carrot tissue produced by sodium azide concentrations of approximately the same order as those affecting *Lemna* leaves.

The inhibitory effect on the course of chloroplast movements has a pronounced dual character. The obtained results show that the inhibitors used inhibit only those reactions for which the starting off chloroplast arrangement is the profile position and in which, if conditions were normal as in the controls, the final arrangement would be fully horizontal (the parastrophe — epistrophe and apostrophe — epistrophe reactions—Fig. 4).

The opposite reactions (the epistrophe — parastrophe and epistrophe — apostrophe) are not affected by the inhibitors. Special notice must be given to the parastrophe — apostrophe reaction. Earlier investigations (Zurzycka and Zurzycki 1953) show that when *Lemna trisulca* cells with the parastrophe chloroplast arrangement are placed in darkness the first response to the new conditions is epistrophe, and the arrangement characteristic for darkness is not reached till later. However, all the three poisons used here inhibit the first part

Fig. 4. Epistrophe — parastrophe and parastrophe — epistrophe reactions in normal and in hydroxylamine treated cells. Abcissae — time in mins, ordinates — % of chloroplasts in horizontal position.

Fig. 5. Parastrophe — apostrophe reactions in normal untreated cells and in cells treated with various hydroxylamine concentrations. Abcissae and ordinates as in fig. 4.

of this reaction, the change to epistrophe. The inhibition is complete in higher hydroxylamine or sodium azide concentrations and less marked in weaker concentrations (Fig. 5).

The dual character in the chloroplast reaction to the inhibitors used which is revealed by the present experiments once again corroborates that in *Lemna trisulca* there are two types of phototactic reactions. A similar

duality was ascertained in the response to temperature, mineral salts, light and other stimulants.

The question now arises with which process of gaseous metabolism are connected such reactions as the parastrophe — epistrophe, apostrophe — epistrophe, or parastrophe — apostrophe reactions, all distinctly inhibited by the poisons used. As these reactions are always inhibited when the poison used produces a marked reduction in photosynthesis rate regardless of its effect on respiration which may be inhibited (sodium azide, berberine sulphate) or normal (hydroxylamine) it seems that on the basis of the results obtained the reactions having at the start the profile chloroplast arrangement are connected with photosynthesis. However, the results obtained in the case of the parastrophe — apostrophe reaction indicate that it would be more accurate to speak in terms of a relationship of the inhibited reactions with the capability for photosynthesis than with photosynthesis itself.

Notwithstanding the numerous efforts it was neither possible to discover poisons which would selectively inhibit respiration nor to interrupt respiration completely with the poisons used. The reduction of the respiration rate by approximately 70% which was the maximum obtained has no particular effect on phototactic movements. It is therefore to be assumed that the residual respiration fully covers the energetic requirements of these movements. A similar phenomenon is reported by Allen and Price (1950) in the slime mould *Physarum polycephalum*, in this species the reduction of respiration by 3/4 through lessening the partial oxygen pressure or through the application of some inhibitory substances does not inhibit plasmatic movements. Diametrically different conditions prevail in the case of cyclosis in the cells of higher plants where plasmatic circulation is strictly united with respiration and where even a small drop in respiration rate produces an inhibition of this movement (Bottelier 1934, Thimann and Sweeney 1938, Gorenflot 1947).

5. SUMMARY

1. The effect of three enzymatic inhibitors on respiration and photosynthesis in *Lemna trisulca* leaves was tested. It was found that hydroxylamine hydrochloride inhibited photosynthesis without affecting respiration rate, sodium azide had a strong inhibitory effect on photosynthesis and a weaker one on respiration, and berberine sulphate affected little photosynthesis and inhibited strongly respiration.

2. Observations were made of phototactic chloroplast reactions in selected concentrations of the poisons which inhibited in a known manner photosynthesis or respiration. It was found that:

a) a 70% reduction in the respiration rate brought no change in the phototactic movements,

b) a strong reduction or the complete blocking of photosynthesis inhibited or stopped entirely those phototactic movements which started with the profile chloroplast arrangements (parastrophe — epistrophe, parastrophe — apostrophe and apostrophe — epistrophe), and had no effect on phototactic movements beginning from the horizontal chloroplast position (epistrophe — parastrophe, epistrophe — apostrophe reactions).

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STRESZCZENIE

1. Zbadano działanie trzech inhibitorów enzymatycznych na oddychanie i fotosyntezę liści *Lemna trisulca*. Stwierdzono, że chlorowoderek hydroksylaminy hamuje fotosyntezę nie zmieniając intensywności oddychania, azidek sodu hamuje silnie fotosyntezę a słabo oddychanie, zaś siarczan berberyny wywiera stosunkowo słabsze działanie na fotosyntezę, hamując silnie oddychanie.

2. Przebadano przebieg reakcji fototaktycznych chloroplastów w wvbranych stężeniach inhibitorów, hamujących w znany sposób fotosyntezę względnie oddychanie. Stwierdzono, że:

a) redukcja oddychania o około 70% nie ma wpływu na ruchy fototaktyczne,

b) silne zahamowanie względnie zupełna redukcja fotosyntezy powoduje zahamowanie lub zupełne wstrzymanie ruchów, przy których pozycją wyjściową jest położenie profilowe chloroplastów (parastrofia — epistrofia, parastrofia — apostrofia, apostrofia — epistrofia), natomiast jest bez wpływu na ruchy rozpoczynające się od pozycji płaskiej (epistrofia — parastrofia, epistrofia — apostrofia).

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