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Cinematographic Studies on Phototactic Movements of Chloroplasts

Badania kinematograficzne nad fototaktycznymi ruchami chloroplastów

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1. INTRODUCTION

Cinematographic techniques and the analysis of films are a most effective tool for the study of processes taking place in cells. The method is especially useful in those cases when the researcher is concerned with processes developing relatively slowly. Such is the nature of phototactic movements of chloroplasts and therefore it seemed reasonable to expect that if cinematographic techniques were used in this case more knowledge would be gained primely on the mechanism of these movements. With the exception of one more or less general report (Zurzycki and Zurzycka 1953) concerned mainly with methods and describing the general character of phototactic chloroplast movements in one species only, there are no detailed researches on this problem. The present work was carried out between 1952 and 1955 with the aim of investigating by means of cinematography problems referring to phototactic movements. It was concerned with:

a) the extension of investigations on phototactic movements of chloroplasts to species other than *Lemna trisulca,*

b) investigations on two main phototactic reactions, i. e. epistrophe — parastrophe and parastrophe — epistrophe, as cinematographic techniques have been applied hitherto to the former of the responses only,

c) the effect on the movements of particular chloroplasts, of various physico-chemical factors influencing the course of phototactic reactions (considered in their statistical aspect).

2. MATERIALS AND METHODS

The basic material for the investigations was as before *Lemna trisulca* obtained from a pond in the Botanical Garden of the Jagellonian University and cultivated subsequently in an aquarium. The other species also used for experiments were *Funaria hygrometrica, Elodea densa* and

Arabis arenosa. The reactions were filmed with accelerations ranging from 1/2 to 1/1000 (K u h l 1949) according to the rate of the reactions. The negatives were obtained on an irreversible 16 or 35 mm film band. The method followed in analysing the films was the same as already reported in an earlier paper, except that the velocity curves were now plotted in the time — distance system of coordinates.

3. RESULTS

3.1. THE EPISTROPHE-PARASTROPHE REACTION IN VARIOUS SPECIES

3.1.1. *Arabis arenosa*. The leaves of the plants were prepared in the manner described elsewhere (Z u r z y c k i 1955). The light intensity for inducing the reaction was 15000 lux and the acceleration 1/1000 (i. e. one frame per minute). The reaction was relatively slow and the majority of the chloroplasts reached the lateral cell walls only after 1—2 hours. The movements as seen on the screen seem to be a slow and uniform gliding away of chloroplasts to the side walls. The chloroplasts move either radially and symetrically away from the centre or the majority

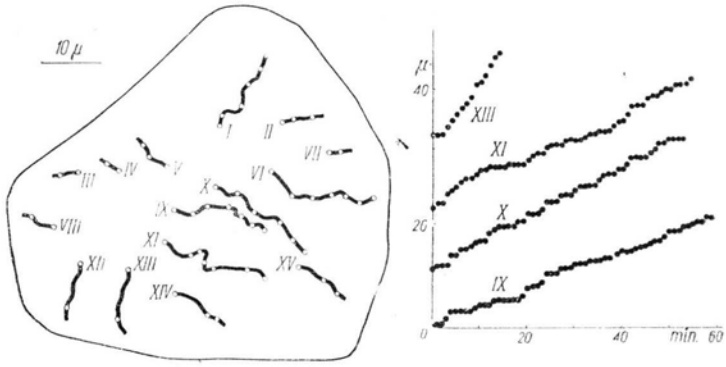

Fig. 1. *Arabis arenosa*. Left, paths traced by chloroplasts in cell. Points mark the position of chloroplast centres at 10 minute intervals. Right, distance — time curve for several chloroplasts.

of chloroplasts lying near the centre move in one direction whereas the others move to the nearest side wall. The analysis of the film revealed that the chloroplast movements begin immediately the light is switched on. The paths traced by the chloroplasts are fairly straight and slightly waved, though, there are no loops and changes of direction. The average velocities of chloroplasts ranged from 0,16 to 1,18 μ/min. The velocities of the particular chloroplasts are too fairly uniform. The mean velocity for 12 chloroplasts in 3 cells was 0,417 μ/min. The highest momentary velocity recorded was 1,6μ/min.

3.1.2. *Funaria hygrometrica.* The movements were filmed with an acceleration of 1/480, i. e. one frame every 30 seconds. Light intensity was 25000 lux. In this case too the movement as seen on the screen gives the impression of a smooth gliding away to the side walls, though the movements are far less regular than in *Arabis arenosa.* The analysis of the film also shows that the paths of the chloroplasts are less regular. Although movements towards the nearest side wall usually predominate, the paths are less straight, but loops are quite exceptional. The velocity of chloroplast movements is not as uniform as in the previous case. Very

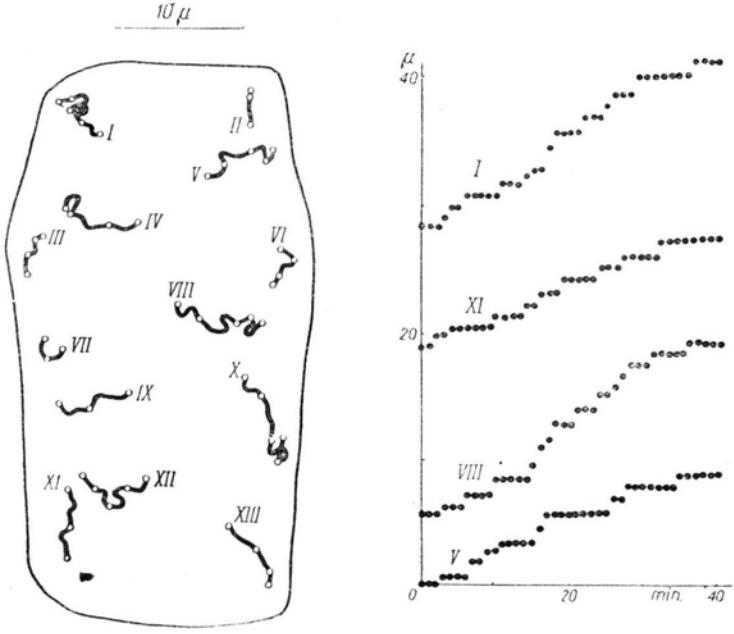

Fig. 2. *Funaria hygrometrica.* Left, paths traced by chloroplasts (points mark positions of chloroplasts at 10 min. intervals). Right, distance — time curve for several chloroplasts.

often during 30 seconds a chloroplast changed its position considerably and remained motionless sometimes even for the next several minutes then it moved rapidly and stopped again. The mean velocity of 16 chloroplasts in 4 cells was 0,245 μ/min. The mean velocities of particular chloroplasts ranged from 0,15 to 0.45 μ/min and the momentary highest velocity was 1,5 μ/min.

3.1.3. *Lemna trisulca.* The detailed characteristic of the chloroplast movements and their changeability will be made further on in this paper. There only as an example the reaction in response to light intensity of 10000 lux is described. It was filmed with an acceleration of 1/80 (one

frame every 5 seconds). As seen on the screen the movements of chloroplasts appear highly entangled and make the impression of a disorderly and directionless escape to the side walls. Only some chloroplasts move without change of direction to the nearest side wall but all the others move about in a disorderly fashion, often changing directions and tracing loops. These movements cease only when the chloroplasts contact a side wall, though in some rare cases chloroplasts already in position on a side wall begin moving again right across the cell to the opposite wall. The

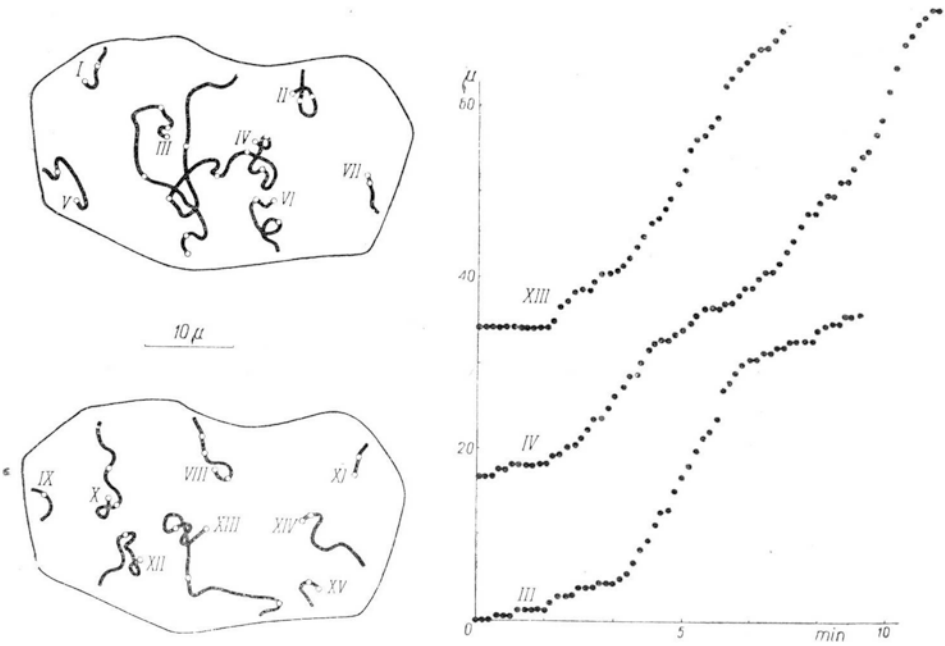

Fig. 3. *Lemna trisulca*. Left, paths traced by chloroplasts (points mark positions of chloroplasts at intervals of 100 sec). Right, distance — time curve for several chloroplasts.

detailed analysis also confirms the high intricacy of the paths and the frequent changes in direction. In many cases the chloroplasts reach not the nearest but indeed, the most distant side wall. The velocity of the movements is also very variable. The mean velocity in the cases examined was 5,41 μ/min, ranging in particular instances from 3,9 to 6,7 μ/min and the highest velocity recorded was 26,4 μ/min.

3.1.4. *Elodea densa*. For the experiments the big cells from the underneath surface of leaves were used. In these cells besides chloroplasts movements also the cytoplasmic streaming is distinctly visible owing to the presence of cytoplasmic granules. This circumstance made a close examination of chloroplast movements very promising as the possibility

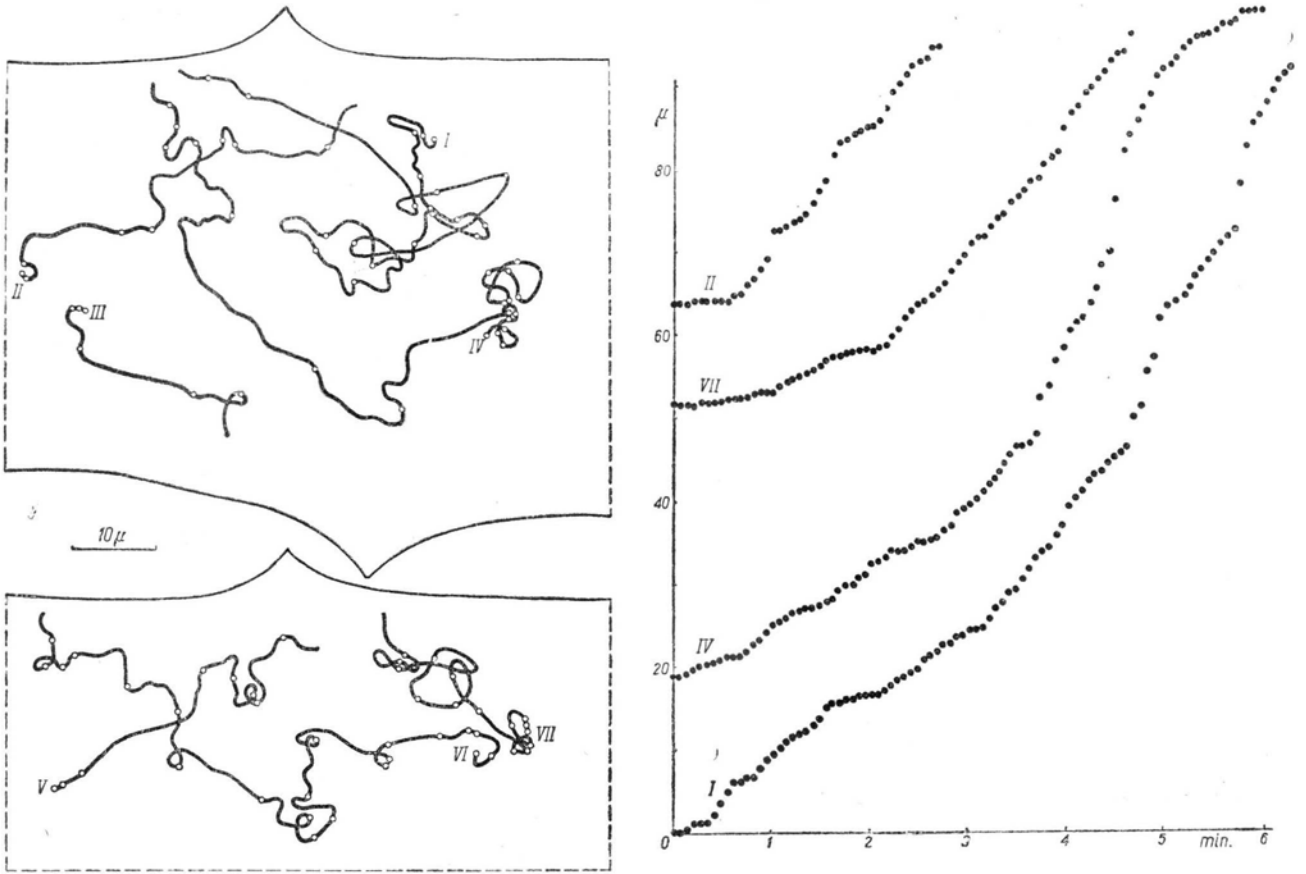

Fig. 4. *Elodea densa*. Left, paths traced by chloroplasts (points mark positions of chloroplasts at intervals of 100 sec.). Right, distance — time curve for several chloroplasts.

arose that if there were a similarity between the cytoplasmic streaming and phototactic chloroplast movements, it would be observed.

In *Elodea densa* the movements of chloroplasts are relatively rapid and consequently they were filmed with an acceleration of 1/16 (exposures at one second intervals) or even of 1/2. Light intensity was 800 lux. In the projection on the screen the movements of chloroplasts make the impression of a disorderly escape. The chloroplasts move on the outer cell wall chaotically over considerable distances and with a distinctly changing velocity. At other times they trace intricate meanders. Very often, especially in the later stages of the reaction, groups of chloroplasts can be seen moving in one direction with approximately uniform velocity. The detailed analysis confirmed the impression from the screen projection. The paths of chloroplasts are very tortuous (fig. 4, where, however only some few chloroplasts are marked in). The velocities are also greatly variable but intervals without any movements at all are an exception. The mean velocity for 15 chloroplasts was 25,02 μ/min, ranging from 19,6 to 29,3 μ/min, and the maximum velocity was 336 μ/min.

The mean and maximum velocities of chloroplasts during the epistrophe-parastrophe reaction in the species examined are shown in Table 1.

Table 1

Species	Mean velocity of chloroplasts μ/min	Maximum velocity of chloroplasts μ/min
Arabis arenosa	0,417	1,6
Funaria hygrometrica	0,245	1,5
Lemna trisulca	5,41	26,4
Elodea densa	25,02	336,0

As a general conclusion it can be said that both the velocity and the character of chloroplast movements in their escape to the side walls is highly variable and depends on the species used for observations. The mean velocity of chloroplast movements ranged from 0,1 to 30,0 μ/min, and during the short lasting peaks could even reach 300 μ/min. The transient maximum velocities of chloroplasts exceeded the mean velocity by as much as 3—5 times (*Arabis, Funaria* and *Lemna*) or even 6—8 times (*Elodea*).

On the whole the slower the chloroplasts move the less complex and more regular are their paths, though, this is not a rule without exception. The different character of chloroplast movements in the various objects can be correlated neither with the size of chloroplasts and cells nor with their anatomical structure. Probably, the character of chloroplast movements is a specific trait peculiar for every species.

3.2. VARIABILITY OF CHLOROPLAST MOVEMENTS DURING THE EPISTROPHE-PARASTROPHE REACTION IN *LEMNA TRISULCA*

A detailed analysis of films obtained at various times and for a wide of experimental conditions shows that the velocity of chloroplast movements varies greatly. This variability is well illustrated by the mean velocities of chloroplasts in the different cells which range from 0,48 to 7,4 μ/min. However at some one stage of the vegetative season and in strictly established conditions plants from one population display fairly constant velocities of chloroplasts. For instance the velocities recorded

on June 18, 1952 were	7,2	7,6	7,4	7,1	mean 7,3	μ/min
on Sept. 9, 1955 were	1,29	1,46	1,22	1,43	mean 1,395	μ/min

From a closer inspection of chloroplast movements it appears that in the case of the epistrophe — parastrophe reaction in *Lemna trisulca* the velocity of chloroplasts depends primely on two factors: light intensity causing the reaction and the physiological state of the plants. As has been

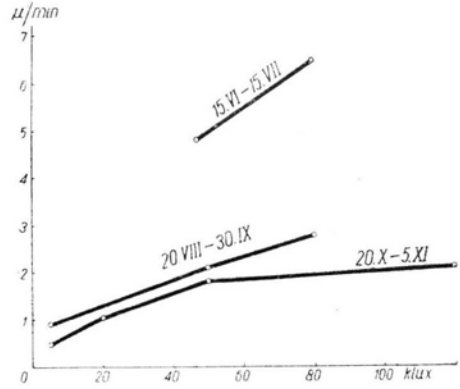

Fig. 5. *Lemna trisulca*. Dependence of mean chloroplast velocity in epistrophe-parastrophe reaction on light intensity and the physiological state of plant. Ordinates — velocity in μ/min abscissae — light intensity in klux.

demonstrated elsewhere the latter factor changes distinctly during one vegetative season (Zurzycka and Zurzycki 1953). The mean chloroplast velocities obtained from numerous experiments carried out at various seasons and for various light intensities are shown in Fig. 5. It follows from these curves that the velocity of chloroplast movements is highest in the spring and summer but drops distinctly in autumn and late autumn. At all seasons the velocity is relatively low, when the light intensity bringing out the response is low, and increases as light becomes stronger. The important conclusion of a methodological significance which emerges from these results is, that a series of several experiments and control observations must be carried out approximately the same time of the vegetative season and with the same material. The absolute values obtained for the velocities of chloroplasts are of relative significance,

whereas only the values obtained in respect to the control have a fundamental significance for the characteristic of chloroplast movements in the epistrophe — parastrophe reaction.

The patterns traced by chloroplasts do not change greatly, with the exception of the reactions produced by very weak light but this will be mentioned later. The paths are in some instances less and in others more complicated, their intricacy being fairly variable, but no differences of direction are noticeable. This variability in the intricacy of the patterns can be correlated neither with the stages of the vegetative season nor with the rate of the movements.

3.3. VARIABILITY OF MOVEMENTS IN THE COURSE OF THE PARASTROPHE-EPISTROPHE REACTION

The return of the chloroplasts from the side to the outer wall of the cells takes place in a somewhat different manner. As seen on the screen it makes the impression of a steady gliding of chloroplasts along straight

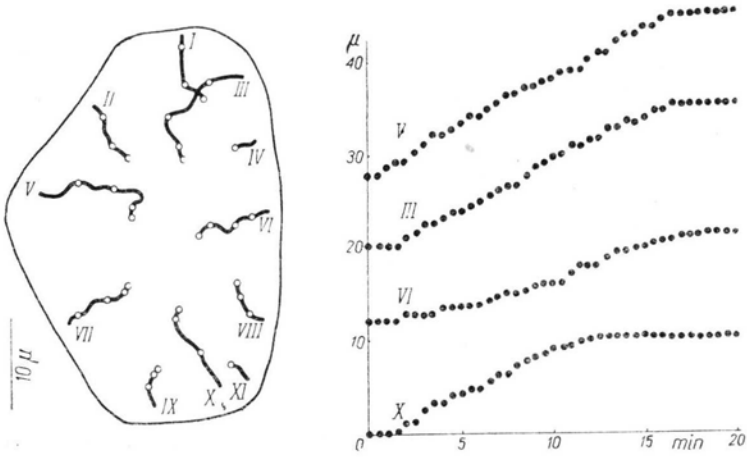

Fig. 6. *Lemna trisulca*, the parastrophe-epistrophe reaction. Left, paths traced by chloroplasts (points mark positions of chloroplasts at 5 min. intervals). Right, distance-time curve for several chloroplasts.

lines from the side walls to the centre of a cell. The analysis shows that the paths are not quite straight but wave somewhat, though, they are far more direct and regular than in the case of the epistrophe — parastrophe reaction (Fig. 6).

The velocities too are much more constant and do not change so distinctly as in the opposite reaction. This applies also to the mean velocities of chloroplast movements which at the same time are lower than in the epistrophe-parastrophe reaction, more constant and less variable. Thus,

the mean velocities of chloroplasts range within limits of 0,5 to 1,0 μ/min and seem to depend only very slightly on the intensity of light and the physiological state of the plants, the two factors which affect so strongly the considerable variability in the epistrophe — parastrophe reaction.

3.4. MORPHOLOGICAL TYPES OF PHOTOTACTIC MOVEMENTS

The cinematographic techniques and the analysis of variability in the chloroplast movements in the course of the epistrophe — parastrophe and parastrophe-epistrophe reactions have made it possible to distinguish two morphological types of chloroplast movements in *Lemna trisulca*. The characteristic features of the two reaction types are compared in Table 2.

Table 2

	Type I characteristic for the epistrophe-parastrophe reaction	Type II characteristic for the parastrophe-epistrophe reaction
The paths of chloroplasts	Intricate, usually in meanders, frequent changes in direction	Less complicated, slightly wavy, no changes in direction
Velocity	Variable, frequent intervals without movements	More steady
Influence of external factors on velocity	Very distinct	Hardly any

Type I is characteristic for the epistrophe-parastrophe reaction, whereas, type II for the parastrophe-epistrophe one.

In fig. 7 the cycle epistrophe-parastrophe-epistrophe is shown, the reactions taking place directly one after the other in one cell. In several instances it was possible to identify the same chloroplasts in both reactions. From the velocity curve it appears that the same chloroplast moves in the two successive reactions along different paths and with various velocities.

However, it has been observed that in some rare cases the epistrophe-parastrophe reaction may develop according to type II, while the parastrophe-epistrophe reaction according to type I. The statistical aspect of the conditions prevailing in this respect is shown by Table 3 which gives the corresponding percentages for film records of 96 epistrophe-parastrophe and 33 parastrophe-epistrophe reactions. In the Table only the percentages of reactions following the patterns of type I and II are

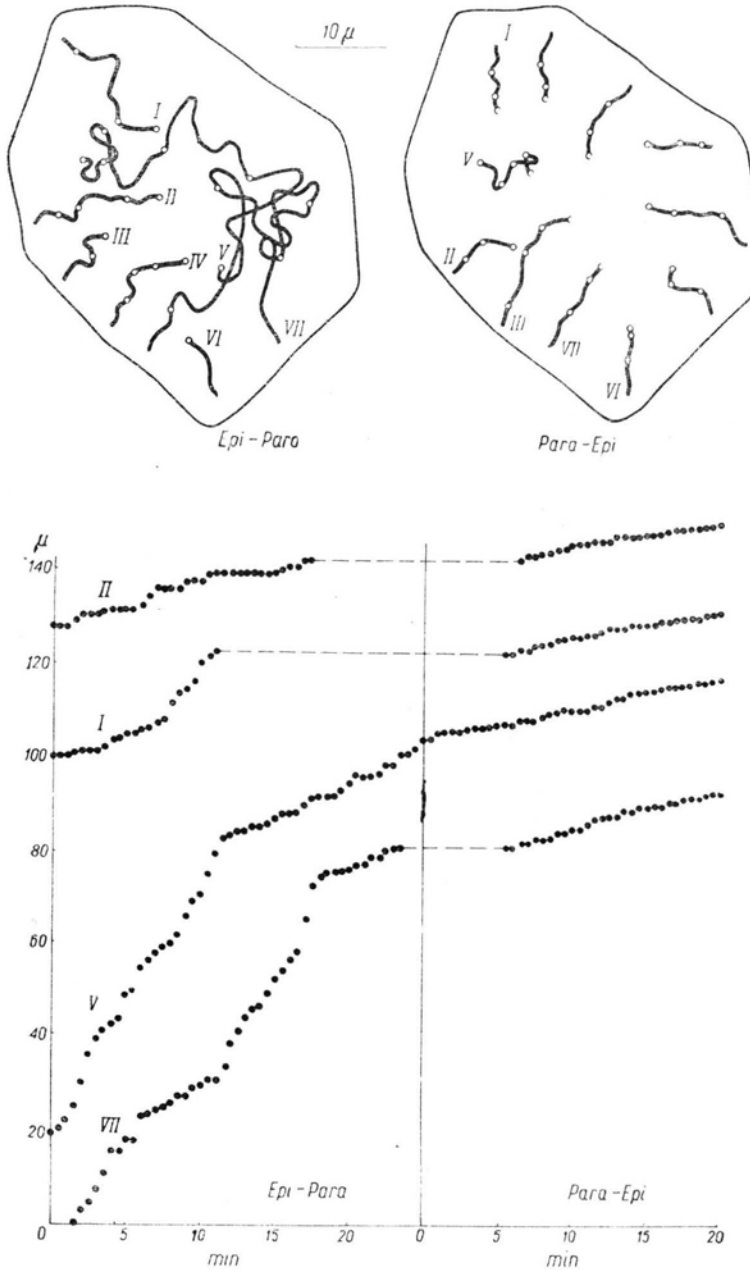

Fig. 7. *Lemna trisulca*. Left, course of the epistrophe-parastrophe reaction (above — points at 5 min. intervals, below distance - time curve). Right the parastrophe-epistrophe reaction in the same cell (above — points at 5 min. intervals, below — distance - time curve).

given, the percentage of reactions of intermediate character between the two types are not included.

Exceptions from the typical course in the epistrophe-parastrophe reaction are observed almost exclusively when the reaction is in response to relatively weak light (e. g. 5000 lux). Deviations from type II in the

Table 3

	Type I	Type II
Epistrophe — parastrophe reaction	78,1%	13,5%
Parastrophe — epistrophe reaction	9,2%	87,8%

parastrophe-epistrophe reaction are observed under the influence of potassium ions and histidine.

Similar, though far less pronounced morphological differences were observed in *Funaria hygrometrica*. In the leaf cells of this moss the paths of chloroplasts in the epistrophe-parastrophe reaction were more intricate, and straighter in the opposite reaction (Fig. 8). It therefore seems

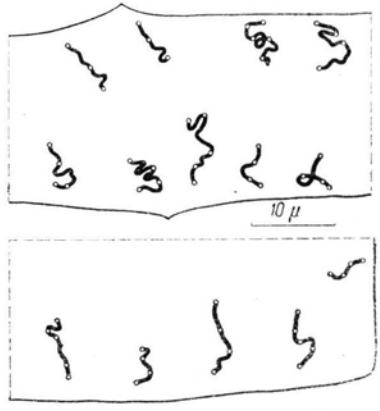

Fig. 8. *Funaria hygrometrica*. Paths of chloroplasts in the epistrophe - parastrophe reaction (above) and the parastrophe-epistrophe reaction (below). Points at 10 min. intervals.

probable that the two morphologically different types of movements are not associated with one species but are of a more general nature, characteristic too for phototactic reactions of other species.

3.5. INFLUENCE OF PHYSICO-CHEMICAL FACTORS ON THE PHOTOTACTIC MOVEMENTS OF CHLOROPLASTS

Hitherto statistical techniques were used in researches on the influence of physico-chemical factors on phototactic movements of chloroplasts.

Cinematographic techniques were used in the study of this problem in order to compare earlier results with the data on the dynamics of the movement of particular chloroplasts in cells acted upon with different physico-chemical factors.

3.5.1. *Light.* It was shown in an earlier paper that the epistrophe-parastrophe phototactic reaction proceeded more rapidly when the light was stronger than when the light was weaker (Zurzycka and Zurzycki 1953). To obtain a better interpretation of the results then obtained the course of the phototactic response has been once again examined with both statistical and cinematographic techniques for light intensities of 150, 500, 5000, 20000, 50000 and 120000 lux. The data assembled in Table 4 illustrate the results obtained for a light intensity range of 5000 to 120000 lux, i. e. for intensity limits causing parastrophe.

Table 4

Light intensity	Mean time of phototactic reaction	Mean velocity of chloroplasts	Variability in velocity on single chloroplasts	Relative velocity of chloroplasts
5000 lux	11,6 min	0,443 μ/min	0,21—0,43 μ/min	21%
20000 „	11,4 „	1,037 „	0,68—1,64 „	49%
50000 „	9,05 „	1,76 „	1,30—2,06 „	83%
120000 „	8,8 „	2,12 „	1,29—3,50 „	100%

It is to be noted as a general conclusion that the rate of the reaction as obtained with the statistical method increases together with light intensity. There are no significant differences in the times of reactions only in light intensities of 5000 and 20000 lux. The observations were made on autumn material and this explains the relatively small differences in the times of reactions and also the relatively small velocities of chloroplasts. The mean velocities of chloroplasts in the investigated light intensities differ between themselves far more than the times of reactions. The nature of the differences in the mean velocities of the particular chloroplasts indicates the significance of these differences. The particular chloroplasts move with a fairly uniform velocity diverging only slightly from the mean value which is proportional to the increase in light intensity similarly as is the time of reaction.

On the other hand, the paths of the chloroplasts in light intensities of 50000—120000 lux are very similar, highly intricate and it is difficult to notice any differences between them. For light intensity of 5000 lux,

however, the reactions proceed along the morphological type II (gliding) in all 5 cases observed. This explains why in spite of the much lower velocity the time of the reaction at 5000 lux differs little from that at 20000 lux because the straighter and shorter paths compensate the lower velocity.

The return parastrophe-epistrophe reaction was observed at light intensities of 150 and 500 lux and generally speaking its course conforms with the type II morphological pattern. Both the rate of the reaction and the velocity of chloroplasts are far less dependent on external factors. In the case of experiments at low light intensity of 150 lux the chloroplasts moved somewhat less rapidly, but the material examined was not large enough so that the conclusions it implies cannot be regarded as definite.

It has already been pointed out that the parastrophe-epistrophe reaction is far less dependent on the vegetative season. This is clearly illustrated by the table below listing the velocities of chloroplast movements in the epistrophe-parastrophe and parastrophe-epistrophe reactions at various vegetative stages. The reactions were filmed at light intensities of 50000 and 500 lux respectively.

Table 5

Time of the year	Velocity of chloroplasts in the epistrophe - parastrophe reaction (50000 lux)	Velocity of chloroplasts in the parastrophe - epistrophe reaction (500 lux)
July 1954	4,95 μ/min	0,90 μ/min
September 1955	2,50 „	0,75 „
November 1955	1,75 „	0,78 „

3.5.2. *Temperature.* In an ealier investigation the authors (Zurzycka and Zurzycki 1950) demonstrated that the phototactic reactions of chloroplasts had various courses at different temperatures. It was found that whereas the epistrophe-parastrophe reaction was very clearly correlated with temperature and its rate greatly increased together with rising temperature, the parastrophe-epistrophe reaction was, within limits of error, independent of temperature for a wide range of temperatures! In the present investigation the course of the reactions and the velocity of chloroplasts were observed at temperatures of 10, 20 and 30°C. The observations were made on a uniformly heated table (Bajer and Molè-Bajer 1953), the temperature being regulated by a flow of water from a Höppler ultrathermostat. The results for both reactions are summarized in Table 6.

Table 6

Temperature	Time of epistrophe-parastrophe reaction	Mean velocity of chloroplasts in epistrophe-parastrophe reaction	Relative velocity in epi-para reaction	Time of parastrophe-epistrophe reaction	Mean velocity of chloroplasts in para-epi reaction
10°	22,2 min	0,67 μ/min	50,8%	—	—
20°	11,3 „	0,98 „	76,5%	7,9 min	0.74 μ/min
30°	7,8 „	1,28 „	100,0%	6,7 „	0,78 „

Simultaneously to the rise of temperature the time of epistrophe-parastrophe reaction is greatly reduced and the much velocities of chloroplasts increase. In the parastrophe-epistrophe reaction a rise in temperature by 10°C affects neither the rate of the reaction nor the mean velocity of chloroplasts. A detailed analysis shows that there are no significant differences in the patterns of the chloroplast paths. It is thus to be concluded that in the case of the epistrophe-parastrophe reaction the differences in the rate of reactions caused by temperature are due to the different velocities with which the chloroplasts move. In the case of the parastrophe-epistrophe reaction the velocity of chloroplast movements is independed of temperature and for this reason the rate of the reaction remains unaffected.

3.5.3. *The influence of calcium and potassium ions.* In the course of earlier work (Zurzycka and Zurzycki 1951) it was found that the ions of some metals, by changing the viscosity of the cytoplasm had different effects on phototactic reactions. The epistrophe-parastrophe reaction is strictly related with the viscosity of the cytoplasm, whereas there is no such relation in the case of the parastrophe-epistrophe reaction. In the course of the present work only the experi-

Table 7

	Epistrophe — parastrophe reaction			Parastrophe — epistrophe reaction		
	Time of reaction	Mean velocity of chloroplasts	Relative velocity of chloroplasts	Time of reaction	Mean velocity of chloroplasts	Relative velocity of chloroplasts
K^+	7,0 min	3,70 μ/min	185%	—	0,73 μ/min	99%
Control	8,6 „	2,00 „	100%	5,7 min	0,74 „	100%
Ca^{++}	15,8 „	0,95 „	47,5%	6,2 „	0,80 „	108%

ments with calcium and potassium salts were repeated as these two salts have an entirely opposite influence on the viscosity of the cytoplasm. The experimental procedure was the same as that described earlier, i. e. the experimental material was immersed for six hours prior to observa-

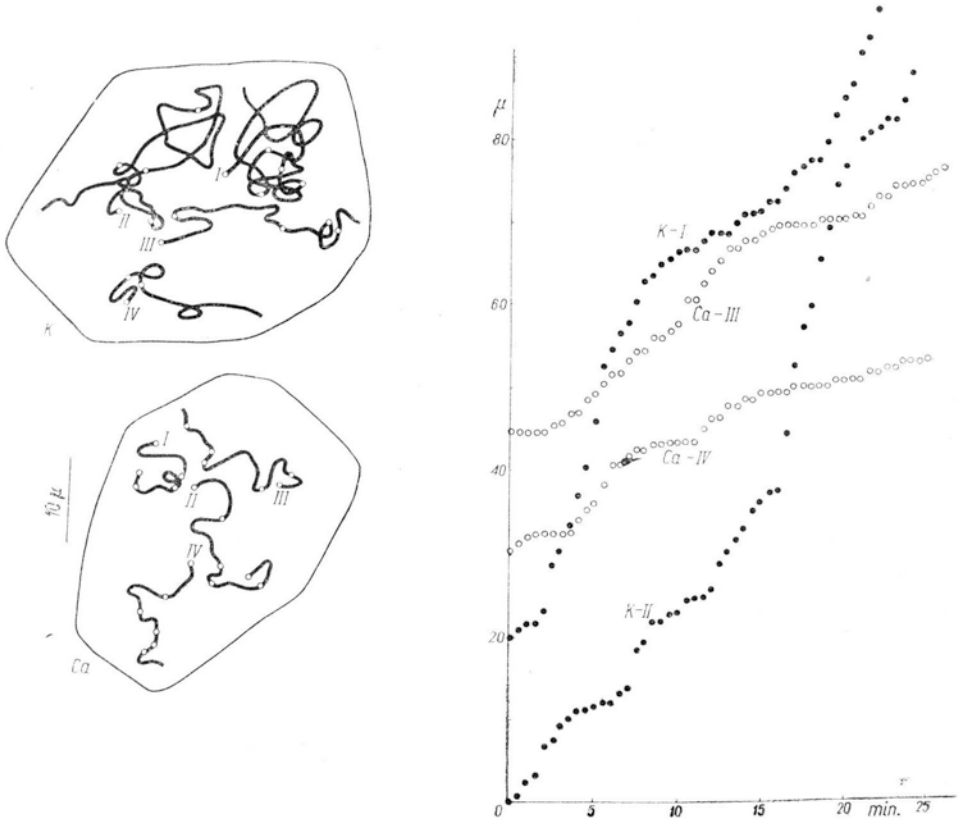

Fig. 9. *Lemna trisulca*. Course of the epistrophe-parastrophe reaction in the presence of calcium and potassium ions. Left, paths of chloroplasts (points at 5 min. intervals). Right, distance — time curve.

tion, in a solution of calcium or potassium salt. The reactions were filmed at 50000 lux. The changes in the rate of the reaction and in the velocity of chloroplasts are illustrated by the data in Table 7.

These results support once again the earlier results. Calcium ions by increasing the viscosity of the cytoplasm slow down considerably the rate of the epistrophe-parastrophe reaction and potassium ions by liquefying the cytoplasm accelerate the reaction. The ions have a similar effect on the velocity of chloroplast movements, but the acceleration or retardation of chloroplasts as measured on the screen is much greater than the results obtained from statistical analyses (almost twice as great).

Also the paths traced by chloroplasts are very different. Under the influence of potassium ions they are even more complicated and tortuous and consequently longer, whereas under the influence of calcium the chloroplasts they move along straighter paths and do not describe loops, their paths being more related to type II. The pattern traced by chloroplasts under the influence of calcium or potassium ions is shown in Fig. 9.

Table 8

	Epistrophe-parastrophe reaction			Parastrophe-epistrophe reaction		
	Time of reaction	Mean velocity of chloroplasts	Relative velocity of chloroplasts	Time of reaction	Mean velocity of chloroplasts	Relative velocity of chloroplasts
Control	9,5 min	1,75 μ/min	100%	8,4 min	0,76 μ/min	100%
Histidine	7,8 min	2,30 ,,	132%	6,9 min	0,91 ,,	120%

The tortuous paths of chloroplasts under the influence of potassium ions has an opposite effect as the increased velocity and consequently the chloroplasts remain much longer in the flat position. However, the greater velocity is the predominant factor and therefore the reaction as a whole is accelerated. In the case of calcium ions the reduced velocity of chloroplasts is counteracted by the straighter paths, but here again the former factor predominates and consequently the whole reaction is prolonged. In the course of the parastrophe-epistrophe reaction the paths of chloroplasts do not deviate from the pattern in the controls. There was only one exception when under the influence of potassium ions the paths of the chloroplasts were sufficiently tortuous to qualify them as type I. The velocity of chloroplasts during the parastrophe-epistrophe reaction in solutions of calcium and potassium salts is exactly the same as in the controls and there is therefore no change in the rate of the reaction.

3.5.4. *Histidine.* Unpublished results from experiments on the mechanism of phototactic movements indicate that some aminoacids accelerate both the epistrophe-parastrophe and the parastrophe-epistrophe reactions. To illustrate this effect experiments on phototactic reactions in histidine solutions were repeated. Prior to observations the material was placed for 20 minutes in a histidine solution, the concentration being 10^{-2} m/l. The results of the analyses are summarized in Table 8.

As is apparent from the above data the movements of chloroplasts in the reaction epistrophe-parastrophe are accelerated and consequently the time of the reaction is shortened. The accelerated velocity and the

shorter time of the reaction are also observed in the parastrophe-epistrophe reaction which is a most remarkable effect in view of the fact that this reaction is relatively independent of external conditions. Histidine causes the paths of chloroplasts to be even more complicated than

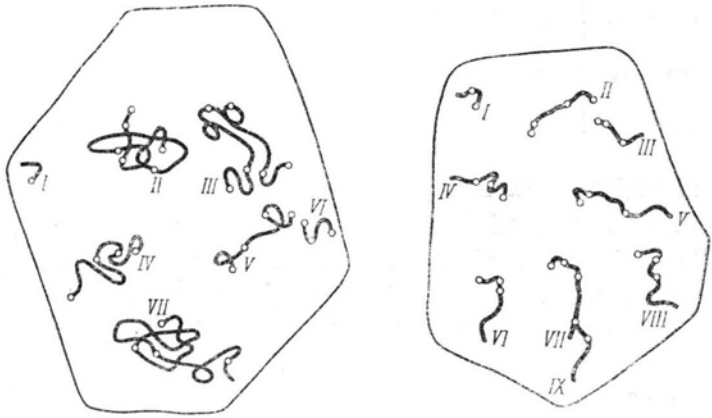

Fig. 10. *Lemna trisulca*. Paths of chloroplasts in the epistrophe-parastrophe reaction (left) and the parastrophe-epistrophe reaction (right) in the presence of histidine. Points at 5 min. intervals.

in the control material. The same effect is obtained too in the case of the parastrophe-epistrophe reaction so that frequently (in 35% of cases) the pattern of chloroplast movements is morphologically of type I.

3.5.5. *Hydroxylamine*. When investigating the influence of enzymatic inhibitors of photosynthesis on the phototactic movements of chloroplasts it was found that such a typical inhibitor of photosynthesis as hydroxylamine, in concentrations of 10^{-2} m/l had no influence on the epistrophe-parastrophe reaction, but entirely inhibited the opposite reaction. In the latter case the chloroplasts remain on the side walls, although the intensity of light corresponds to the flat arrangement of chloroplasts. In the present experiments this property of hydroxylamine has been confirmed. The rate of the reactions and the velocity of chloroplasts in cells acted upon with hydroxylamine are presented in Table 9.

The time of reaction, the velocity and the paths of chloroplasts in the epistrophe-parastrophe reaction show no significant differences in respect to the controls. On the other hand in the parastrophe-epistrophe reaction the percentage of chloroplasts in the initial position does not change and the chloroplasts which had previously remained on the outer walls move a little but without any specified direction.

Table 9

	Epistrophe-parastrophe reaction			Parastrophe-epistrophe reaction		
	Time of reaction	Mean velocity of chloroplasts	Relative velocity of chloroplasts	Time of reaction	Mean velocity of chloroplasts	Relative velocity of chloroplasts
Control	8,6 min	2,00 μ/min	100%	5,7 min	0,74 μ/min	100%
Hydroxylamine	8,0 „	2,12 „	106%		0,15 „	203%

3.5.6. *Phenylurethan.* The unpublished results obtained in the course of an investigation on the influence of narcotics on phototactic movements of chloroplasts show that phenylurethan in 5 mmol concentration retards considerably the epistrophe-parastrophe reaction, whereas in the case of the parastrophe-epistrophe reaction it acts similarly as hydroxylamine by inhibiting completely the return of chloroplasts to the flat position. The analysis of the cinematographic record of the behaviour of chloro-

Table 10

	Epistrophe-parastrophe reaction			Parastrophe-epistrophe reaction		
	Time of reaction	Mean velocity of chloroplasts	Relative velocity of chloroplasts	Time of reaction	Mean velocity of chloroplasts	Relative velocity of chloroplasts
Control	9,5 min	2,10 μ/min	100%	7,2 min	0,84 μ/min	100%
Phenylurethan	37,0 „	0,28 „	16%		0 „	0%

plasts at this concentration of phenylurethan shows a correlation between the results of the statistical method and the movements of particular chloroplasts. This is illustrated by Table 10.

The paths of chloroplasts during the epistrophe-parastrophe reaction do not differ from those in the controls, whereas in the opposite reaction the chloroplasts remain motionless.

3.5.7. *Return of chloroplasts after centrifugation.* By centrifugation all the chloroplasts are forced into one part of the cell and after centrifugation is stopped they return to their normal position. It was demonstrated by Diannelidis (1950) that ethyl ether inhibits the return

of centrifugated chloroplasts. As both ethyl ether and phenylurethan inhibit the phototactic response of chloroplasts, it seems possible that the mechanism governing the return of centrifugated chloroplasts may be similar to the mechanism of phototactic movements. Because of this the return of centrifugated chloroplasts was studied by means of cine-

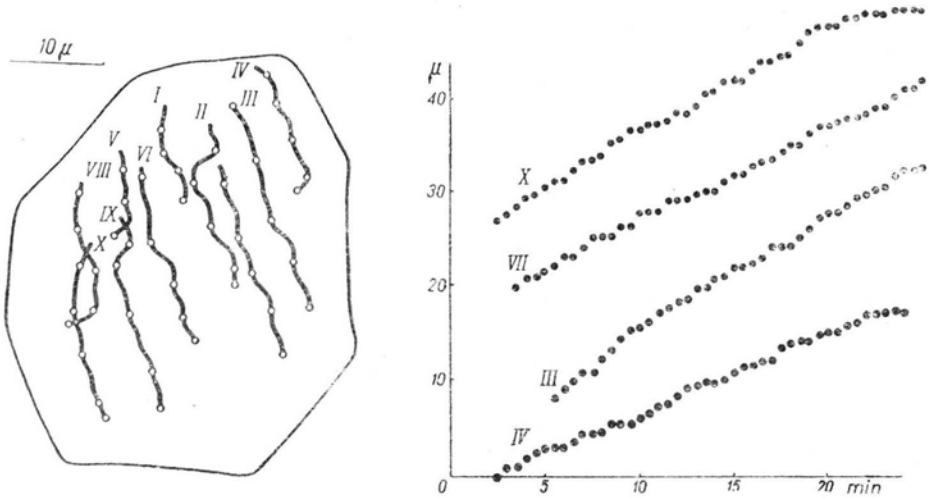

Fig. 11. *Lemna trisulca.* Displacements of chloroplasts in weak light (500 lux) after centrifugation. Left — paths of chloroplasts (points at 5 min. intervals). Right, distance-time curve.

matography both in weak (500 lux) and strong (50000 lux) light. The return of chloroplasts in faint light as seen on the screen appears as a slow uniform gliding of the chloroplasts in one direction. The analysis of the film record shows that the paths of chloroplasts are almost straight,

Table 11

Kind of movement	Mean velocities in various cells			Mean velocity
Epistrophe — parastrophe reaction	0,845	0,624	0,801 μ/min	0,760 μ/min
Return after centrifugation	0,866	0,782	0,750 ,,	0,798 ,,

slightly wavy and nearly parallel. The pattern of these paths resemble the phototactic movements of type II characteristic for the parastrophe-epistrophe reaction. The velocity of the movements is highly uniform and in this respect the return of chloroplasts differs from the morphological type II. At the same time it is very remarcable that the velocities

of the returning chloroplasts are exactly the same as the velocities in the parastrophe-epistrophe reaction. The similarities of chloroplast velocities in the parastrophe-epistrophe reaction and in the return after centrifugation are compared in Table 11.

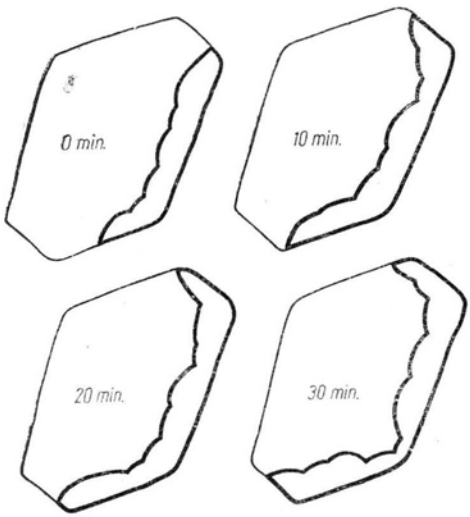

Fig. 12. *Lemna trisulca*. Displacement of chloroplasts in strong light (50000 lux) after centrifugation. Successive diagrams show chloroplast arrangements at 10 min. intervals.

If after centrifugation the chloroplasts are subjected to strong light then there is no return to the outer cell walls. Instead, after some time the chloroplasts arrange themselves around the cell by moving along the side walls without changing their profile arrangement.

3.6. THE DYNAMICS OF THE MOVEMENTS OF INDIVIDUAL CHLOROPLASTS

The cinematographic analysis makes possible a detailed investigation of particular chloroplasts. Some of details obtained in this manner throw a new light on the mechanism of chloroplast movements. The most valuable in this respect were the observations on *Elodea densa* and the experiments on the effects of physico-chemical factors. At this stage of work some facts were established on the margin of the investigations described above making possible a better understanding of the phototactic chloroplast movements.

3.6.1. *Relation of the size of chloroplasts to the velocity of movements.* It has been found in the course of studies on phototactic movements of chloroplasts in various species that the differences in the velocity of these movements cannot be explained by the differences in the size of chloroplasts. However, the circumstances are quite different when the velocity of movements and the size of chloroplasts in one species are con-

sidered. In one of the filmed cells of *Lemna trisulca* marked differences in the size of neighbouring chloroplasts were observed. When the velocities of these chloroplasts were analyzed it was found that the smaller ones moved much faster than the larger. This is shown in Table 12.

Table 12

Chloroplast	Diameter in μ	Mean velocity in μ/min
1.	7,8	1,2
2.	7,4	1,9
3.	5,2	3,7
4.	5,4	3,5

Inasmuch as these chloroplasts were in the direct neighbourhood of one another and on the whole moved in concordant directions it can be assumed that the conditions influencing them were the same and consequently their velocity can be associated with their size. However, in general the differences in the size of chloroplasts in *Lemna trisulca* are much smaller than in this special case and it is very difficult to note any such correlation in other cells.

3.6.2. *Changes in the direction of chloroplast movements in Lemna trisulca*

When a chloroplast is assymmetric or its starch grain is located eccentrically it is easy to see whether it pivots on its axis while changing the direction of movement. Already in the course of earlier work it was found that sometimes a chloroplast may spin round in the course of forward

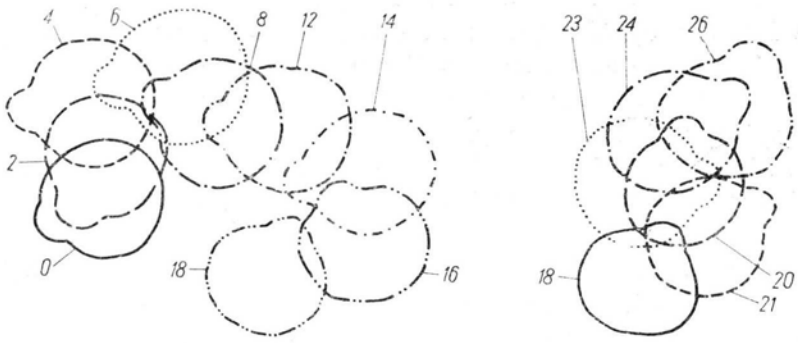

Fig. 13. *Lemna trisulca*. Movements of an asymmetric chloroplast (the starch grain is not at the centre) in the epistrophe-parastrophe reaction. Numbers 2, 4, 6, etc. mark the position of the chloroplast after 200, 400, 600 etc. seconds.

motion. An example of a chloroplast with an eccentric starch grain changing the direction of its movement is shown in Fig. 13. As can be seen the chloroplast moves at first with the side where there is no starch in front, but when the direction changes it moves backwards without spinning round. The spin does not take place till when the chloroplast is moving.

3.6.3. *Correlation between cytoplasmic and chloroplast movements in Elodea densa*

The movements taking place inside *Elodea* cells were filmed with an 100 x immersion objective and 10 x eyepiece and small acceleration (1/2). This made possible a study of chloroplast movements on the background of the motion of the granulosities in the cytoplasm. An example showing these movements is illustrated by fig. 14. The full results from analyses of the relation between the streaming of the cytoplasm and the phototactic chloroplast movements will be reported elsewhere, nevertheless,

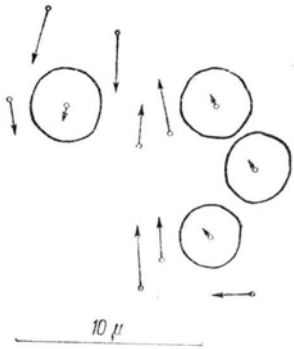

Fig. 14. *Elodea densa*. Movements of chloroplasts and of the cytoplasmic granulosities. Arrows mark the direction and the distance travelled in 1 second.

it is already apparent that three most remarquable facts have been revealed with the cinematographic technique:

a) The direction of chloroplast movements is usually concordant with the direction of the movements of the surrounding cytoplasm.
b) The chloroplast movements are slower — ofter much slower — than the cytoplasmic movements.
c) The highest velocities of chloroplasts at the temporary peaks agree with the mean velocity of the cytoplasmic movements.

3.6.4. *Agreement in the direction of the movements of particular chloroplast in the cells of Lemna trisulca*

During the epistrophe — parastrophe reaction the paths traced by chloroplasts are absolutely chaotic. However, when the vectors of the temporary velocitites are plotted it appears that they are so directed as if there were in the cell currents going in one, constantly changing di-

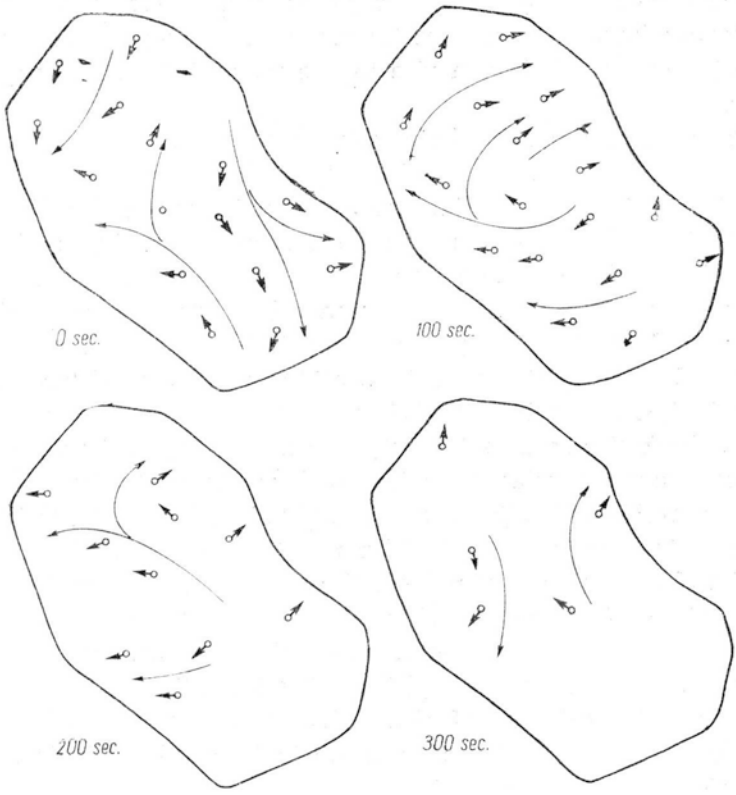

Fig. 15. *Lemna trisulca*. Temporary directions of chloroplast movements in the epistrophe-parastrophe reaction. ○→ marks the position of a chloroplast centre and the direction of its movement in the next 5-10 seconds. Continuous lines accentuate the common directions for various chloroplasts. The course of the reaction in this cell is shown in fig. 3.

rection. Sometimes the direction of these currents changes very decisively. Fig. 15 illustrates the directional currents in a cell of *Lemna trisulca* recorded at intervals of 5 or 10 minutes.

4. DISCUSSION

Analyses of phototactic chloroplast movements in *Arabis arenosa*, *Funaria hygrometrica*, *Lemna trisulca* and *Elodea densa* show that the differences in these movements can be classified into two groups: a) the different complexity of paths traced by chloroplasts in various species and b) the different velocities of chloroplast movements.

Usually the simpler paths are associated with the smaller or medium velocities of chloroplast movements. This effect is apparent also in the cells of one species. The parastrophe-epistrophe reaction in *Lemna tri-*

sulca is characterized by straighter paths and lower velocities of the chloroplasts, whereas the greater tortuousness of the paths in the opposite reaction is accompanied by a rise in the velocities of chloroplast movements.

In the case of the two phototactic reactions (epistrophe-parastrophe and parastrophe-epistrophe) in *Lemna trisulca*, which have been investigated in considerable details two reaction types may be distinguished on the basis of the evidence assembled from cinematographic records.

Type I is characteristic for the epistrophe-parastrophe reaction which begins with the flat arrangement of chloroplasts natural for dim light. Morphologically this type is characterized by the highly tortuous paths and the changeable velocities of the particular chloroplasts. The physiological characteristic of this reaction type is its dependence, in respect to both the rate of the reaction and the velocity of the chloroplasts, on numerous external factors such as the intensity of light, temperature, metal ions, histidine and the physiological state of the plants.

Type II is characteristic for the parastrophe-epistrophe reaction in which the chloroplasts return from the profile arrangement induced by strong light to a flat one. The characteristic features of this reaction are the gliding and slower movements of the chloroplasts, the more uniform velocity and the relatively straighter paths. Both the course of the whole reaction and the velocity of chloroplast movements are here greatly independent from the action of external factors and the influence of the physiological state of the plant.

Movements of type II sometimes occur in the epistrophe-parastrophe reaction under the influence of factors altering the physiological state of the cytoplasm or the rapidity of chloroplast movements (e. g. under the influence of calcium ions or not very strong light). On the other hand, reactions of type I occur sometimes, though less frequently, in the parastrophe-epistrophe reaction e. g. under the influence of potassium ions or histidine.

In view of this difference in the behaviour of chloroplasts in response to various external factors it seems probable that the mechanism of both phototactic types is different.

By comparing the results obtained for *Lemna trisulca* and *Elodea densa* it appears that the mechanism of the epistrophe-parastrophe reaction may be associated with the streaming of the cytoplasm. This explanation is supported by the following evidence.

a) It has been found by comparing directly the movements of the cytoplasm and chloroplasts in *Elodea densa* that the directions of chloroplast movements and of the cytoplasmic streaming are concordant at

a given time and part of the cell, but the chloroplasts move much more slowly. Although, the temporary peak velocities of chloroplasts may equal the mean velocity of the cytoplasmic movements, no instance has been recorded where the former was greater than the later.

b) In *Lemna trisulca* no direct correlation can be demonstrated between the chloroplast movements and cytoplasmic streaming as the cytoplasm in this plant is highly homogenous and consequently hardly visible. Evidence for the existence of plasmatic currents of a similar nature as the streaming of the cytoplasm in *Elodea* is provided by plotting the vectors of chloroplast movements at a given moment. From the vector it appears that in chloroplast movements there are short lasting „currents" of variable directions. Plasmatic currents in *Funaria hygrometrica* of the kind today defined as cytoplasmic streaming was reported already by Knoll (1908) and Boresch (1914). The former of these writers even stressed the possible connection of these currents with the phototactic movements in *Funaria.*

c) The increased velocity of chloroplasts under the influence of factors liquefying the cytoplasm indicates that chloroplast movements are facilitated by more liquid and less viscous medium.

d) The spinning of chloroplasts which is not necessarily associated with the change of direction also supports the hypothesis that the chloroplasts move with the cytoplasmic currents. On the other hand these observations contradict an earlier hypothesis on phototactic movements according to which the chloroplasts are passively pulled by cytoplasmic fibres.

The parastrophe-epistrophe reaction seems to be less related with the streaming of the cytoplasm but rather with relaxation of the stresses produced in the cytoplasm under the influence of strong light. This explanation is supported by the following evidence.

a) The velocity of the chloroplast movements when they return from the profile to the flat arrangement is exactly the same as their velocity when they return after centrifugation when the fibres of the cytoplasm stretched by the action of the centrifugal force contract.

b) The reaction is inhibited by factors liquefying excessively the cytoplasm and consequently disturbing its structure (hydroxylamine, phenylurethan).

c) The relatively straight paths of the chloroplasts during the reaction.

d) The independence of the velocity of chloroplasts in their return from external conditions.

The results obtained in the course of the present investigation throw some light on the mechanism of phototactic chloroplast movements.

Dynamic plasmatic structures such as fibres, meshworks etc. have been observed in the cells of many plants which have chloroplasts adapted to phototaxis (K n o l l 1908, B o r e s c h 1914). On the other hand, it has been found that in these plants strong light reduces the viscosity of the cytoplasm (V o e r k e l 1934 on *Funaria hygrometrica,* V i r g i n 1952 and 1954 on *Elodea densa*). Light strong enough to produce parastrophe causes immediately a drop in the viscosity of the cytoplasm (V i r g i n 1954) and consequently a relaxation of the plasmatic fibres. As a result photodinesis (S c h w e i c k e r d t 1928) begins or the cytoplasmic streaming is intensified. The chloroplasts are released from the fibres which held them in place and start moving chaotically together with the currents of cytoplasmic streaming prevailing at the moment. In the shaded portions of the cells on the side walls (S e n n 1909) the destruction of the cytoplasmic fibres is less extensive. When the chloroplasts in the course of their random movements finally reach these places they are arrested there. The final effect of this process is the complete displacement of chloroplasts to the side walls, i. e. parastrophe.

The drop in the viscosity of the cytoplasm causes too an ununiform distribution of the cytoplasm in the cell and consequently produces intracellular stresses similar to those caused by centrifugation. When the light intensity drops the stresses are equalized by the contraction of the stretched out plasmatic fibres. This contraction causes a passive movement of chloroplasts in the cell, i. e. in epistrophe.

This explanation has so far the nature of a work hypothesis only and it will be the aim of future research work to check its assumptions and if it proves correct to develop it further.

5. SUMMARY

1. Cinematographic techniques were used for studying phototactic chloroplast movements in several plant species, the changeability of these movements in *Lemna trisulca* and the effect of physico-chemical factors on the dynamics of these movements.

2. Various species displayed differences in the character of phototactic movements referring both to the complexity of the paths and the average velocities of chloroplasts. In connection with this trait the species can be arranged in a sequence according to the increasing complexity of the paths chloroplasts (*Arabis arenosa, Funaria hygrometrica, Lemna trisulca, Elodea densa*). On the whole the more tortuous paths are associated with greater velocity of chloroplast movements. The mean chloroplast velocities are as follows: in *Arabis arenosa* 0,417 μ/min, in *Funaria hygrometrica* 0,245 μ/min. in *Lemna trisulca* 5,41 μ/min., in *Elodea densa* 25,02 μ/min.

3. In *Lemna trisulca* two morphological types of phototactic reactions are observed: a) the type characteristic for the epistrophe-parastrophe reaction (tortuous paths, velocity greatly variable and affected

by external conditions and the physiological state of the plant ranging from 0,5 to 7,4 μ/min), and b) type characteristic for the parastrophe-epistrophe reaction (paths rather straight, velocity fairly constant ranging from 0,6 to 1,0 μ/min). Moreover, in the latter case the velocity is far less dependent on external factors and the physiological state of plants. The return of chloroplasts after centrifugation is analogous to the response of type II.

4. Several observations referring to the dynamics of chloroplast movements are reported in a) connection with the relation between the size of the chloroplasts and the velocity of their movements, b) the pivoting of chloroplasts round their axis when the direction of movement changed, c) the correlation between cytoplasmic streaming and chloroplast movements, and d) the periodic changes in the direction of chloroplast movements.

5. On the basis of the results a work hypothesis is attempted for explaining the mechanism of phototactic movements. According to this reactions of type I (epistrophe-parastrophe) are associated with the streaming of the cytoplasm, whereas those of type II (parastrophe — epistrophe) are associated with the equalizing of stresses arising in the cytoplasm under the influence of strong light and the subsequent contraction of the cytoplasmic fibres.

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STRESZCZENIE

Praca niniejsza wykonana w latach 1952—1955 miała na celu opracowanie przy pomocy metody kinematograficznej trzech problemów z dziedziny ruchów fototaktycznych chloroplastów, a mianowicie:

A. Rozszerzenie badań nad przebiegiem ruchów fototaktycznych chloroplastów na inne obiekty niż opisana poprzednio *Lemna trisulca.*

B. Zbadanie dwu zasadniczych reakcji fototaktycznych: epistrofia-parastrofia i parastrofia-epistrofia. Dotychczasowe badania kinematograficzne, wykonane przez autorów, dotyczyły wyłącznie pierwszej z tych reakcji.

C. Poznanie wpływu różnych czynników fizykochemicznych, które wywierają działanie na przebieg reakcji fototaktycznych (traktowanych statystycznie) na ruchy indywidualnych chloroplastów.

A. Przy pomocy metody kinematograficznej zbadano przebieg reakcji epistrofia-parastrofia u *Arabis arenosa, Funaria hygrometrica, Lemna trisulca* i *Elodea densa.* Obserwacje obrazów na ekranie oraz dokładna analiza dróg i szybkości poszczególnych obiektów pozwoliły na ustalenie średnich szybkości ruchów chloroplastów. Wynoszą one dla: *Arabis arenosa* 0,417 μ/min, *Funaria hygrometrica* 0,245 μ/min, *Lemna trisulca* 5,41 μ/min i *Elodea densa* 25,02 μ/min. Maksymalne szybkości chwilowe przekraczają szybkość średnią 3—5 x (*Arabis, Lemna, Funaria*) a nawet 6—8 x (*Elodea*). Drogi chloroplastów u *Arabis arenosa* są stosunkowo proste, zwykle lekko faliste, bez pętli, zwrotów i zmian kierunku. U *Funaria hygrometrica* analiza wykazuje charakter ruchów podobny jak u *Arabis arenosa,* ale drogi są bardziej powyginane, pętle dróg należą natomiast do rzadkości. Obserwuje się często okresy stabilizacji, a potem pokony-

wanie w krótkim czasie dużych odcinków drogi. U *Lemna trisulca* ruch chloroplastów jest bardziej zawiły i wygląda na ekranie jak bezładna i bezkierunkowa ucieczka, kończąca się ustaleniem chloroplastów na ścianach bocznych. Tylko niektóre chloroplasty zachowują kierunek ruchu ku najbliższej ścianie bocznej, inne poruszają się bezładnie, często zmieniając kierunek ruchu i opisując pętle. U *Elodea densa* chloroplasty wędrują po górnych ścianach komórek chaotycznie, z wybitnie zmienną szybkością, drogi ich ruchu są długie, często tworzą zawiłe pętle.

Zarówno szybkość jak i charakter dróg chloroplastów są więc w wysokim stopniu zależne od rodzaju badanego obiektu. Na ogół im mniejsza jest szybkość poruszania się chloroplastów, tym bardziej proste i regularne są ich drogi.

B. Badania nad przebiegiem reakcji epistrofia-parastrofia i parastrofia-epistrofia u *Lemna trisulca* pozwoliły na wyróżnienie dwu typów morfologicznych reakcji. Typ I (epistrofia-parastrofia) charakteryzują drogi zawikłane, zwykle z pętlami i częstymi zmianami kierunku i szybkości chloroplastów zmienne (0,48—7,4 μ/min.), z częstymi długimi okresami zastoju. Wpływ czynników zewnętrznych na ten typ ruchu jest bardzo wyraźny. Typ II (parastrofia-epistrofia) charakteryzują drogi znacznie prostsze, lekko faliste, bez zmian kierunku. Na ekranie ruch robi wrażenie równomiernego wpływania chloroplastów ze ścian bocznych na górną. Szybkości chloroplastów są bardziej stałe (wahania w zakresie 0,5 do 1,0 μ/min). Czynniki zewnętrzne wywierają na drugi typ ruchów wpływ znikomy.

Analiza zmienności ruchów typu I pozwoliła na ustalenie ważnego metodycznego faktu, mianowicie, że szybkość ruchów zależy także od stanu fizjologicznego rośliny. Szybkość ruchu chloroplastów jest największa w okresie wiosennym, a wartość jej zmniejsza się wyraźnie w okresie jesiennym i późno-jesiennym. Stąd wynika konieczność przeprowadzania serii doświadczeń (wraz z kontrolą) w danym okresie sezonu wegetacyjnego i na tym samym materiale. Ustalono bowiem, że w takim wypadku szybkości ruchów chloroplastów mają wartości bardzo stałe.

C. Zbadano przy pomocy metody statystycznej i kinematograficznej wpływ szeregu czynników fizykochemicznych na ruchy fototaktyczne chloroplastów.

Światło. Zakres badanych intensywności światła mieścił się w granicach 150—120000 luksów. Stwierdzono, że szybkość reakcji epistrofia-parastrofia obliczona metodą statystyczną wzrasta wraz z intensywnością światła. Średnie szybkości chloroplastów w zbadanych intensywnościach różnią się między sobą w sposób daleko wybitniejszy niż czasy reakcji. Drogi ruchów poszczególnych chloroplastów w zakresie 50000—120000 luksów są bardzo podobne. Tylko w stosunkowo słabym świetle (5000 luksów) następuje pewne uproszczenie dróg.

Temperatura. Wraz ze wzrostem temperatury (badania przeprowadzano w 10°, 20° i 30°C) ulega skróceniu czas reakcji epistrofia-parastrofia, podobnie ze wzrostem temperatury wzrastają i średnie szybkości chloroplastów. Drogi ruchu nie różnią się między sobą.

Jony wapnia i potasu. Jony wapnia, zwiększające lepkość plazmy, obniżają znacznie szybkość reakcji epistrofia-parastrofia, jony potasu, działające upłynniająco na plazmę, przyspieszają tę reakcję. Podobne zjawisko obserwujemy i w odniesieniu do szybkości chloroplastów.

Drogi chloroplastów, w wypadku działania jonami wapnia, są bardziej wyprostowane i bez pętli, pod wpływem jonów potasu są bardziej skomplikowane.

Histydyna. Szybkość ruchu chloroplastów w reakcji epistrofia-parastrofia ulega zwiększeniu pod działaniem histydyny.

Hydroksylamina. W jednej z prac poprzednich stwierdzono, że hydroksylamina, będąca typowym inhibitorem fotosyntezy, nie wywiera wpływu na przebieg reakcji epistrofia-parastrofia. W niniejszych badaniach właściwość ta została potwierdzona — szybkość chloroplastów a także charakter ich dróg nie wykazują żadnych istotnych różnic w porównaniu z kontrolą.

Fenyluretan wyraźnie opóźnia przebieg reakcji epistrofia-parastrofia, co znajduje swój wyraz w znacznym obniżeniu szybkości ruchu chloroplastów.

W reakcji parastrofia-epistrofia, w jej przebiegu, szybkości chloroplastów i charakterze ich dróg nie obserwujemy żadnych zmian w odniesieniu do kontroli. Tylko pod wpływem histydyny występuje niewielki (o 20%) wzrost szybkości chloroplastów oraz skomplikowanie ich dróg.

Obserwacje nad dynamiką ruchu chloroplastów pozwoliły na powiązanie mechanizmu reakcji epistrofia-parastrofia z ruchem ślizgowym protoplazmy. Za taką koncepcją przemawiają fakty następujące:

a) Bezpośrednie porównanie ruchu protoplazmy i chloroplastów u *Elodea densa* wykazało, że kierunki ruchu chloroplastów są zgodne z kierunkami ruchu ślizgowego protoplazmy w danym momencie i w danej części komórki, przy czym chloroplasty poruszają się znacznie wolniej. Ich maksymalna szybkość chwilowa może dorównywać średniej szybkości ruchu protoplazmy, lecz nie obserwowano nigdy, aby ją przewyższała.

b) Na istnienie podobnych prądów protoplazmatycznych u *Lemna trisulca* wskazuje fakt, że wykreślając aktualne kierunki ruchu chloroplastów metodą wektorów, uwidaczniamy w komórkach *Lemna* krótkotrwałe, zmienne co do kierunku „prądy" w ruchu chloroplastów.

c) Zwiększenie szybkości chloroplastów pod wpływem czynników upłynniających protoplazmę wskazuje na łatwiejsze poruszanie się chloroplastów w mniej lepkim ośrodku.

d) Stwierdzenie faktu, że obrót chloroplastów nie zawsze jest skorelowany ze zmianą kierunku ruchu, przemawia również za hipotezą poruszania się chloroplastów z prądem plazmy.

Reakcja parastrofia-epistrofia wydaje się być związana nie tyle z ruchem ślizgowym plazmy, ile ze zwolnieniem napięć wywołanych w protoplazmie przez działanie silnego światła, ponieważ:

a. Szybkość powrotu chloroplastów z pozycji profilowej do płaskiej jest identyczna jak szybkość obserwowana przy powrocie odwirowanych chloroplastów (średnia szybkość chloroplastów w reakcji epistrofia-parastrofia 0,760 μ/min, szybkość powrotu chloroplastów po odwirowaniu 0,799 μ/min).

b. Reakcja ta zostaje wstrzymana przez czynniki upłynniające w zbyt wysokim stopniu protoplazmę i zaburzające w ten sposób jej strukturę (hydroksylamina, fenyluretan).

c. Przy reakcji tej mamy stosunkowo proste drogi.

d. Szybkość ruchu chloroplastów w wysokim stopniu jest niezależna od czynników zewnętrznych.

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