ACTA SOCIETATIS
BOTANICORUM POLONIAE
Vol. XLII — nr 3
1973

The action spectrum in chloroplast translocation in multilayer leaf cells

ZBIGNIEW LECHOWSKI

Institute of Molecular Biology, Jagiellonian University, Kraków

(Received: March 5, 1973)

Abstract

By measurement of light transmittance through a leaf as criterion of chloroplast translocation, the action spectrum of *Ajuga reptans* was established. In the spectrum obtained, a correction was introduced for leaf autoabsorption calculated on the basis of the Beer-Lambert law. The action spectrum has two maxima: at $\lambda = 375$ nm and $\lambda = 481$ nm. The range above 502 nm has no significant effect on chloroplast translocation. Comparison with other objects examined demonstrated that in multilayer leaf cells riboflavin seems also to be a photoreceptor active in this process.

INTRODUCTION

One of the main problems requiring elucidation as regards the influence of light on chloroplast translocation is the mechanism of this process. The outset point in this problem is the nature of the active photoreceptor and its localization in the cell. It is possible to identify the active photoreceptor by establishing the action spectrum. The distribution of the action maxima allow in some extent to conclude as to the light-absorbing pigments. Investigations on numerous objects lead to conclusions regarding the chemical nature of the photoreceptor. In reference to the character of the photoreceptors controlling the movements of chloroplasts two groups of plants have been distinguished:

a) algae: *Mougeotia* and *Mesotaenium,*

b) all other objects examined.

The movements of chromatophores in *Mougeotia* and *Mesotaenium* are exceptional both from the anatomical and physiological aspect. In the remaining objects it has been demonstrated that only the shortwave range below 530 nm is active in the translocation caused both by weak and strong light (Haupt and Schönfeld, 1962; Fischer-Arnold 1963; Zurzycki 1962, 1967a; Mayer 1964; Seitz 1967). Some discrepancies in the obtained action spectra have been noted in red light.

All authors agree that, as regards movement induced by weak light, the above mentioned range is inactive (Faminizin, 1867; Senn 1908; Voerkel 1933; Zurzycka 1951; Zurzycki 1962, 1967a; Fischer-Arnold 1963; Mayer 1964).

The influence of red light of high intensity is controversial. On the one hand, Senn (1908), Babuskin (1955), Haupt and Schönfeld (1962) did not demonstrate the influence of this radiation range on chloroplast translocation, and the results of their experiments were the same as of experiments in darkness. Another group of authors (Böhm 1856; Frank 1871; Lindsbauer and Abramowicz 1909; Zurzycka 1951; Zurzycka and Zurzycki 1951; Zurzycki 1962; Mayer 1964; Seitz 1967) have demonstrated on the objects studied that the action of red light differs widely from that of darkness.

The investigations performed so far concerned mainly objects with a relatively simple anatomical structure of assimilative organs. Information on the active spectral range influencing translocation of chloroplasts in the cells of multilayered leaves of land plants is scarse. Senn (1908) and Seybold (1956) mention solely that the shortwave range is active. The only action spectrum obtained to date for a typical representative of this group of plants, *Nicotiana tabacum*, is reported by Babuskin (1955). It was established, however, by a simple method which arouses serious doubts, and the result is so much different that it cannot be compared with other investigated objects. It seemed, therefore, necessary to perform experiments in order to establish the action spectrum for a representative of this group of plants in order to fill the gap in the literature. As criterion of chloroplast translocation, light transmittance through the leaf was adopted.

MATERIAL AND METHODS

The experiments were performed on well developed leaves of *Ajuga reptans*. The material for the experiments was collected from a natural habitat exposed to moderate insolation. Before starting the experiments the leaves were adapted to weak white light (60—80 erg $cm^{-2}s^{-1}$) for a period of 18—24 h.

The leaves were irradiated with monochromatic light in a special apparatus. The apparatus has been described in an earlier paper (Lechowski 1970). As source of light served a 750 W 110 V projector lamp or a HBO-50 lamp. A liquid filter with a 5-cm distilled water layer and an appropriate interference filter were built into the optic system. IL Zeiss interference filters with the following transmission maxima were used: 350, 375, 400, 426, 436, 442, 452, 463, 475, 481, 493, 502, 530, 543, 560, 628, 650, 673 and 703 mm. Half-width transmission of the filters was 5—10 nm. The light intensity was regulated by changing the voltage supplying the lamp by means of an autotransformer. Radiation intensity was measured before and after irradiation of the leaf with a Zeiss VTh-8 thermoelement.

After 2 h of exposure to monochromatic light of a given wavelength and radiation intensity, transmittance of the leaves was measured for $\lambda = 436$ nm. The measurements were performed with an opal plate (Shibata 1958, 1959; Zurzycki 1962). Details of the measurement are described in an earlier paper (Lechowski 1970).

Each transmittance value given in this paper is a mean from 5 measurements. As basis for determining the activity of the particular wavelengths, served the radiation intensity producing the same percentual increase in transmittance, always measured at wavelength 436 nm. As such a numerical criterion a radiation intensity which caused a transmittance increment equal to $\Delta = 3$ per cent was used. Within this range of radiation the curves plotted have a linear course. The maximal transmittance increase for the *Ajuga reptans* leaf is about 6 per cent (Lechowski 1970).

The corresponding radiation intensities were read from the diagrams at the intercept of the curve representing transmittance changes versus radiation intensity with the line plotted for changes of transmittance equal to $\Delta = 3$ per cent.

In the final calculation, the law of Einstein-Warburg was taken into account, according to which, radiation activity is proportional to the number of quanta absorbed by the system. Critical radiation intensities for the particular wavelengths are expressed in quanta $cm^{-2}s^{-1}$. The respective conversions were achieved by multiplying the critical radiation value expressed in erg $cm^{-2}s^{-1}$ by the number of quanta per 1 erg.

The reciprocal of critical density of the quanta ($1/I_c$) was adopted as relative radiation activity of the particular wavelengths.

The leaves show a high radiation absorption, therefore, for the final calculation a correction for autoabsorption was introduced. This correction was calculated on the basis of Beer-Lambert's law with the assumption that the leaf is a homogenous medium. This is a considerable simplification but it was necessary in order to apply the Beer-Lambert law. Up till now no data are available in the literature concerning the course of the light absorption gradient in leaves, that is why, in the calculations, the thickness of the absorption layer was assumed as equal to 1/5, 1/3 and 1/2 of leaf thikcness. The following formula served for calculation:

$$I = I_O \cdot e^{-kcl} \tag{1}$$

where

I — radiation intensity transmitted through system,
I_O — intensity of incident radiation,
e — base of natural logarithms,

k — absorption coefficient (its value depends on the wavelength of the light used)
c — concentration of light-absorbing substance,
l — thickness of absorption layer.

When the definition of transmittance is introduced according to which $T = \frac{I}{I_0}$, results from (1) that

$$T = e^{-kcl} \tag{2}$$

If we assume the absorption layer thickness of the leaf $l = 1$, the foregoing formula may be written as

$$T = e^{-kc} \tag{3}$$

For transmittance calculation for various thicknesses of the leaf absorption layer (l') the same formula may be written as

$$T_{l'} = e^{-kcl'} \tag{4}$$

Changing to logarithms both sides of eq. (3) we get

$$\log T = -kc \log e, \tag{5}$$

This equation may be expressed in the form

$$\log 1/T = kc \log e \tag{6}$$

It results analogically from (4) that

$$\log. 1/T_{l'} = kcl' \, 0.4343 \tag{7}$$

When (6) and (7) are compared we get

$$\log 1/T_{l'} = l' \log 1/T. \tag{8}$$

The values $1/T_{l'}$ and further $T_{l'}$ were found by means of logarithmic tables.

$T_{l'}$ may be interpreted as the part of incident radiation intensity which passed through leaf tissue equal in thickness to the absorption layer l'.

As basis for quantitative calculation, the transmittance value of leaves adapted to conditions of weak light intensity was taken. Transmittance measurements were performed for particular wavelengths.

In order to establish the light beam I' which produces in a leaf of l' thickness the pertinent reaction, the $T_{l'}$ values obtained were substituted into formula (1).

The activity of the particular wavelengths was expressed in the form of the $1/I_c$.

RESULTS

The family of curves obtained representing the dependence of the changes in transmittance of the leaf on radiation intensity of the particular wavelength is shown in Fig. 1. For wavelength 350 nm only two points were obtained on the curve, it was impossible to get any more because of technical difficulties in obtaining higher radiation intensities. The curve for this wavelength is prolonged by a dashed line in order to determine critical intensity by way of extrapolation.

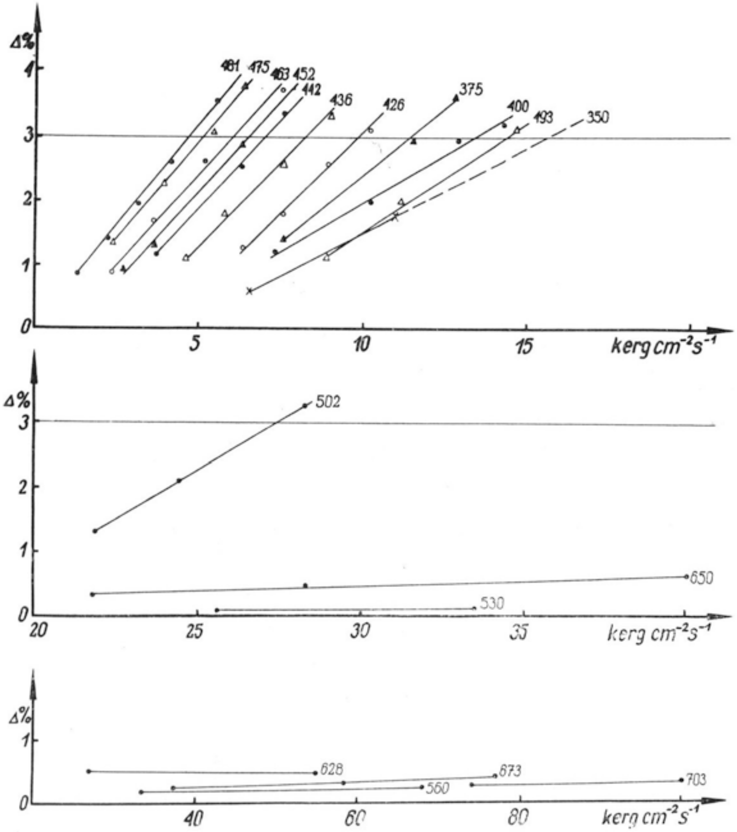

Fig. 1. Light transmittance increment in *Ajuga reptans* leaf versus radiation intensity for particular wavelengths. Figures along curves denote length of light wave

By the action of light of less efficient wavelengths such as 350, 400, 493 and 502 nm, curves with smaller slope were obtained. Light of wavelength above 502 nm has no significant effect on changes in transmittance, even when high radiation intensities are applied. The differences in transmittance values obtained for these wavelengths remain small in spite of application of increasing radiation intensities, they vary

for the range 530—560 nm from 0.04 to 0.08 per cent

for the range 628—703 nm from 0.4 to 0.61 per cent.

Table 1

Numerical values of action spectrum in the translocation of *Ajuga reptans* chloroplasts

λnm	I_c x 10^{15}	$1/I_c$ x 10^{-16}	T %	$1/I_c$ without the correction for leaf autoabsorption		
				1/5	1/3	1/2
				$^1/I'_c \cdot 10^{-17}$	$^1/I'_c \cdot 10^{-16}$	$^1/I'_c \cdot 10^{-16}$
1	2	3	4	5	6	7
350	2.7606	0.7244	0.52	1.0368	0.2090	0.5515
375	2.1640	0.9242	1.17	1.1248	0.2035	0.4273
400	2.7014	0.7402	1.48	0.8596	0.1507	0.3043
426	2.1143	0.9428	1.12	1.1602	0.2107	0.4456
436	1.8235	1.1966	1.07	1.3590	0.2488	0.5302
442	1.5811	1.2648	1.35	1.4958	0.2656	0.5443
452	1.5217	1.3142	1.41	1.5413	0.2720	0.5534
463	1.4231	1.4052	1.45	1.6380	0.2881	0.5837
475	1.2448	1.6066	1.74	1.8060	0.3099	0.6079
481	1.1635	1.7188	1.77	1.9264	0.3298	0.6464
493	3.6018	0.5552	2.35	0.5877	0.0969	0.1811
502	6.9448	0.2878	3.80	0.2769	0.0428	0.0738

The lack of quartz optics and difficulties in obtaining high radiation intensities made it impossible to extend the investigations to the entire UV range.

The results of transmittance measurement in leaves adapted to weak illumination for the particular wavelengths utilized for calculation of the correction for leaf autoabsorption are shown in table 1, col. 4.

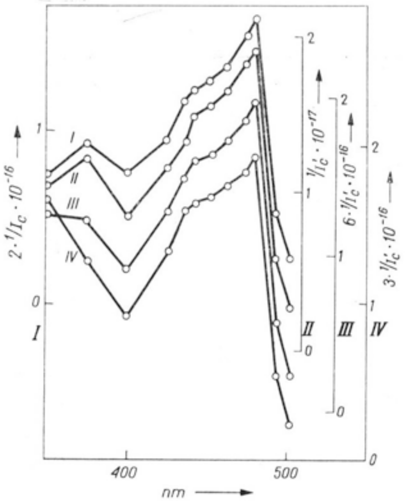

Fig. 2. Action spectrum in chloroplast translocation in *Ajuga reptans*. Curves: I — without correction for autoabsorption, II — with correction for autoabsorption calculated for 1/5 of leaf thickness, III — with correction for autoabsorption calculated for 1/3 of leaf thickness, IV — with correction for autoabsorption calculated for 1/2 of leaf thickness

The numerical values of the action spectrum without the correction for leaf autoabsorption are given in table 1 col. 3. Columns 5, 6 and 7 list the numerical data after introduction of the correction for autoabsorption for the layers 1/5, 1/3 and 1/2 of leaf thickness.

The action spectrum curve in the process of translocation of *Ajuga reptans* chloroplasts is shown in Fig. 2. This curve shows that shortwave radiation is active in regulation of chloroplast translocation, that is the UV and visible light range up to about 502 nm. Within this range two activity maxima may be seen: in the near UV at $\lambda = 375$ nm and in the visible range at $\lambda = 481$ nm.

Curves II, III and IV present the action spectrum after introduction of the correction for leaf autoabsorption. The shape of the curves is practically analogous with the exception of the UV range.

Since a leaf is a multilayer structure, it is hard to decide which of the versions calculated is the most correct. It is certainly not the curve without correction for autoabsorption, but it will neither be the curve accounting for the greatest thickness of the absorption layer. Analysis of the so far obtained action spectra for other objects seems to indicate that curve II may be considered as most representative.

DISCUSSION

The particular parts of the spectrum exert different influences on chloroplast translocation. Typical translocations to weak and strong light positions occur under the influence of the shortwave part of the spectrum (Zurzycki 1962, 1967a; Haupt and Schönfeld, 1962; Fischer-Arnold 1963; Mayer 1964; Seitz 1967). In Fig. 3 the action spectra obtained to date in chloroplast translocation are compared with the absorption curve of riboflavin. When the action spectrum for *Ajuga reptans* is compared with those obtained for other objects and the absorption of riboflavin, a far-reaching similarity is seen. The suggestion of Haupt and Schönfeld (1962) that riboflavin is a photoreceptor controlling chloroplast movements has been confirmed in numerous studies. The action spectrum for *Ajuga reptans* shows a certain deviation in the visible part of the spectrum in longwave range.

In a number of other action spectra also a certain discrepancy is observed between the absorption curve of riboflavin and the position of the particular action maxima within the visible range. For instance Mayer (1964) obtained for the land plant *Selaginella Martensii* by another method the main maximum within this range at $\lambda = 472$ nm. Similarly Schönbom (1963) obtained in the movements of the *Mougeotia* chromatophore induced by the action of strong light, a maximum at $\lambda = 470$ nm.

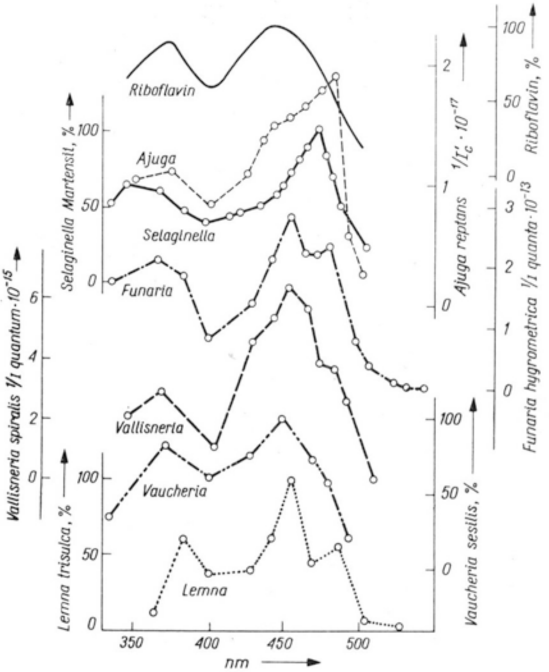

Fig. 3. Comparison of action spectra in chloroplast translocations, obtained for various objects and of riboflavin absorption curve with action spectrum obtained for *Ajuga reptans* (Haupt and Schönfeld, 1962; Fischer-Arnold, 1963; Zurzycki, 1962, 1967a; Mayer, 1964; Seitz 1967)

In the action spectrum curve of *Lemna trisulca, Funaria hygrometrica* (Zurzycki 1962, 1967a) and *Vallisneria spiralis* (Seitz 1967) additional maxima were found at about 485 nm. It is striking that the differences concern only the 450—490 nm range. The deviations in the action spectrum cannot be explained as the result of the dispersing effect of the cells.

Mayer (1964) interprets the shift of the main maximum as the result of light absorption by the flavo-protein complex, what would cause a shift of absorption towards longer waves. Explanation of the causes of the deviation observed for *Ajuga reptans* is difficult at the present state of investigations.

The action spectrum obtained by Babuskin (1955) for *Nicotiana tabacum* is in complete contradiction to our results. The cause of this should be sought in the method used by Babuskin, who adopted as criterion of chloroplast translocation the degree of blackening of the photographic plate after illumination of the leaf with various spectral ranges. The suppositions of this author that the system controlling the movements of chloroplasts consists in photosynthetic pigments, found no confirmation in the investigations of other authors whose results suggest the involvement of riboflavin as active photoreceptor. This is supported by:

a) the analogy between the action spectra and absorption curve of riboflavin, both in the visible and the far UV ranges (Zurzycki 1967a);

b) the agreement between the chloroplast reaction and the optical properties of flavin molecules (Mayer 1964; Zurzycki 1967a),

c) another argument is the fact that the extremally low radiation intensities are active in certain chloroplast arrangements, that is the effect of light is multiplied owing to enzymatic activity. Numerous enzymes are known to contain flavin, but none have been found including carotenoids (Zurzycki 1972).

Riboflavin is also an active photoreceptor in the process of light -induced change of viscosity of the cytoplasm (Virgin 1952, 1954; Seitz 1967) and of photodinesis (Botelier 1934; Seitz 1964, 1967).

It is possible that the primary processes causing changes in viscosity, photodinesis and chloroplast translocation are the same.

This seems to be confirmed by the agreement of the action spectra obtained on the same object and the equal quantum effect in the shortwave part of the spectrum (Seitz, 1967). On the other hand, the secondary processes causing movement of the chloroplasts would be different than in the case of photodinesis or viscosity change. This seems to find confirmation in the fact that prolongation of the illumination time exerts a stronger action than a corresponding increase of radiation intensity (Seitz, 1967).

The longwave range of the spectrum is not active in chloroplast translocation. Red light seems to be ineffective as far as the end effect of translocation is concerned (Zurzycki, 1962). The activity of this range is noticeable when the course of movements in time or the effect after a relatively short illumination with this light are taken into account and compared with the effect in darkness (Lindsbauer and Abramowicz 1909; Zurzycka 1951). This range does not exert a phototactic only a photokinetic effect, and its influence depends on the radiation intensity (Zurzycki 1962). In the present experiments the kinetics of action of red light was not investigated only changes in transmittance after setting in of equilibrium. It was established that the increase in transmittance is much higher as compared with that in the range of medium wavelengths and with that in darkness.

The data of Seitz (1967) for *Vallisneria spiralis* also show slight translocation of chloroplasts under the influence of this range. From the experiments of Zurzycki (1962) and Seitz (1967) it results that maximum photokinetic activity occurs at about 680 nm. Investigations on photokinesis of algae demonstrated that in some cases also the action maximum lies in the red part of the spectrum (Wolken and Skin 1958). Comparing the results of chloroplast photokinesis with those obtained for algae, Zurzycki (1962) advances the conclusion that in both cases photosynthetic pigments play a role via photophosphorylation. Light absorption by the chlorophyll system simultaneously exerts an influences within the shortwave range where cumulation of these two processes, phototaxis and photokinesis occurs (Zurzycki 1962; Seitz 1967).

It is claimed in the latest studies that, beside its kinetic action, red light causes conformational changes in the chloroplasts leading to their contraction (Heber 1969). The extent of these changes depends on the radiation intensity and on the presence or absence of electron receptors. The relation between electron transport and conformational changes has been demonstrated by Izawa and Good (1966a,b).

The results of Heber's experiments show that chloroplast contraction in N_2 occurs at low intensity of red light. Addition of oxygen inhibits this reaction which may be in some extent eliminated by application of higher intensity red light. The kinetics of the reaction determined by measurement of transmittance of the chloroplast suspension indicates that the maximal effect is reached in 40—60 sec.

It is believed that oxygen is the acceptor interrupting electron transport on the pathway between photosystem I and $NADP^+$. As result of oxygen reduction ATP is formed which is capable of penetrating from the chloroplasts to the cytoplasm (Santarius and Heber 1965) affecting the rate of chloroplast translocation.

The influence of this radiation via the photophosphorylation process is indicated by the action spectrum of longwave light (Zurzycki 1962, 1964) and the results of experiments with photophosphorylation inhibitors which abolish the accelerating action of red light (Zurzycki 1965).

The connection between photostructural reactions and photophosphorylation is based on the fact that similar changes as those occurring under the influence of light may be induced by the action of ATP (Itoh et al., 1963).

The author is deeply grateful to Professor Jan Zurzycki for his valuable advice and guidance in the course of this work.

REFERENCES

Babuskin L. N., 1955. Spektrofototaksisa chloroplastow, DAN SSSR, 103: 333—335.

Böhm J. A., 1856. Beiträge zur nächeren Kenntnis des Chlorophylls, Sitzgsber, Akad. Wiss. Wien, Math.-naturwiss. Kl. 22: 479—512.

Botelier H. P., 1934. Über den Einfluss äusserer Faktoren auf die Plasmaströmung in der *Avena* — Koleoptile, Rucueil trav. bot. neérl. 31 : 474 — 582.

Faminzin A., 1867. Die Wirkung des Lichtes und der Dunkelheit auf die Vertetilung der Chlorophyllkörner in der Blättern von *Mnium* sp., Ib. wiss. Bot. 6: 45 — 49.

Fischer-Arnold G., 1963. Untersuchungen über die Chloroplastenbewegung bei *Vaucheria sessilis,* Protoplasma 56: 495-520.

Frank B., 1871. Über lichtwärts sich bewegende Chlorophyllkörner, Bot. Ztg. 29: 209 — 225.

Haupt W., und Schönfeld I., 1962. Über das Wirkungsspektrum der „negativen Phototaxis" der *Vaucheria* — Chloroplasten, Ber. d. Deut. Bot. Ges. 75: 14—23.

Heber M., 1969. Conformational changes of chloroplasts by illumination of leaves in vivo, Bioch. Biophys. Acta 180: 302 — 319.

Itoh M., Izawa S., Shibata K., 1963. Shrinkage of whole chloroplasts upon illumination, Bioch. Biophys. Acta 66: 319—327.

Izawa S., Good N. E., 1966a. Effect of salts and elektron transport on the conformation of isolated chloroplasts. I. Light — Scatering and volume changes, Plant Physiol. 41: 533 — 543.

Izawa S., Good N. E., 1966b. Effect of salts and elektron transport on the conformation of isolated chloroplasts. II. Elektron mikroskopy, Plant Physiol. 41: 544 — 552.

Lechowski Z., 1970, Some aspects of chloroplast movement in leaves of terrestrial plants, Acta Soc. Bot. Pol. 39: 453 — 468.

Lindsbauer K., und Abramowicz E., 1909. Untersuchungen über die Chloroplastenbewegungen, s. — B. Acad. Wiss. Wien, Math. — naturwiss. Kl. 118: 137—182.

Mayer F., 1964. Lichtorientierte Chloroplasten-verlagerungen bei *Selaginella Martensii,* Z. f. Bot. 52: 346—381.

Santarius H. A., Heber M., 1965. Changes in the intracellular leavels of ATP, ADP, AMP and Pi and regulatory function of the adenylate system in the leav cells during photosynthesis, Bioch. Bioph. Acta 102: 30—54.

Schönbom E., 1963. Untersuchungen über die starklichtbewegung des *Mugeotia* — Chloroplasten, Z. f. Bot. 51: 233—276.

Shibata K., 1958. Spectrophotometry of intact biological materials, Jour. of Biochem. 45: 599—623.

Shibata K., 1959. Spectrophotometry of translucent biological materials — opal glass transmission method, in methods of biochemical analysis ed by D. Glick, 7: 77—109.

Seitz K., 1964. Das Wirkungsspektrum der Photodinase bei *Elodea canadensis,* Protopl. 58: 621—640.

Seitz K., 1967. Wirkungsspektrum für die Starklichtebewegung der Chloroplasten, die Photodinese und die lichtabhängige Viscositätsänderung bel *Vallisneria spiralis* ssp. *torta,* Z. f. Pflanz. 56: 246—261.

Senn G., 1908. Die Gestalts- und Lageveränderung der Pflanzen Chromatophoren, Leipzig.

Seybold A., 1956. Hat die Chloroplastenverlagerungen in Laubblättern eine Bedeutung? Naturwiss. 43: 90—91.

Virgin H. I., 1952. An action spectrum for the light induced changes in the viscosity of plant protoplasm, Physiol. Plant. 5: 575—582.

Virgin H. I., 1954. Further studies on the action spectrum for light induced changes in the protoplasmic viscosity of *Helodea densa,* Physiol. Plant. 7: 343—353.

Voerkel S. H., 1934. Untersuchungen über die Phototaxis der Chloroplasten, Planta 21: 156—205.

Wolken J. J., Skin E., 1958. Photomotion in *Euglena gracilis.* I. Photokinesis, II. Phototaxis., J. Protozool. 5: 39-46.

Zurzycka A., 1951. The influence of the wave lenght of light on the movements of chloroplasts in *Lemna trisulca* L., Acta Soc. Bot. Pol. 22: 17—37.

Zurzycka A., Zurzycki J., 1951. Investigation onto phototactic movements of chloroplasts in *Selaginella Martensii* Spring., Bull. Acad. Sc. Cracowie B. I: 235—251.

Zurzycki J., 1961. The influence of chloroplast displacements on the optical properties of leaves. Acta Soc. Bot. Pol. 30: 503 — 527.

Zurzycki J., 1962. An action spectrum for the light dependend movements of chloroplasts in *Lemna trisulca,* Acta Soc. Bot. Pol. 31: 489 — 538.

Zurzycki J., 1964. The affects of simultaneous action of the short and long wave parts of spectrum on the movements of chloroplasts, Acta Soc. Bot. Pol. 33: 133—139.

Zurzycki J., 1965. The energy of chloroplast movements in *Lemna trisulca* L., Acta Soc. Bot. Pol. 34: 637 — 666.

Zurzycki J., 1967a, Properties and localization of the photoreceptor active in displacements of chloroplasts in *Funaria hygrometrica.* I. Action spectrum, Acta Soc. Bot. Pol. 36: 133—142.

Zurzycki J., 1967b, Properties and lokalization of the photoreceptor active in displacements of chloroplasts in *Funaria hygrometrica.* II. Studies in polarized light, Acta Soc. Bot. Pol. 36: 143—152.

Zurzycki J., 1972, Primary reactions in the chloroplasts rearrangements, Acta Protozool. Vol. 11: 189—199.

Author's address:
Dr. Z. Lechowski
Institute of Molecular Biology,
Jagiellonian University, Cracow,
31-001 Kraków, Grodzka 53, Poland

Widmo działania w translokacjach chloroplastów w komórkach liścia wiolowarstwowego

Streszczenie

Stosując metodę pomiaru transmitowanego przez liść światła jako kryterium translokacji chloroplastów opracowano widmo działania dla *Ajuga reptans.* W uzyskanym widmie działania uwzględniono poprawkę na autoabsorpcję liścia, która wyliczona została z prawa Beera-Lamberta. Krzywa widma działania wykazuje dwa maksima: dla $\lambda = 375$ nm i $\lambda = 481$ nm. Zakres powyżej 502 nm nie wywiera istotnego wpływu na translokacje chloroplastów. Na podstawie porównań z innymi zbadanymi obiektami stwierdzono, że również w komórkach liścia wielowarstwowego ryboflawina jest fotoreceptorem czynnym w tym procesie.