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Action spectrum in sporulation of slime-mold *Physarum nudum* Macbr.

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Our knowledge concerning the action of light on the slime-molds is rather scanty. Not only the number of species studied under this aspect is limited but also the part played by radiation in the development of slime-molds and the mechanism of its action are imperfectly known. In previous studies carried out by the author on the slime-mold *Physarum nudum* the indispensibility of light in inducing sporulation has been demonstrated. The part played by white light and the dependence of the minimum light dosis on the age of the plasmodium and the effects of other factors influencing its development have been established. These researches are continued and the present paper summarises the results of a study which was undertaken with the aim 1) to obtain the action spectrum of sporulation, 2) to determine the photoreceptor system involved in this process.

Gray (1938, 1953) was the first botanist who carried out studies on sporulation of *P. polycephalum* plasmodia which were exposed to coloured light. He found that in the visible spectrum the activity is restricted to short wavelengths, in contrast to inactive red light. According to Straub (1954) and Lieth (1954, 1956) the radiations inducing the sporulation process in *Didymium nigripes* include: the near ultraviolet, the blue and the red radiations; deprived of activity are the green and infrared radiations. It follows from these results that the activity of the red light depends upon the species. It is active for *Didymium nigripes* and not active for *P. polycephalum*.

In view of these divergences it was considered necessary to make similar researches on other species. It must be also pointed out that so far no exact action spectrum of slime-molds sporulation is known. Consequently, a study was made with the aim to obtain the action spectrum in sporulation of the studied species.

MATERIAL AND METHOD

The plasmodia of the myxomycete *P. nudum* Macbr. provided the experimental material. The growth conditions of the laboratory cultures of this species were described in a previous paper (Rakoczy 1962). The method presented in the present paper was a slight modification of the procedure described in the paper 1962 and was based on the

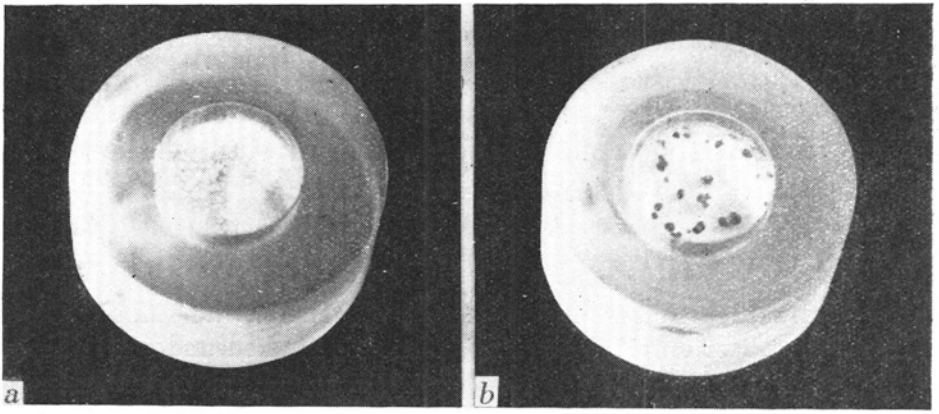

Fig. 1. Plexiglass vessels with a plasmodium on filter paper — *a*, with mature sporangia — *b*

fact that twelve-days old plasmodia are ready for the perception of the light stimulus inducing the sporulation process.

The areas of the plasmodium fragments exposed to light were small; this was a consequence resulting from the necessity of irradiating the plasmodia with monochromatic light of high intensity. Such light was obtained by using a system of lenses concentrating the light beam on a small area.

Twelve-days old plasmodia cultured in the dark were used for irradiation. These plasmodia were transferred by means of a metal spatule on to a piece of filter paper moistened with distilled water and subsequently placed in darkness.

Discs of twelve mm diameter were cut from the plasmodium as soon as it migrated on to the filter paper (usually after 3—5 hours). For irradiation, these discs were placed in special plexiglass vessels (Fig. 1)

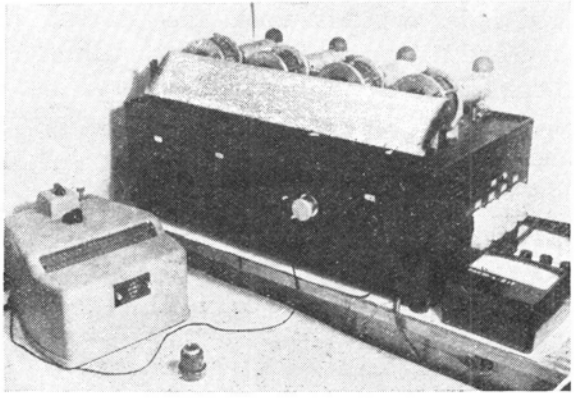

Fig. 2. Apparatus for irradiation with monochromatic light (cover taken off). In the third chamber photoelement connected with galvanometer. Next to the galvanometer thermopile

which in turn were put into Petri dishes with a small amount of water in order to assure a humid atmosphere.

The apparatus for irradiation (Fig. 2 and 3) consisted of four chambers. Each chamber was light proof and was equipped with an optical system which directed and concentrated the light emitted by a lamp. A heat and an interference filter were mounted in the optical system. Two kinds of lamps were used as light source: the "Osram" projector bulbs 150 W, 110 V (fed through a regulating transformer (for the wavelengths range 362—823 nm), and high pressure mercury lamps HQE — 40-RTT (Berlin) for the range 333—350 nm. Each optical system included a condensor lens (2 × 15 D), a liquid thermo-filter 5 cm thick, a miror which directed the light downwards to the chamber, an interference filter and a collector lens (+ 10 D) Fig. 2). The two last elements were mounted in the upper wall of the light proof chamber. $CuSO_4$ solutions in 2% H_2SO_4 (20 or 100 g per liter) or distilled water were used as thermofilters for the range 400—600 nm and 333—400 nm as well as for red light respectively. Zeiss (Jena) and Schott (Mainz) interference filters were used with the following transmission maxima at: 333, 350, 362, 382, 400, 417, 429, 442, 470, 484, 504, 520, 541, 560, 580, 602, 622, 632, 642, 656, 668, 682.5, 703, 713, 724, 747, 768, 823 nm wavelength. Their maximum transmission ranged from 25—35% and the half width transmission equaled 6.12 nm. In Fig. 4 transmission curves of these filters are presented. The optical system was arranged in such a way as to give a uniform illumination of an area about 14 mm diameter.

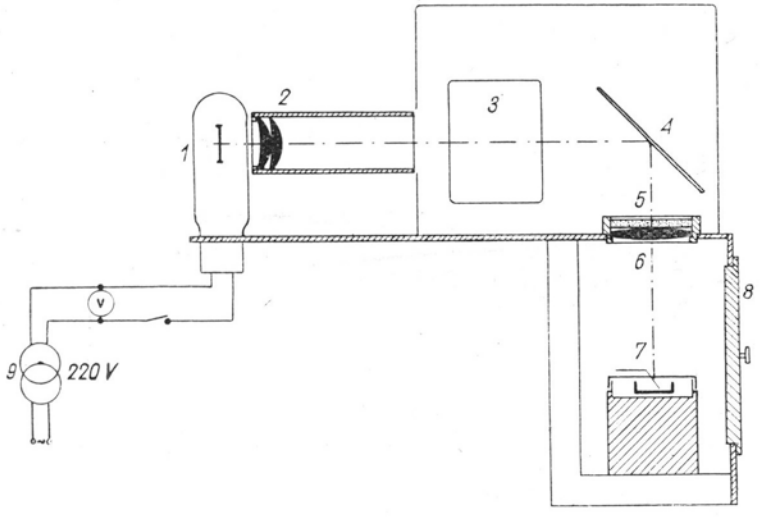

Fig. 3. Scheme of the apparatus used for irradiation with monochromatic light
1 — bulb; *2* — condensor lenses; *3* — liquid filter; *4* — mirror; *5* — interference filter; *6* — colector lens; *7* — plexiglass vessel with plasmodium; *8* — light proof chamber with water coat; *9* — regulating transformer

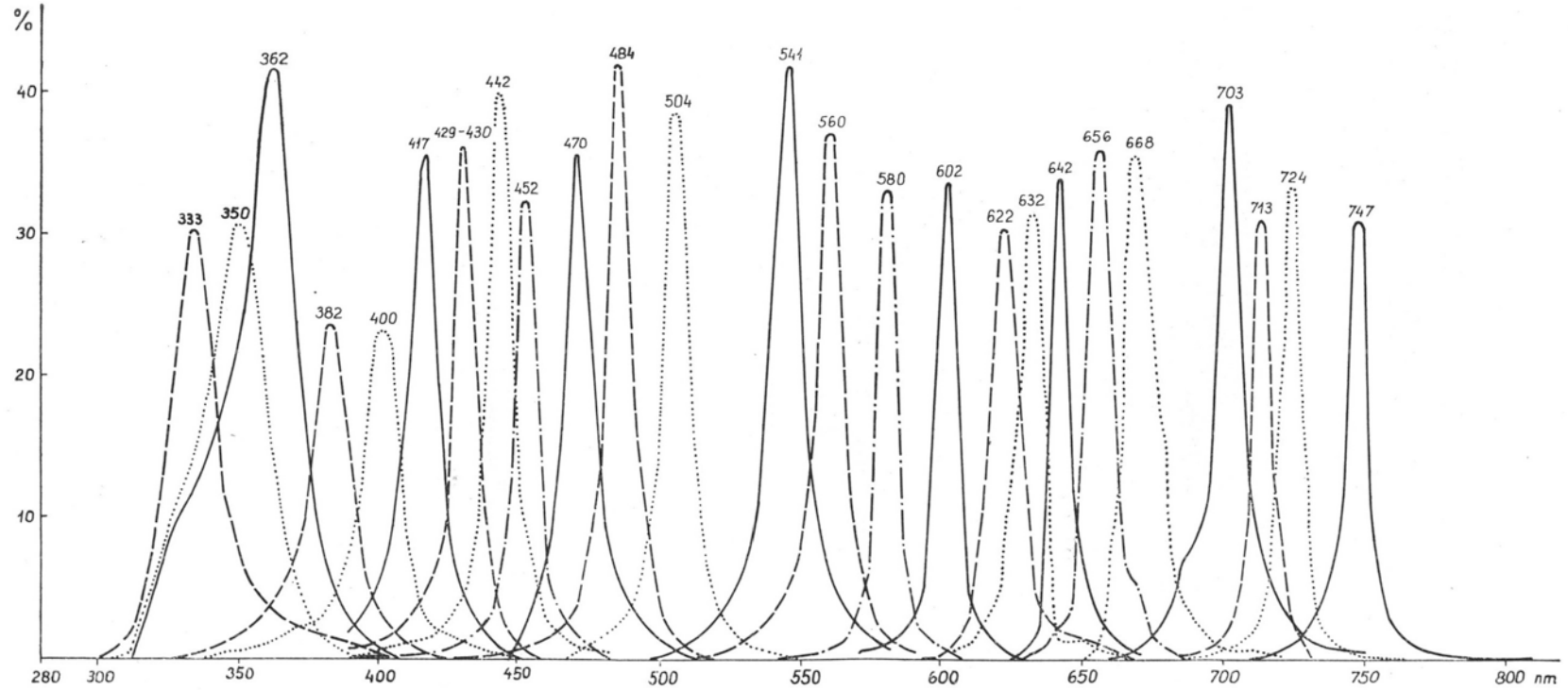

Fig. 4. Transmission of interference filter used for study

X axis wavelength in nm; *Y* axis transmission in %. Numbers denote individual wavelength in nm

The regulation of light intensity was perfomed by changing the voltage at the regulating transformer or, in case of the Hg-lamp, by means of NG and BG (Schott) filters. The walls of the chambers were surrounded with a water coat joined to a Hoepler thermostate, which maintained a constant temperature of 21°C during the exposure of the plasmodium.

The measurement of light intensity was carried out by means of a photocell (Lange) with a diaphragme 12 mm diameter. This photocell was calibrated in ergs/cm²sec for every wavelength by comparing its readings with the readings of a thermopile (Kipp and Zonnen) of known absolute sensitivity. In both cases a Kipp galvanometer (type A-70, Delft, Holand) of inner resistance 70 Ohms and sensitivity 6×10^{-9} A per scale mm was used.

Light intensity was measured twice: before and after irradiation. Differences between both these measurements were insignificant and negligible provided that the actual voltage of the lamps was considerably lower than the nominal one. In case of high load of the lamps these differences could attain 10 percent. In this case the average intensity was calculated and adopted in the experiments. The vessels with plasmodia were placed inside the chambers in the plane of irradiation (Fig. 2). Plasmodia were irradiated for 12 hours. After irradiation they were transferred to a dark thermostat at 21°C in which sporangia (if formed) appeared within 12—24 hours following irradiation. Sporangia were formed either on the filter paper placed on the bottom of the plexiglass vessels or on its wall (Fig. 1).

Results were recorded in terms of percentage of sporulation of the irradiated plasmodia for each wavelength and each light intensity. Exceptionally when the percentages of sporulation showed constant values (for instance 0 or 100%) the experiments were run in 6 replications, whereas in critical cases they were repeated 10—20 times (for ultraviolet and blue-green light). In experiments with red light the number of replications was always higher than 10.

All preparatory operations proceeding the experiments and the periodical control of the irradiated cultures were carried out rapidly in very weak day-light. The control experiments (in darkness) were made in the chambers in which the interference filter was replaced by special black screen whose size was identical with the size of the interference filter.

RESULTS

It was found that different spectral ranges showed distinct differences in their capacity of inducing the sporulation of the slime-mold *P. nudum*. Sporulation was induced by 12 hours irradiation with light of the following spectral ranges: 333—541, and 630—713 nm, whereas the

spectral ranges 541—620 and 724—823 nm were deprived of activity. In their physiological properties these active ranges show quantitative and qualitative differences. The curves in Fig. 5 are representative of the action exercised by three wave lengths belonging respectively to the three active ranges. For instance, for a radiation of 333 nm wavelength already an intensity of 40 ergs/cm²sec is sufficient for inducing a certain percent of sporulation. If this intensity is increased the percent of sporulation increases, attains maximum value and then falls rapidly to zero level if the radiation intensity is still increased. As a rule, however, the maximum is less than 100% and radiation intensities exceeding about 800 ergs/cm²sec do not induce sporulation in any case. This response of the plasmodia is typical of all radiations whose wavelengths are included in the range 333—400 nm.

Plasmodia irradiated with blue light (417 nm) for 12 hours sporulated only if the radiation intensity exceeded 2000 ergs/cm²sec. In the interval 2000—4000 ergs/cm²sec the effect of irradiation was dependent on its intensity, the percent of sporulation of the plasmodia increased concomitantly with the increase of light intensity. Light of 4000 ergs/cm²sec intensity induces 100% of sporulation in all irradiated cultures. A further increase of the radiation intensity to the highest available level did not change these results. Not only blue light but the whole range of short wavelengths radiations of the visible spectrum (417—541 nm) has a similar effect (Fig. 6).

Red light (668 nm) is without influence if its intensity is lower than about 2400 ergs/cm²sec (Fig. 5). Light intensities however exceeding this threshold value increase the percent of sporulation with the effect that a small peak is attained followed by a rapid fall of the sporulation percent for still higher light intensities. It must be also pointed out that for all red radiations (630—713 nm) a similar dependence of sporula-

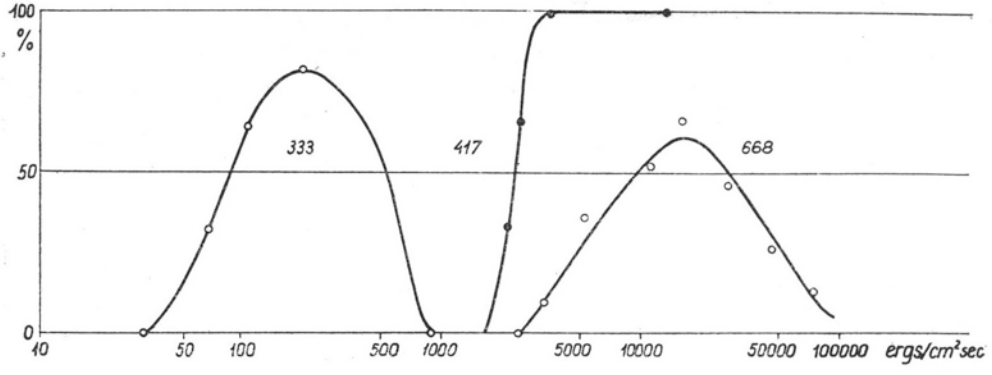

Fig. 5. Dependence of sporulation on the intensity of applied irradiation
X axis — intensity of light in ergs/cm²sec; *Y* axis — percent of sporulation. Numbers on the curves denoted wavelength of radiation in nm

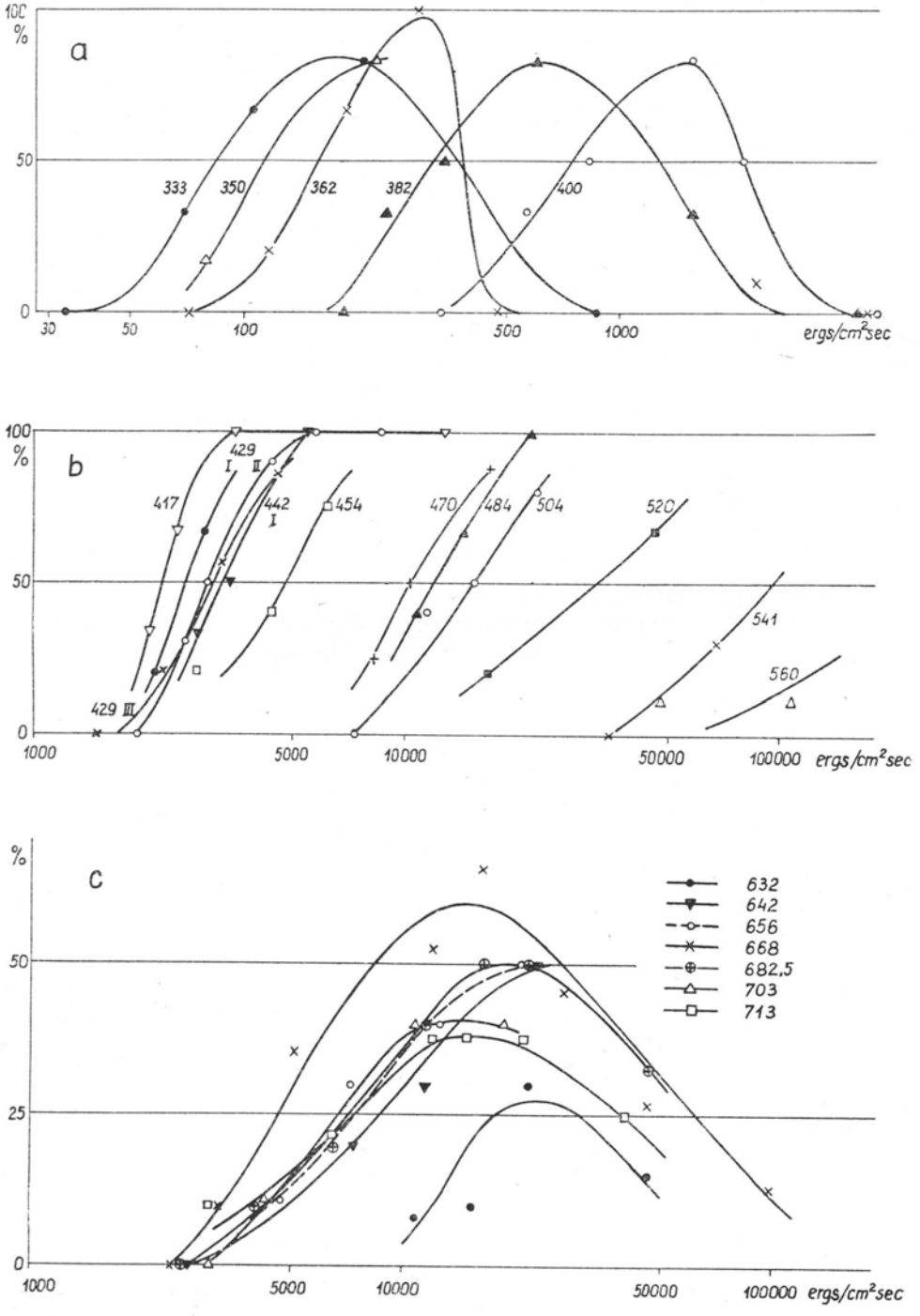

Fig. 6. Dependence of sporulation on the intensity of applied irradiation in 12 hrs dosis for different wavelength: a — UV; b — short wavelength range of visible light; c — red. Numbers on the curves denoted wavelength of radiation in nm

tion upon the light intensity is observed. Another particularity of this range of radiations is that the maximum percent of sporulation is low and rarely exceeds 50% (Fig. 6 c). Accordingly, the shapes of the sporulation percent curves for red radiations are similar to the shapes of the UV curves. The action of UV and red light is characterised by optimum activity curves. In both cases with increasing light intensity the percent of sporulation increases, attains a maximum value and than falls rapidly to zero level. In all cases the maximum value is less than 100%. The light intensities, however required to induce sporulation are rather comparable with the intensities of the blue-green part of the spectrum. The reaction of the plasmodia exposed to visible light is different and is represented on the graph by a maximum curve. The percent of sporulation increases also with increasing light intensity and attains 100% and this value is maintained even for still higher intensities.

In the course of this work it became necessary to find a criterion permitting to compare the action exercised on sporulation by the radiations of different wavelengths. The lowest light intensity of radiation inducing 25% of sporulation was adopted for this criterion. This intensity was found by graphical interpolation; on the graph with the curves representing the percent of sporulation in dependence on the intensity of radiation a straight line parallel to the light axis and corresponding

Table 1

Wave length in nm	Intensity of radiation inducing 25 % of sporulation				Relative activity
	in ergs/cm^{2}sec			in quants/cm^{2}sec $\times 10^{13}$	
	serie I	serie II	serie III		
333	64	-	-	1.07	44.4
350	88	-	-	1.57	30.3
362	130	-	-	2.37	20.06
382	240	-	-	4.63	10.3
400	550	-	-	11.11	4.29
417	-	1960	-	41.16	1.29
429	2200	2450	2350	I 47.74	1
				II 53.16	1
				III 50.9	1
442	2660	-	-	59.31	0.8
454	-	3600	-	82.44	0.64
470	-	8000	-	189.6	0.28
484	-	9300	-	226.9	0.23
504	-	11000	-	280.5	0.18
520	-	19000	-	499.7	0.106
541	-	61000	-	1665.3	0.031
630	-	-	19000	604.2	0.084
642	-	-	8300	268.9	0.189
656	-	-	7500	248.25	0.205
668	-	-	4600	155.02	0.328
682.5	-	-	7200	247.68	0.205
703	-	-	6900	244.95	0.208
713	-	-	7300	262.8	0.194

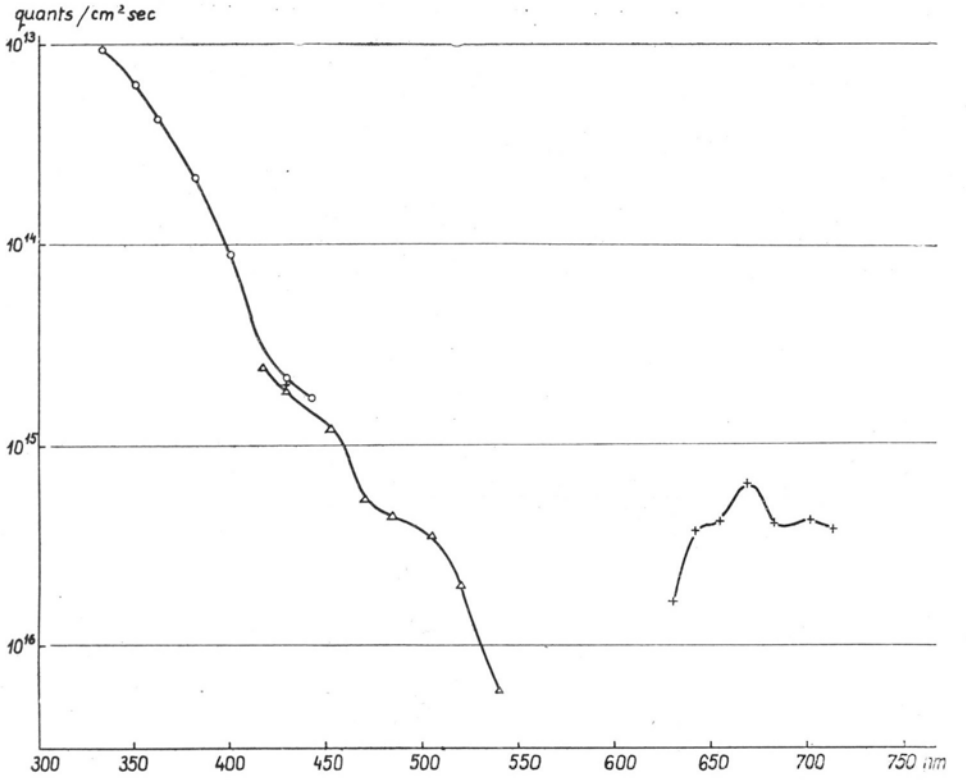

Fig. 7. Dependence of light intensity in quants/cm²sec inducing 25% of sporulation of irradiated cultures on the wavelength

to 25% sporulation was drawn. The intersection point of this parallel line with radiation intensity presents the values we are looking for. In this way the data of Table 1 were obtained.

It has been observed that the slime-mold *P. nudum* is able to reproduce vegetatively for about one year. During this time it shows good growth and manifests identical reactions to environmental factors. However, after longer periods of purely vegetative development the plasmodia grow weaker and become less resistent to infections; they even die, if the period of vegetative development is still prolonged. Therefore it became inavoidable to rejuvenate from time to time the cultures by allowing spores to germinate and to form a new plasmodia. In the course of this study three series of experiments were performed. The object of the series II was the action spectrum of visible short wavelengths light. Fresh material obtained from spores was used in series I in experiments on the action of UV. Experiments with red light form the series III. The sensibility of the plasmodia used in these investigations showed slight differences depending on the series (Fig. 7). In order

to obtain comparable results the sensibility to radiation of 429 nm wavelength was determined for each series and adopted as the basis of comparison. Taking into consideration the E i n s t e i n - W a r b u r g law active intensities of different radiations were expressed in quanta per cm^2 and second, and the radiation 429 nm was adopted as the point of reference. The last column in Table 1 presents the action spectrum which was calculated and shows the ratio of intensity of some wavelength expressed in quanta/cm^2sec to the intensity 429 nm (also in quanta/cm^2sec) provided the kinds of both these radiations induce the

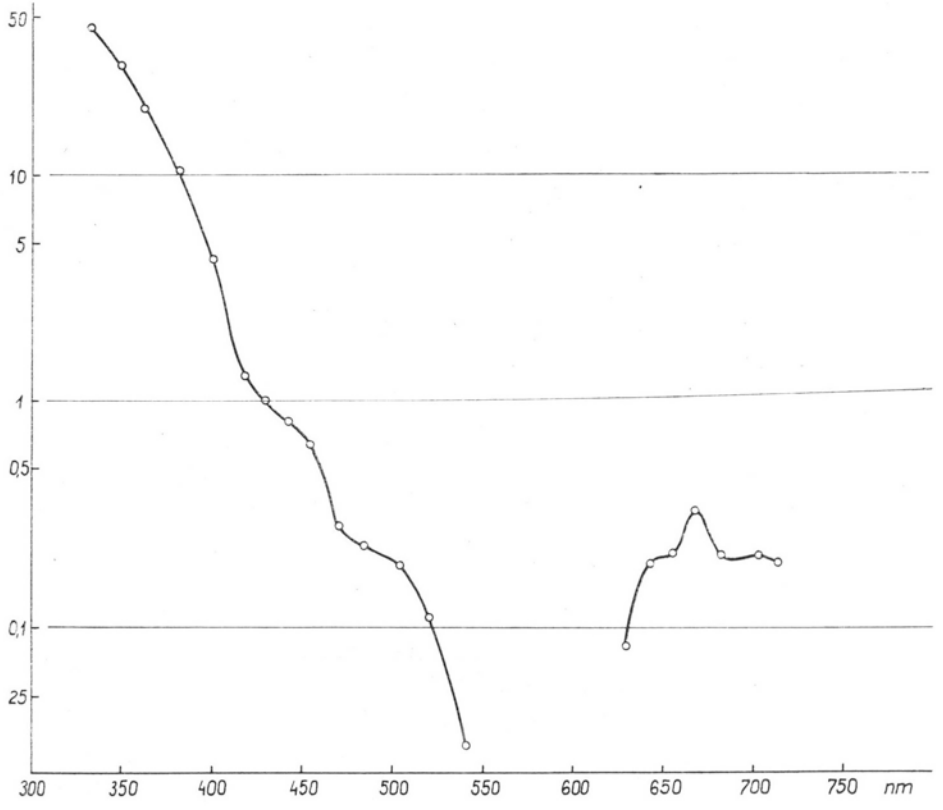

Fig. 8. Action spectrum in sporulation of the myxomycete *Physarum nudum*
X axis — wavelength in nm; Y axis relative activity of radiation. Radiation activity of 429 nm wavelength (= 1) was adopted as reference point, to west light intensity inducing 25% of sporulation was adopted criterion of the action of light

same effect (25% of sporulation). The action spectrum of sporulation of the myxomycete *P. nudum* is presented in Fig. 8. It results from the graph that in the range 333—540 nm biological activity of radiation decreases concomitantly with the increase of wavelength. UV shows maximum activity for the extreme value, viz. 333 nm. Unfortunately the lack of quarz optics made impossible further investigations on the action

of UV of shorter wavelengths. No distinct maxima of activity are visible in the action spectrum in the range 333—540 nm, but a slightly higher activity in the vicinity of 450 and 500 nm seems to be discernible.

Radiations of the long wavelength part of the visible spectrum are also able to induce sporulation of cultures, the maximum activity is obtained for 668 nm. At 622 and 724 nm only occasional sporulation was observed; it did not exceed 10% of irradiated cultures.

A change of colour occuring in irradiated plasmodia deserves special notice. Twelve days old plasmodia grown in darkness were characterised by yellow-orange colour. A change of colour was observed in plasmodia which were exposed to irradiation of some spectral ranges and of intensities inducing a high percent of sporulation. The colour changes

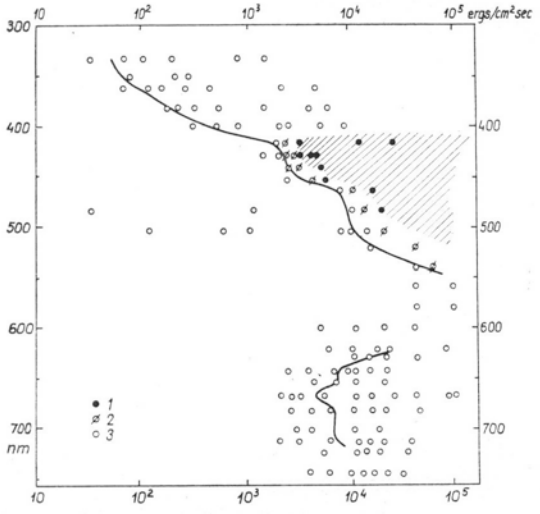

Fig. 9. Scheme presenting the degree of changes of colour of the plasmodium *Physarum nudum* in dependence on the intensity of applied irradiation
X axis light intensity in ergs/cm²sec; *Y* axis wavelength in nm. *1* — intensive change of colour from yellow-orange to olive brown; *2* — slight change of colour occuring in a part of plasmodia only; *3* — lack of change of colour

into bright or intensive olive-brown. It appears on Fig. 9, presenting the results of these observations, that without effect on the change of colour are the UV radiations in the range 333—400 nm and the red radiations.

Probably the above stated different character of dependence of the sporulation percent on the intensity of radiation of different wave lengths (417—540 nm and UV and red) is causatively connected with the ability of the plasmodium to change its pigments composition.

DISCUSSION

Only few investigations on spectral ranges active in the process of sporulation were carried out.

Gray (1938) was the first botanist, who initiated systematic research on the action of chromatic light on the sporulation of slime-mold *P. polycephalum*. The glass filters which he used, however, were of low selectivity and transmitted a high percent of light of different wavelengths. Later he made a study on the action of strictly monochromatic light on the sporulation of the same species but only three kinds of the radiations of the following wavelengths were investigated: 436, 546 and 577—579 nm. In the same paper the relations between the wavelength of light and the percent or the time of sporulation were established. The shorter the wavelength of the incident radiation the shorter the time elapsing between the moment of irradiation and the moment of sporulation and the higher the percent of sporulation. In 1941 Gray found also that a given dosis of non-monochromatic UV radiation retards the sporulation of the slime-molds which characterised by non-pigmented plasmodia and shortens the time of sporulation of those species which have yellow pigmented plasmodia.

Daniel and Rusch (1962) using differential filters confirmed the results of Gray that the spectral range 350—520 nm is capable of inducing sporulation in pure cultures of *P. polycephalum*.

An other species, *Didymium nigripes*, was studied by Straub (1954) who found that not only UV and blue, but also red radiations stimulate the sporulation.

Detailed studies on the same species were performed by Lieth (1954) who used glass filters, and showed that the sporulation was induced by near UV, blue and red radiations while green and infrared radiations were inactive. Moreover, the green light showed antagonistic action with respect to red light.

The relation between the percent of sporulation and the intensity of chromatic light was also investigated by Lieth, this relation being represented by a S- shaped curve. The results of our study agree with the results of Lieth only in the range of short wavelengths. In Lieth's experiments with red light transmitted by a RG 5 filter the percent of sporulation was proportional to the light intensity and attained 100. The results presented in this paper show an other type of relation.

It is obvious that the comparison of the activities of different monochromatic radiations requires the knowledge of their absolute intensities. This condition is fulfilled in Gray's experiments, which however were limited to three wavelengths. As a matter of fact the results of our study are in agreement with Gray's results in the range of radiations used by this worker. In Gray's experiments a low percentage of

sporulation was observed in the range 577—579, whereas in our research this range was deprived of activity. These slightly different responses are probably ascribable to differences in the sensibilities of the investigated species and to differences in the growth conditions.

The indispensibility of light for inducing sporulation is an indirect evidence of the presence in the plasmodia of a light absorbing system whose optical properties can be deduced to a certain extent from the action spectrum. These properties were determined by Gray (1953) and Wolf (1959) for *P. polycephalum* and by Lieth (1956) for *Didymium nigripes*, but only Wolf established a detailled absorption spectrum limited, however, to the UV and blue part of the spectrum. He was able to extract two components (I and II) from the plasmodia and basing on the results of Gray he came to the conclusion that the component I is responsible for sporulation. Assuming that the pigments systems in both species are identical, then it follows from this assumption that in *P. nudum* rather component II plays the role of the light absorbing system. This inference is based on the fact that for this species UV light is more active than blue or violet radiations.

Gray (1938) reported a discolouration of plasmodia exposed to direct sun light. After transferring however, the plasmodia to darkness the yellow colour returned. It is not possible to decide which factor — the light intensity, or the higher temperature (or both) is responsible for observed discolouration of plasmodia.

It has been found in an earlier work on the combined action of light and temperature that plasmodia of *P. nudum* transferred to 30°C were discoloured (lost their colour) and died within 6 hours of irradiation. In 26°C the plasmodia were not discoloured but were strongly injured (splitted veines, clumped). Irradiated for 6 hours, they survived the period of irradiation, but after transferring to darkness they were unable to sporulate in the normal time. Similar protoplasmic injuries and discolouration of the plasmodia were observed to occur in darkness under the influence of higher temperatures. It cannot be ruled out that the effects described by Gray (1938) were also caused by the direct action of sunlight.

Colour changes of the plasmodia of *Fuligo septica* were described by Baranetzki (1876) and Gray (1938) and were also observed in our laboratory in specimens maintained at the temperature 21°C. It is, however, not possible to draw definite conclusions from these observations.

A change of colour (from yellow into bright or deep olive-brown) was also observed to occur in plasmodia irradiated with white light (Rakoczy 1963). It was found that this change of colour was without influence on the subsequent sporulation or its absence. For instance cultures placed in light for 6 or 7 days (from the moment of reinoculation) showed

marked changes in their colour, but were not able to sporulate after being transferred to darkness.

On the contrary in 12 or 14 days old cultures their colour does not change after 12 hours of irradiation, and the plasmodia (after transferring into darkness) show 100 percent sporulation. An identic change of colour was observed to occur in plasmodia irradiated with visible monochromatic light provided that its wavelength is short and its intensity high and capable of inducing a high percent of sporulation. In these conditions, however, sporulation did not always occur in spite of a change of colour. Such a change was not observed in plasmodia exposed to UV or red light. It seems justified to connect this fact with the above discused difference in the action of UV and red light on sporulation on the one hand and visible light of short wavelengths on the other. A hypothesis may be forwarded that the photochemical system involved in sporulation process is easily injured by radiations of high intensity and the brown pigment plays the role of a protecting agent. This hypothesis explains the optimum character of the curves representing the percent of sporulation as a function of the light intensity (Fig 6 a and 6 c) of plasmodia exposed to UV or red radiations. If, however, the brown pigment protecting the photoreceptor system is formed then not only 100% sporulation is attained but this level is maintained even for very high light intensities.

It follows from above mentioned experiments with white, UV, and red light that the presence of this pigment is not indispensible for inducing sporulation.

Since in natural conditions light contains always a sufficient amount of short wavelengths radiations, the formation and the functioning of this protective system is assured.

I wish to express my most sincere thanks to Professor dr. F. Górski and Professor dr. J. Zurzycki for their valuable advices in the course of this work and Mrs. W. Maczek for technical assistance.

SUMMARY

Dependence of sporulation of the slime-mold *P. nudum* on wavelength and light intensity has been stated.

Interference filters were used to obtained monochromatic radiation. Lowest light intensity inducing 25% of sporulation was as adopted criterion of comparing the light activity in this process.

Radiation intensities inducing this effect are lowest for 333 nm (about 64 ergs/cm²/sec) they gradually increase concomitantly with a wavelength attaing highest value at 541 nm. In red light the maximum effect is attained at 668 nm and at this wavelength 25% of sporulation is attained at 4600 ergs/cm²/sec. The character of the action of UV and red light differs from that in the range of the short wavelength of visible part of spectrum. These differences consisted in a change of colour of the plasmodium under the influence of visible short wavelength part

of spectrum and no change under the influence of UV and red light. Moreover, inhibiting influence of UV and red in supraoptimal intensities has been established, whereas in the short wavelength range of the visible spectrum no inhibiting effect occured.

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Widmo czynne w procesie zarodnikowania śluzowca Physarum nudum

Streszczenie

Materiałem użytym do badań były plazmodia śluzowca *Physarum nudum* hodowane w ciemności. Stwierdzono, że światło jest konieczne dla wyzwolenia procesów zarodnikowania tego gatunku i kilkugodzinny impuls świetlny wystarcza dla wyzwolenia procesów sporulacji. Do badań nad widmem czynnym w pro-

cesie tworzenia zarodni użyto plazmodiów pochodzących z 12-dniowych kultur z ciemności. Plazmodia takie przenoszono na wilgotną bibułę filtracyjną i na tym podłożu poddawano naświetlaniu promieniowaniem monochromatycznym.

Naświetlanie przeprowadzano w komorach, do których skierowane było światło za pomocą odpowiedniego układu optycznego. Promieniowanie monochromatyczne izolowano za pomocą filtrów interferencyjnych. Źródło światła stanowiły lampy projekcyjne lub lampy rtęciowe. Pomiaru światła dokonywano za pomocą fotoelementu wycechowanego w ergach/cm²sek dla każdej długości fali przez porównanie z termostosem. Przebadano około 30 długości fali począwszy od 333—823 nm. Czas naświetlania wynosił 12 godzin, po czym plazmodia umieszczano ponownie w ciemności. Rejestracja doświadczeń polegała na obliczeniu procentu zarodnikowania naświetlanych kultur dla danej długości fali i intensywności światła.

Stwierdzono zależność zarodnikowania od długości fali i intensywności promieniowania. Zdolne do wyzwolenia zarodnikowania jest promieniowanie od 333—541 nm oraz od 630—713 nm, podczas gdy promieniowanie w zakresie od 541—620 i 724—823 nm jest pozbawione aktywności.

Dla porównania aktywności promieniowania w badanym procesie przyjęto tę najniższą intensywność promieniowania, która wywołuje zarodnikowanie 25% naświetlanych kultur. Intensywności te są najniższe dla 333 nm i stopniowo wzrastają osiągając najwyższe wartości dla promieniowania o długości fali 541 nm. W zakresie czerwieni maksimum zarodnikowania przypada na 668 nm.

Charakter działania poszczególnych zakresów spektralnych jest różny. Krzywe obrazujące zależność procentu zarodnikujących kultur od natężenia promieniowania UV i czerwieni wykazują maksima z reguły leżące poniżej 100% w przeciwieństwie do podobnej krzywej dla zakresu widzialnego krótkofalowego, która osiąga 100% i nie wykazuje spadku przy wyższych intensywnościach. Ponadto stwierdzono zmianę barwy plazmodium podczas naświetlania promieniowaniem z zakresu krótkofalowej widzialnej części widma, a brak takiej zmiany podczas naświetlania ultrafioletem i czerwienią.