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The effect of light on the fructification of the slime-mold *Physarum nudum* Macbride as influenced by the age of the culture

by

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INTRODUCTION

Since the techniques of culturing slime-molds became sufficiently standarized to allow their current use in the laboratory practice, many investigations were carried out on the influence of external conditions on the fructification process of the above organisms.

Usually only the two last stages in the developmental cycle of slime-molds are taken for the investigations eg. the plasmodium phase, and phase of formation of sporangia — as the effect of environmental conditions on various developmental stages — such as sprouting of spores, formation of swarmcells, myxamoebae, or plasmodia — might be quite different in each case. Such aproach is also dictated by some technical details of culturing slime-molds in the laboratory, as new cultures are usually obtained by means of reinoculation of a fragment of an old plasmodium onto fresh media. This results in a "rejuvenescence" of the plasmodium which henceforth starts a new cycle in its vegetative development.

In the present paper by the a g e o f t h e p l a s m o d i u m we understand the time which elapses from the moment of the reinoculation of the plasmodium onto fresh media, and by the t i m e o f f r u c t i f i c a t i o n — the period measured from the moment of reinoculation of the culture, to that moment when sporangia are black.

As it can be seen from the thus far collected evidence, many factors can influence the time of fructification. C a m p (1937) observed its considerable reduction in *Physarum polycephalum*, which was caused by the exhaustion of the media of nutritive compounds. The correlation between the pH of the substrate and temperature on one side, and the time of fructification on the other, was stated by G r a y (1939). More detailed investigations in this respect, were carried out by S e i-

friz and Russel (1936), who studied the effect of various factors on the culture media, pH of the substrate, temperature, gamma irradiation, and mechanical damage. They conclude that the slime-molds possess similarly to the majority of living organisms, an endogenous developmental cycle, and that all the mentioned above factors can only modify the time of fructification, causing its retardation or acceleration — provided they act within limits where the development is at all possible.

Among the various factors which influence the fruiting of slime-molds, light occupies a special position. Many investigators (Gray 1938, Sobels and Van der Brugge 1950, Lieth 1954) have found that slime-molds with white or colourless plasmodia can fructify both in light and in darkness, whereas the forms possessing coloured plasmodia do not fructify in the dark. The light represents therefore a factor qualitatively different from the others, because its lack not only modifies the time of fruiting but even renders impossible the fructification at all.

More detailed studies of the effect of light on the fructification, were carried out by Gray (1938, 1953) on *Physarum polycephalum*, by which Wolf (1961) detected a new type of pigment, and on *Didymium eunigripes* (Lieth 1954, 1956).

In the present work we used as the object of study the slime-mold *Physarum nudum* Macbride. It was chosen for experimentation as preliminary investigations revealed its slightly different reaction on light in comparison with species studied previously. It revealed also a certain regularity in development and fructification which secured a relatively accurate accomplishment of the experiments.

The aim of the present work was to study the effect of light on the process of fructification in relation with the age of the plasmodia.

MATERIAL AND METHOD

The myxomycete *Physarum nudum* was cultured in our laboratory since January 1961. It is characterised by yellow pigmented plasmodia and undergoes in the laboratory conditions a full developmental cycle. The stock cultures were grown in a thermostate in darkness, at 21°C. The cultures were kept in Petri dishes of a diameter 7.5 cm which contained 15 ccm of media each prepared out of commercial oats flakes. They were made according to Howard's (1931) without the addition of phosphate buffer. The plasmodia were reinoculated every 8 days onto fresh, sterilised media, by cutting out by means of a specially designed metal spatula, pieces of about 0.5 square cm. Both the sort of media

and the age of the parent plasmodium were choosen as optimal after preliminary experiments.

The proper experiments were carried out on the material obtained from the stock culture in the manner described above. The cultures were grown in a specially designed thermostat (fig. 1) divided horizontally into two compartments. The upper chamber *A* was illuminated by means of four 25 W fluorescent lamps, emitting white light. Its

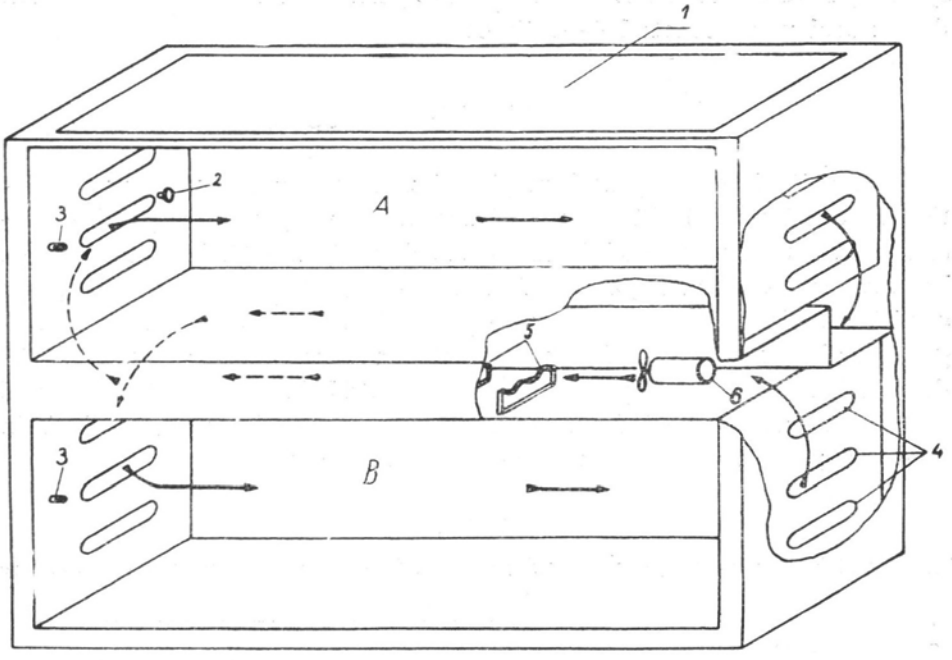

Fig. 1. Diagram of thermostat used for experiments. *A* — upper illuminated chamber; *B* — lower dark chamber. *1* — ground glass window; *2* — thermoregulator; *3* — thermometers; *4* — openings of air chanels; *5* — heaters; *6* — blowers. The arrows indicate the direction of air circulation

intensity measured at the level of the Petri dishes amounted to about 4510 ergs/cm^2/sec. The lower part *B* of the thermostat, was completely blacked out. A thermostat of such construction has this advantage that not only temperature but also other factors which are more difficult to control (eg. air humidity) are practically uniform all over the whole space. This was obtained by a continuous, air circulation between the two compartments. A complicated system of air channels, as well, as the covering of walls inside the box with a black, matt varnish, assured a complete darkness in the lower chamber in the thermostat.

The main series of the experiments consisted in growing plasmodia

in both chambers and transferring them at different age, as well as for different periods, from light into darkness, or in the reverse order. The results of these experiments were registered mainly by measuring the time of fruiting — that means the time counted from the moment of the reinoculation of the plasmodium, to the moment when black sporangia were formed. Besides that, the percentage of fruiting was estimated that means — the percentage of Petri dishes on which sporangia were formed. Each series of experiments consisted of 10 Petri dishes and was repeated 4—5 times.

RESULTS

Plasmodia *Physarum nudum* placed from the moment of reinoculation in continuous light developed sporangia very regularly. The time of fructification amounted to about 9,5 days (Table 1). In the darkness however sporangia were never formed in any of the cultures. In those conditions plasmodia also grew very regularly, showing a normal migration phenomenon on the surface of the substrate for about 10—12 days, after which the protoplasm aggregated into large clumps and the reticulum contracted. In consequence plasmodia usually died in 15—20 days, developing sclerotia only occasionally.

Table 1

The time of fruiting and the place of the formation of fruiting bodies in relation to the culture conditions

The period of culture in the dark (days)	The period between exposure to light and the formation of sporangia (hours)	Time of fruiting (hours)	Approximate number of sporangia and their localisation
0	224 ± 4.86	224	250—300 On glass
2	197 ± 12.28	245	,, ,, ,, ,,
4	157 ± 10.53	243	,, ,, ,, ,,
6	124 ± 13.11	268	,, ,, ,, ,,
8	52 ± 17.87	244	,, ,, ,, ,,
10	31 ± 6.26	271	,, ,, ,, ,,
12	28 ± 3.67	329	,, ,, The majority on the agar.
14	30 ± 4.23	366	100—200 On the agar

The above observations point out on the light being an indispensable factor for the process of sporulation of the slime mold *Physarum nudum* and of the other yellow pigmented species. In order to examine whether the influence of this factor is indispensable during the whole

vegetative period or only during a certain restricted phase of it, experiments were carried out by culturing the plasmodia in the dark for 2, 4, 6, 8, 10, 12, and 14 days, followed by subsequent exposition onto light. Results of these experiments are presented in the Table 1 and Fig. 2. The formation of fruiting bodies was observed in all cultures in spite of their remaining for 2—14 days in complete darkness. Only in the case of the 14 days culture, a certain percent (0—30%) of the plasmodia usually died even after exposure to light, or at least a part of the protoplasma collapsed, whereas the other part developed normal

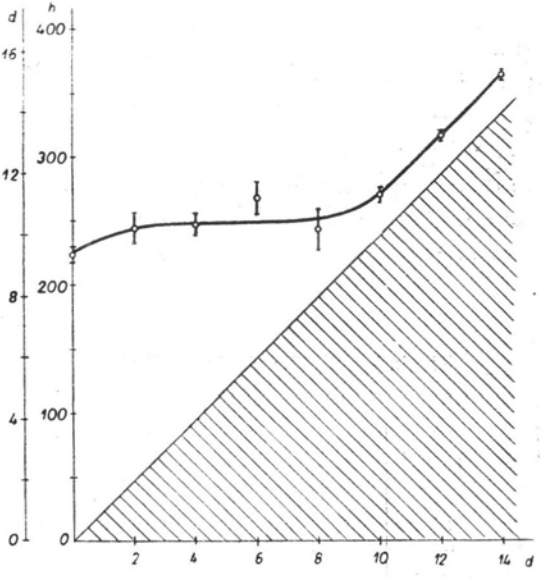

Fig. 2. Dependence of the time of fructification (y-axis — scales in hours and days) on the age of plasmodium (x-axis) at which the cultures were transferred to the light. The dashes mark the mean error

fruiting bodies. The above results clearly indicate that the light although indispensable for the fruiting process, need not be supplied during the whole culture period. For plasmodia which remain in the dark for 0—8 days long, being afterwards transferred under light — the time of fructification does not undergo any changes (Fig. 2). Nevertheless the remaining in the darkness for much longer periods extends the duration of the fruiting time proportionally to the duration of the time spent in darkness plus about 30 hours in light required to form the fruiting bodies. In this last case characteristic is also a much greater regularity in the time of fructification, which expresses itself in a larger standard error at the initial part of the curve (Fig. 2), followed by its considerable reduction in the second part.

The above described experiments authorise a supposition that light is apparently a superfluous factor in the first stage of the vegetative development of the plasmodium. It seems indispensable first after the

maturation of plasmodia, when they become ready for the induction of processes, which lead to the morphogenesis of sporangia. This period is attained with the investigated species, and at the conditions above described, in about 8 days. For separate plasmodia it may be somewhat shorter or more prolonged which depends on their individual variability. Just after reaching it they pass into an induction phase resulting in a sensibility to light. The time of fructification also shows a rather large scale of individual variations. Provided the dark period is longer than 8 days, all plasmodia become ready to pass into a generative phase of development. However as the induction of the fruiting process, and the morphogenesis of the fruiting bodies, require about 30 hours time — the time of fructification is prolonged when the plasmodia are kept in the dark for more than 8 days. A reduced dispersion of particular estimations points for the elimination of individual variations in the vegetative phase of growth. This may be explained on the basis of attaining by all the plasmodia a state of readiness for induction, at which exposing them to light initiates a new developmental phase, proceeding simultaneously in the majority of individuals in a series.

Table 2

The influence of periodic irradiation on the sporulation in relation to the age of the plasmodium

The period of culture in the dark (days)	Time of irradiation in hours: 3		4.5		6		12		24	
	Per cent of fruit.	Time of fruit.	Per cent of fruit.	Time of fruit.	Per cent of fruit.	Time of fruit.	Per cent of fruit.	Time of fruit.	Per cent of fruit.	Time of fruit.
8	No sporulation									
10	No sporulation								50	280
12	No sporulation				35	329	100	330	100	329
14	No sporulation		40	363	69	359	100	368	100	263

For testing whether light is really superfluous for the fructification of plasmodia in the earlier period of their development, before they are ready for induction — the cultures were grown for 7 days in light, being transferred afterwards to darkness. No fructification was observed in any case. Plasmodia died in 15—18 days, similarly to those kept for

the whole time in the dark. Also the results of the application of the 24 hour's time of irradiation on plasmodia of different age, supports the formulated before supposition. Applying continuous light conditions for 24 hours onto plasmodia at the age of: 2, 4, 6 and 8 days, followed by transferring them into darkness, was never effective in initiating sporulation. The 24 hours light period applied onto plasmodia, grown in the dark for 10 days, resulted in the sporulation of about 50 per cent of the cultures and 100 per cent of those kept previously in the dark for 12 and 14 days. In the described experiments sporangia were developed by old plasmodia after a definite period of exposure to light, but their formation and maturation took place already after transferring them into darkness. It might be therefore supposed that light is not

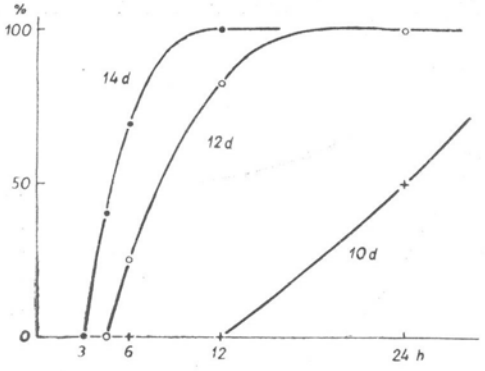

Fig. 3. Dependence of the percentage of fruiting (y-axis) on the duration of light period (x-axis) for dark cultivated plasmodia of 10, 12 and 14 days age

necessary during the whole period of the plasmodium phase for the formation of fruiting bodies, but that only a short light impulse (induction) is already sufficient to initiate the process of fructification. All the later stages of the developmental cycle could thus easily proceed in the dark. If that is true it is important to know how long must be the light impulse, and whether it depends on the age of the plasmodium. We tried to solve this problem by applying light impulses of 3, 4.5, 6, 12 and 24 hours onto plasmodia, grown in the dark for 10, 12 and 14 days.

In each case the percentage of cultures, bearing sporangia, as well as the time measured from the moment of the beginning of irradiation — to the moment when sporangia were black, were estimated. Results are presented on the Table 2 and Fig. 3. Data inserted in Fig. 3 clearly show a reciprocal relationship between the age of the plasmodium and the length of light period, necessary for the initiation of the fruiting process. The duration of the necessary light impulse diminishes with the proceeding age of the culture, whereas the period between the beginning of irradiation and the moment of formation of sporangia shows a much looser correlation with the age of plasmodia (Fig. 4). The

duration of the light impulse, which is sufficient for the induction of fructification in 50 per cent of cultures, can be estimated by interpolation on the curves presented in Fig. 3. It amounts to about 5 hours for plasmodia 14 days old, — 10 hours for 12 days old plasmodia, and less than 24 hours for the plasmodia of 10 days of age (Fig. 4). For testing whether the effect of light during the induction period, complies with the law of total energy = light intensity × time ($I \times t$), 12 days old plasmodia were exposed for 6 hours on the full light (100 per cent intensity) — for 12 hours, 22 min. onto light of 48.5 per cent of the initial intensity, and 25 hours onto light of only 24 per cent intensity of the initial value. Light intensity was reduced in all cases by means of covering the Petri dishes with the neutral filtres, prepared out of a blacked wire screen. The times of irradiation were adequately adapted to the transmission values of filtres, in order to

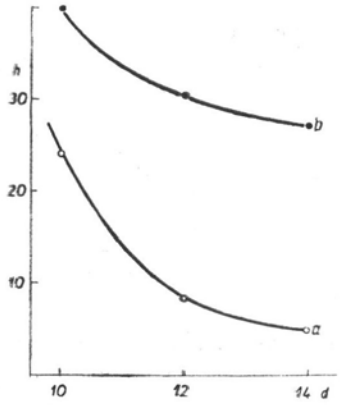

Fig. 4. Dependence of the length of light period necessary for inducing 50% of fruiting (curve ^{a} —○—), and the time necessary for the formation of mature sporangia (curve ^{b} —●—) on the age of culture (x-axis)

keep the product $I \times t$ constant in all cases. As can be seen on the table 3, the effect of short light periods applied at the time of the induction of fruiting, complies with the law in question whithin the investigated range of intensities. The per cent of fruiting remains constant provided the applied amount of light: $I \times t$ = constant.

In further experiments also the effect of different temperatures during the induction period was investigated. Plasmodia were cultured for 12 days in the dark at 21°C, and then exposed to the light for six hours at different temperatures: 11°C, 21°C, 26°C, and 31°C. — after which they were once more placed in the dark at 21°C. The results of this experiment are summarized in Table 4. The temperature of 31°C proved too high as the plasmodia irradiated for 6 hours at this temperature did not develop any sporangia. On the other hand the percentage of fruiting in all the remaining series of the experiment, was constant. The temperature coefficient: Q_{10} is equal to about unity.

Table 3

The law of the quantity of light at the induction of sporulation. The age of the plasmodium — 12 days. Full intensity of light = = 4510 erg/sq. cm × sec

Relative light intensity	Time of irradiation (hours)	Per cent of fruiting	Time of fruiting (hours)
100	6	36.2	314
48.55	12.36	35.4	315
24.1	24.9	35.4	314

Table 4

The influence of temperature on fructification at the induction period. The age of the plasmodium — 12 days. Time of irradiation at the induction stage — 6 hours

Temperature induction period	Per cent of fruiting	Temperature coefficient : Q_{10}
11°C	36	
21°C	40	1.11
26°C	36	0.81
31°C	—	—

Table 5

The time of fruiting in relation to the amount of media

Diameter of the Petri dish sq. cm.	Area of the Petri dish sq. cm.	Time of fruiting (hours)
5.5	21.4	160 ± 10.25
7.5	44.2	201 ± 11.7
9.5	71.0	222 ± 6.98
14.5	165.0	235 ± 6.0

In all the above experiments the culture conditions remained unchanged, as described in the methodical part of the paper. Results obtained by Camp (1937) who found a close correlation between the time of fruiting and the amount of nutrient media in *Physarum polycephalum*, inspired the author to investigate the same problem for the slime-mold *Physarum nudum*. The cultures were grown on standard media in continuous light, on Petri dishes of different diameter (5.5 — 14 cm). Hence their area differed 8 times. The appropriate amounts of nutritive media

differed within a similar range. As can be seen from the results presented in the Table 5, the time of fructification of the investigated plasmodium was shortest on the smallest dishes and most prolonged on the largest ones. The differences however are not very great. The 8 — fold difference in area (and the amount of media) is accompanied by only 25 per cent increase in the time of fruiting.

This means that contrary to *Physarum polycephalum*, at which the amount of media exerts a decisive effect on the time of fruiting, in the investigated species it plays only a secondary role.

DISCUSSION

Results of the present work confirm a general regularity in the developmental cycle of slime-molds, which is expressed in a requirement of light for the induction of sporulation processes in species with coloured plasmodia. Gray (1938) first showed that all the four tested species with yellow plasmodia (*Physarum polycephalum, Physarum tenerum, Fuligo septica, Leocarpus fragilis*) require light for the completion of their developmental cycle, whereas 10 species with colourless plasmodia can fructify also in the dark.

These findings were confirmed later by Sobels and van der Bruge (1950), who proved the indispensability of light for the fructification of *Physarum polycephalum* and *Badhamia utricularis*. The same was found by Lieth (1954, 1956) and Straub (1954) for *Didymium eunigripes*, as well as by Gray (1961) for *Physarum flavicomum*. Only Seifriz and Russel (1936) claimed *Physarum polycephalum* being able to fructify also in the dark. More recent investigations however, carried out by Gray (1938, 1953), Sobels and van der Brugge (1950) does not confirm that result *.

The observed fact that light is not necessary during the whole developmental period of slime-molds, for the induction of sporulation, comply with the data of Sobels and van der Brugge (1950, and Straub (1954). The data of Straub (1954), on the action of light impulses may be also valid for other species. Accordingly to him, *Didymium eunigripes*, kept for 10 days in the dark, and then exposed for 5 hours to light of 1000 Lux intensity, fructifies in 38.5 per cent, whereas the application of 10 hours light impulse results in 100 per cent fructification. The application of light after prolonged periods of culture in the darkness allows a more exact determination of light

* Recently Daniel and Rusch (1962) have found that in pure cultures of *Physarum polycephalum* a light period of 2 hours duration is necessary for inducing the subsequent fructification in darkness.

requirements. At the same time it reduces the dispersion of experimental data, contributing to the obtaining of much more precise results, than in the case of cultures grown in continuous light of different intensities or under periodical irradiation. Furthemore it also allows to correlate the light requirements with a definite developmental phase.

On the basis of above experimental data it may be possible to formulate a working hypothesis concerning the mechanism of the light action on the fruiting process. The period of the vegetative growth, which in the case of the plasmodium *Physarum nudum* lasts for about 8 days long, leads to the increase of its fresh weight. In this period the presence or absence of light does not affect the subsequent development of the plasmodium. After 8 days it attains a maximum and at the same time a most vigourous appearence. It is therefore not a matter of chance that this very moment was chosen for taking material for the experiments. Starting at this moment, the production of a hypothetic substance *A* beginns, which is continuously accumulating in the plasmodium. Maybe an excessive accumulation of this substance is one of the reasons of the often observed collapsing of the cultured plasmodia. For the development of the sporangia another substance *B* is necessary which is formed out of *A* under the influence of light:

Vegetative growth → substance *A*
↓ light
substance *B* → sporulation

The effect of light depends on the age of the plasmodium, as the production of the substance *B* is proportional to the initial concentration of the substance *A*, — in conformity with the general law of kinetics of the chemical reactions. This is schematically represented in Fig. 5. Thus the production of the same amount of the substance *B*, necessary for the whole cycle of formation of fruiting bodies, requires much more time in an 6 — 10 days old plasmodium than in an older one (12—14 days old). This is also in accord with the observed reduction in the length of the required light impulse parallely to the increasing age of the culture (Fig. 3). For the initiation of processes leading to the morphogenesis of sporangia, a certain amount of the substance *B* is required. Its production, accordingly with the above argumentation, require a longest time in the 8 days old plasmodia, and least time in those 14 days old. The period of morphogenesis is rather constant and amounts to about 25 hours (Fig. 5 — marked with brackets). Hence the time measured from the moment of the exposure to light, depends in a much greater extent on the age of the plasmo-

dium, and the curve illustrating this relationship approaches asymptotically the value of about 25 hours. A slow production of the substance *B* allows the migration of the plasmodia in search of the optimal sites for fructification (dry places on the glass — table 1), whereas its quick production results instantly in morphogenesis and the fruiting

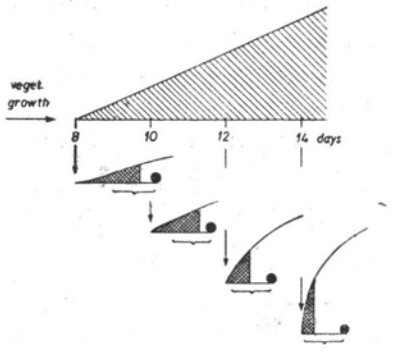

Fig. 5. Graphical description of processes taking place in the fructification of plasmodia. Shaded area — the amout of substance *A* in the dark cultivated plasmodium. The arrows indicate the transferring of the culture at different age to light. Dark shaded area — the amount of substance *B* necessary for fructification. The brackets indicate the ± constant time of sporangia morphogenesis

bodies develop at the same places occupied previously by the plasmodia. The above argumentation has a character of a hypothesis, representing only an attempt for the explanation of the quantitative results. We do not know the nature of both hypothetical substances *A* and *B*, nor the pigments which absorb light in the photochemical reaction.

The experiments carried out by S t r a u b (1954) also indicate for the occurrence of a substance which might stimulate the process of fructification (on our scheme the substance *B*). The obtained results clearly indicate that the transformation of the substance *A* into the substance *B* is limited at the applied conditions by the photochemical reaction. Both, the rather close correlation with the law of the quantity of light (Table 3), and the constant temperature coefficient Q_{10}, equal to one (Table 4), support such intepretation.

In the light of the presented above hypothesis, the results of the experiments of G r a y (1933) upon the influence of light intensity on the time of fruiting by slime-molds, may be explained. The cultures of *Physarum polycephalum* grown in continuous light of various intensities, ranging from 760 to 3400 lm (a 4—5 — fold difference in intensity), revealed only a slight reduction in the time of fruiting (about 25 per cent) as the intensity of the light increased. Assuming that light is not active during the whole vegetative period of growth, the effect of its intensity influences only the short interval of induction and this being rather short in comparision with the former, the reduction in the time of fruiting should not be too great. The same interpretation can be applied to the results obtained by G r a y (1933) with the effects of

interrupted light periods. Periodic irradiation of *Physarum polycephalum* per 8 hours a day increased only for about two days the time of fruiting, in comparision with the cultures kept constinuously under light, whereas "if a direct mathematical relationship existed, they would theoretically require thirty three days, since they were exposed to light only one third of the time".

It must be supposed that in case when the 8 hours light period is not sufficient for the production by the investigated slime-mold of a required amount of the substance *B* necessary for fruiting, it is produced in the light period which follows. We shall therefore expect only a slight prolongation of the time of fructification in the cultures irradiated periodically.

It seems that in the conditions of a normal day light rythmus, according to the data of Miller (1898), Jahn (1901), Howard (1931), Seifriz and Russel (1936), the sporulation occurs most often at night. These last two authors even claim that the observed fact of the migration of plasmodia onto the surface of the media before the fruiting phase, only represents an adaptation for spreading spores, and that rather darkness than light favourites fructification. In the light, however, of more recent data on the fructification cycle of slime-molds with coloured plasmodia, as well as of results of the present work, such view does not seem legitimate. The coloured plasmodia cannot fructify without light, and hence their positive phototaxis in the period which preceedes fructification. On the other hand, the often observed fact of fructification of plasmodia at night (which is not the rule) can be interpreted on the basis of a sufficiently large dosis of light, which they obtain during the day, and which is large enough not only for the initiation of sporulation but also for its completion afterwards in the dark.

SUMMARY

It has been established that light is necessary for fruiting of the yellow pigmented plasmodium of *Physarum nudum*.

Continuous light is not indispensible for the vegetative growth of the plasmodium; light is only necessary in the state of plasmodium maturity for the induction of morphogenetic processes. In the conditions maintained in our research this state was reached after about 8 days. Light is necessary to induce the formation of sporangia, but the further morphological stages may proceed in darkness. The time required for the formation of sporangia is constant and equals about 25 hours. The duration of the light impulse indispensible for the sporangia formation decreases with the age of the plasmodium.

In low light intensities during the period of induction the percentage of fruiting plasmodia is determined by the product $I \times t$, where "I" is the light intensity and "t" is the time of illumination.

Exposition to light of 12 days old plasmodia in different temperatures indicates that the van t'Hoff's coefficient Q_{10} is aproximativelly constant and equals 1.

A working hypothesis referring to the mechanism of light action on the fruiting processes of Myxomycetes has been advanced.

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