

Influence of the light factor on the course of the cell cycle in the successive generations of the antheridial filaments of *Chara vulgaris* L.

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Abstract

The exposure to continuous light causes a rise of the mitotic index in the successive generations of the antheridial filaments of *Chara vulgaris*, whereas culture in darkness leads to a considerable depression of mitosis, and if prolonged, to its complete cessation.

Light reverses the effect of the depression of mitosis caused by darkness: in the 16-, and 32-cell generations mitotic activity reappears as early as after 3 h, but in the 2-, 4-, and 8-cell generations only after 18 h.

The size of the cells in the antheridial filaments of plants exposed to continuous illumination is larger as compared with the control material. After being kept in darkness the cells become smaller. The analysis of the size of the latter suggests the inhibition of growth in initial and final periods of interphase.

In all generations continuous light reduces the duration of the cell cycle while darkness protracts it. The duration of S phase is similar in all generations of antheridial filaments (ca. 16 h) and is not modified by the light conditions. Thus, the light factor seems to interfere mainly with G₂ phase, and its role in the regulation of the cell cycle is correlated with the duration of this phase.

The role of light in the kinetics of the cell cycle of the particular generations of antheridial filaments in *Chara* is discussed in the aspect of the nutritional requirements of cells, hormonal regulation and phytochrome.

INTRODUCTION

In investigations on the mechanisms regulating the kinetics of the cell cycle much attention has been devoted to the analysis of the influence of growth substances, inhibitors, nutritional conditions of the

culture, temperature and light. Physical factors play in these investigations a particular role; they can synchronize mitoses in nonhomogenous cell populations.

Among numerous papers devoted to the physiological role of light of various spectral composition, energy and photoperiod, the literature dealing with the cell cycle and division activity of plant cells constitutes only a marginal problem. Halaban (1972) analysed the mitotic index and the duration of the cell cycle under different photoperiods in *Lemna*. The considerable increase of the heterogeneity of the material after the prolonged period of illumination made it, however, impossible to compare the result with those obtained from the analysis of plants cultivated under short day conditions. The cell division rhythm in the onion root meristem controlled by the light factor was described by Bishop and Klein (1973). The role of the light factor as the modulator of proliferative activity has been described on numerous examples of animal tissues (cf. Scheving and Pauly, 1973).

The investigations on the role of light in the regulation of the cell cycle with the use of spontaneously synchronized cells of antheridial filaments of *Chara vulgaris* as a model, were suggested by the diurnal rhythmic changes in division activity correlated with the alternation of day and night (Godlewski and Maciejewska, 1972). This material dealt with in cytochemical investigations in our Laboratory was found to be exceptionally convenient for the analysis of phenomena accompanying the successive steps of the cell cycle (Olszewska, 1974a). Synthesis of nucleic acids and proteins was analysed by the autoradiographic method in the successive cell generations (Olszewska and Godlewski, 1972), genetic activity of the chromatin was studied (Olszewska, 1974b), and the duration of the cell cycle was established (Godlewski and Olszewska, 1973).

MATERIALS AND METHODS

Chara vulgaris L. was cultivated in an aquarium in water from the natural habitat. Control material in all experiments consisted of plants kept under light for 16 in 24 h (L:D=16:8) with FLORA fluorescent tubes between 6 a.m. and 10 p.m.

Mitotic activity in the antheridial filaments was determined on the basis of analysis of squashes made from antheridia fixed at 2-h intervals with a glacial acetic acid — abs. ethanol mixture (1:3) and stained with 2 per cent orcein solution and 0.1 per cent Fast Green FCF solution according to Zeiling. Plants kept for 4 days under continuous illumination (LL) and those kept in darkness (DD) for 24 h, beginning

with the end of the dark period (L : D : D = 16 : 8 : 24) were compared with the control material (LD).

Mitotic activity was abolished after 72 h of culture without light access. For ascertaining the time period necessary for eliciting resumption of mitosis, the plants were exposed to light and fixed at 3-h intervals. In evaluation of the mitotic index the antheridial filaments more advanced or retarded in development as compared with the dominating generation in the antheridium were not taken into account.

In the autoradiographic investigations on the duration of the cell cycle the control material (LD), and that subjected to continuous illumination (LL) and continuous darkness (DD) consisted of freely floating apical fragments of *Chara* thallus, about 2.5 cm long. After 40 h under experimental conditions the plants were incubated in the solution of ^3H -6-thymidine (^3H -TdR), the concentration of which after mixing with water from the natural habitat was 62 $\mu\text{Ci/ml}$ (5 Ci/mM). Depending on the material the incubation was performed under light or darkness. The material was then thoroughly washed and postincubated in batches in the appropriate light conditions for 15, 20, 25, 30, 35 and 40 h. During the experiment the plants of the combination kept in darkness were aerated. The material was fixed according to the method described above for 40 min. The squashes were covered with liquid photographic emulsion (Ilford K2) and exposed for 8 months. After development the autoradiograms were stained with Unna's mixture.

Cell length was estimated by means of an eyepiece micrometer with an accuracy up to 0.5 μm .

RESULTS

1. Mitotic activity

The character of the diurnal rhythm of the mitotic activity in the antheridial filaments of *Chara* in the control material is that of an extinction wave. Its maximum falls between 1 p.m. and 5 p.m. and there is a deep depression in the early morning hours (Fig. 1). Mean mitotic activity for all the generations expressed by mitotic index is 14.5 per cent (Table 1).

Material subjected to continuous illumination shows a considerable rise of mitotic activity, the mean mitotic index reaching after 96 h of culture a value of 40.3 per cent with simultaneous increase of the amplitude of the diurnal mitotic wave. The smallest number of mitoses, like in the control material, falls to the period corresponding to early morning hours (Fig. 1). Stimulation of the mitotic activity by continuous illumination is more or less pronounced in the particular generations of

the filaments and is relatively weakest in the 32-cell generation (Table 1).

The plants kept in darkness exhibit with time an increasing fall of cell divisions and almost complete extinction of the division wave amplitude (Fig. 1). After 24 h of exposure to darkness the mean mitotic

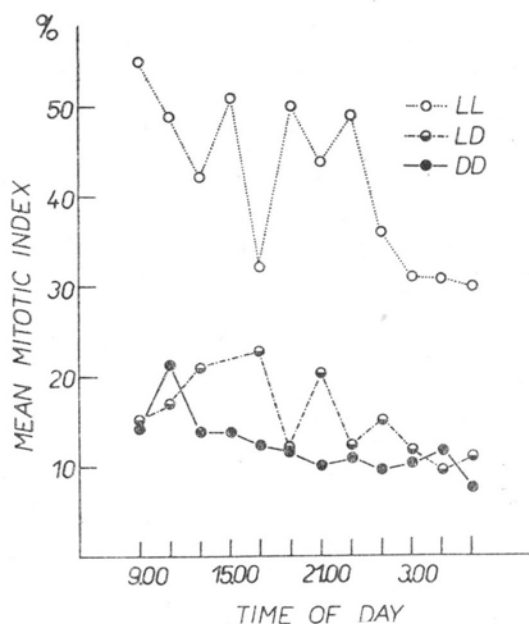


Fig. 1. Mean diurnal mitotic activity in the antheridial filaments of *Chara vulgaris* cultured: under continuous light for 4 days (LL); under alternating periods of light for 16 h, and darkness for 8 h (LD); in continuous darkness for 32 h (DD)

index is 10.3 per cent. The decrease in the number of divisions is particularly pronounced in the 2-cell generation, less so in the 4-, 8-, and 16-cell generations and minimal in the 32-cell generation (Table 1).

Culture in the prolonged period of darkness leads to a complete cessation of mitoses in all generations of the antheridial filaments of

Table 1

Mean diurnal mitotic index (%) in successive 2-, 4-, 8-, 16-, and 32-cell generations of antheridial filaments of *Chara vulgaris* under various light conditions

Generation	2	4	8	16	32	Average
LD	11.9	12.8	14.3	15.1	18.6	14.5
LL	28.3	38.3	48.5	47.1	39.2	40.3
DD	5.1	10.1	9.6	11.6	15.2	10.3

LD — material cultured under alternating periods of light for 16 h and darkness for 8 h.
 LL — material cultured for 4 days under continuous light.
 DD — material cultured for 32 h in continuous darkness.

Chara. After 72 h of culture without light the mitotic activity in the 2-, 4-, 8-, and 16-cell filaments falls to 0 per cent and remains at a 0.5 per cent level in the 32-cell generation. The transfer of plants to light evokes a wave of mitoses. After 3 h, the division is already resumed in 16-, and 32-cell filaments. Earlier stages of antheridial filaments, the 2-, 4-, and 8-cell generations remain in a state of mitotic

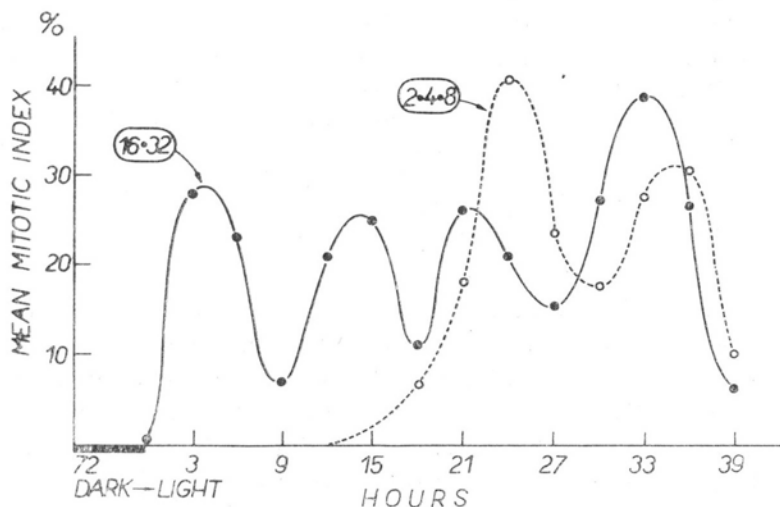


Fig. 2. Induction of mitotic activity abolished by 72-h culture in darkness in the 2-, 4-, and 8-cell generations and in the 16-, and 32-cell generations after exposure to light

depression for a much longer period. The effect of light, i.e. the first wave of new mitoses appears as late as after 18 h. The division activity elicited by light exhibits an undulating character with a concordant course for each of the two groups of the generations inhibited by darkness. The diagrams in fig. 2 show the mean values of the mitotic index for 2-, 4-, and 8-cell generations and 16-, and 32-cell generations.

2. Cell length

The influence of light on cell length in the antheridial filaments is shown in Table 2. The effect of the elongation of the post-telophase cells after 48 h of culture under light, and their shortening after 48 h in darkness is most marked in the early period of the development of the filaments and is relatively least pronounced in the 32-cell generation. The low level of the mitotic activity in the material grown in darkness made it impossible to analyse the cell length in the 2-, and 4-cell generations.

Table 2

Length (μm) of posttelophase cells in successive 2-, 4-, 8-, 16-, and 32-cell generations of antheridial filaments of *Chara vulgaris* under various light conditions

	Generation				
	2	4	8	16	32
	22.0 \pm 0.7 100%	18.0 \pm 0.5 100%	13.8 \pm 0.3 100%	9.8 \pm 0.3 100%	8.3 \pm 0.1 100%
LL	26.0 \pm 0.6 118%	21.1 \pm 0.7 117%	15.9 \pm 0.4 115%	11.0 \pm 0.5 112%	9.1 \pm 0.2 110%
DD	—	—	10.9 \pm 0.3 79%	9.7 \pm 0.3 99%	8.9 \pm 0.2 107%

LD — material cultured under alternating periods of light for 16 h and darkness for 8 h.

LL — material cultured for 42 h under continuous light.

DD — material cultured for 42 h in continuous darkness.

The long period of darkness causes the reduction of the mean length of the interphase cells and changes the distribution of their sizes in all generations of the filaments. This phenomenon manifested by a lowered peak of the middle cell fraction is illustrated for the 2-, and 32-cell generations by the diagrams in Fig. 3. The character of the curves plotted on the basis of histograms from the distribution of the interphase population after 72-h culture in darkness seems to suggest, as compared with the control material, the inhibition of growth of cells in those categories of length, which correspond to the initial and final stages of interphase.

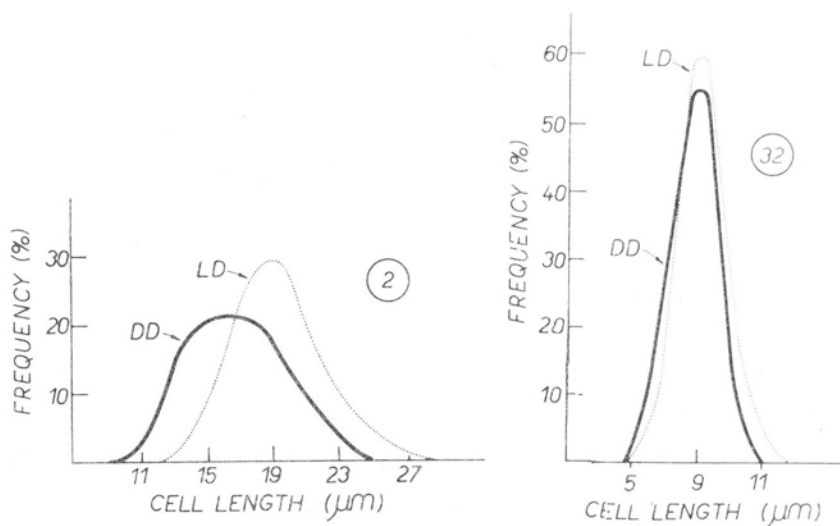


Fig. 3. Distribution of interphase cell sizes in the 2-, and 32-cell antheridial filaments after 72-h culture in darkness (DD) as compared with control material (LD).

The curves are plotted according to the histograms

3. Duration of cell cycle

In each generation of the antheridial filaments of *Chara vulgaris* the cell cycle starts with S phase, the beginning of which falls to the telophase of the preceding generation. Earlier investigations of Olszewska and Godlewski (1972) demonstrated the lack of G₁ phase in interphase. The establishment of the duration of the cell cycle consists in determination of the time period elapsing from incubation in ³H-TdR solution to the appearance of the peak of the new wave of highly radioactive telophases. The per cent of these strongly labeled mitotic figures calculated in the successive hours of postincubation for the particular generations of the antheridial filaments is shown in Fig. 4.

In the successive generations of the antheridial filaments in the control material the duration of the cell cycle is shorter and shorter (Table 3), in agreement with the results of Godlewski and Olszewska (1973). This regularity persists when the culture is exposed to continuous illumination which shortens the duration of the cell cycle in all generations, and most distinctly at the first stages of the development of the filament. The process of differentiation from the 2-cell to the 32-cell filament under continuous light lasts 17 h less than in the control material (Table 3).

Table 3

Duration of cell cycle (h) in successive 2-, 4-, 8-, 16-, and 32-cell generations of *Chara vulgaris* antheridial filaments under various light conditions

Generation	2	4	8	16	32	2—32-celled
LD	40.0 100%	35.5 100%	31.0 100%	28.5 100%	25.0 100%	160.0 100%
LL	36.0 90%	30.5 86%	27.5 89%	25.5 90%	23.5 94%	143.0 89%
DD	—	—	—	45.0 158%	37.0 148%	—

LD — cultured under alternating conditions: 16 h light and 8 h darkness in 24 h.

LL — cultured under continuous illumination.

DD — cultured in darkness.

On account of the extremely small number of mitoses in the 2-, 4-, and 8-cell generations in material grown in darkness, and because of the too short postincubation period for the 16-cell generation, it was only possible to follow the wave of radioactive telophases and to determine the duration of the cell cycle for the 32-cell generation. As results from fig. 4 darkness is a factor inhibiting the kinetics of the cell cycle and its depressive action differs in the successive generations of the

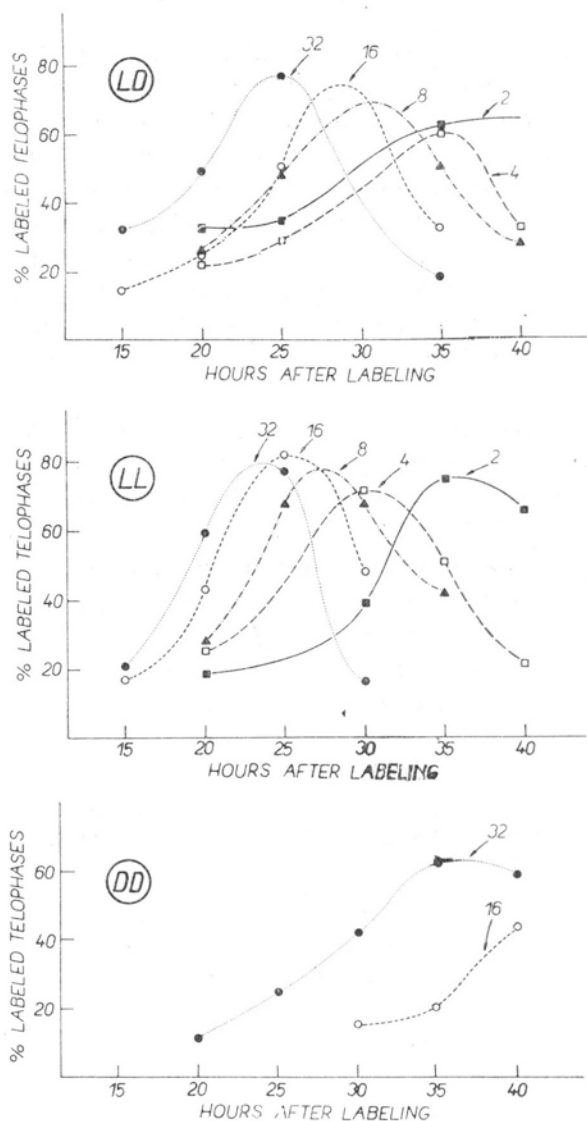


Fig. 4. Per cent of strongly labeled telophases in successive hours of postincubation. LD — control material: 16 h light and 8 h darkness in 24 h; LL — material cultured under continuous light; DD — material cultured in continuous darkness. 2-, 4-, 8-, 16-, 32- — successive generations of antheridial filaments of *Chara vulgaris*

cells. The protraction of the cell cycle in the 16-cell generation seems, on the basis of the course of radioactive telophases, to exceed greatly the reaction of the 32-cell generation, the last of the mitotically active stages in *Chara vulgaris* before the period of spermatogenesis (Table 3).

4. Duration of S phase

Determination of S phase duration by the method of Monesi (1969) is based on the calculation of the proportion of cells labeled after a short incubation with ^3H -TdR. The results are referred to the known duration of the cell cycle as the product of both these values. The number of radioactive cells in proportion to the whole population analyzed after 2-h incubation is shown for the successive generations and experimental combinations in Fig. 5.

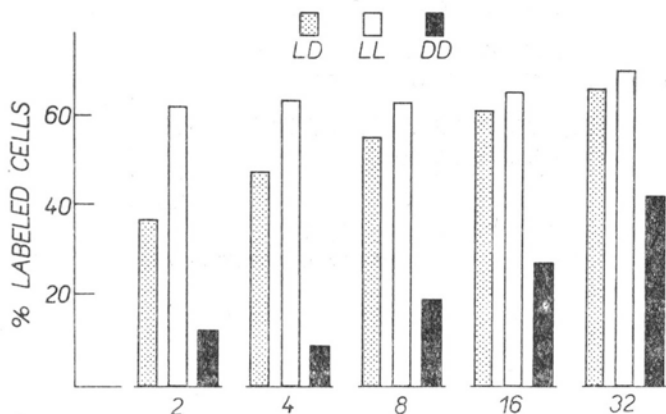


Fig. 5. Per cent of cells labeled with ^3H -TdR in successive generations of antheridial filaments of *Chara* after 2 h of incubation

Duration of the S phase (T_s) was calculated by the formula:

$$T_s = T_c \cdot R \left(1 - \frac{T_i}{T_c} \right),$$

where T_c is duration of the cell cycle, R — per cent of cells labeled with radioactive thymidine after incubation time T_i . The coefficient

$1 - \frac{T_i}{T_c}$ reduces the error resulting from the long, 2-h incubation.

Table 4
Duration of S phase (h)

Generation	2	4	8	16	32
LD	14.1	15.9	16.1	16.2	15.1
LL	21.0	18.2	16.0	16.2	15.0
DD	—	—	—	12.0	14.6

The results of the calculation of S phase duration are shown in Table 4 and Fig. 6 against the background of the cell cycle duration.

In all generations of the antheridial filaments of *Chara vulgaris* the duration of DNA replication is very similar and is not regulated by light conditions. Wider differences are observed in material subjected to continuous illumination at the 2-cell stage, which is the most difficult in the microscopic analysis of the autoradiograms.

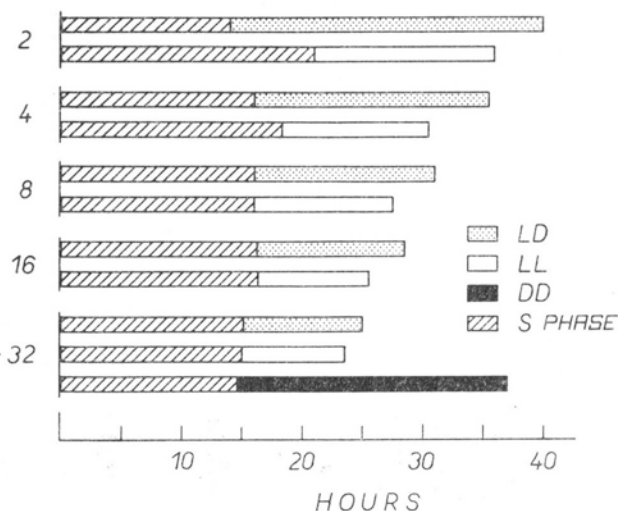


Fig. 6. Duration of cell cycle and S phase in successive generations of antheridial filaments of *Chara vulgaris*. LD — control material; LL — material under continuous illumination; DD — material in continuous darkness

DISCUSSION

The conditions determining cell division are: DNA replication, and the synthesis of the whole set of factors of structural and enzymatic type, including the factor initiating division processes. When the amount of DNA per nucleus is constant in all generations of the antheridial filaments of *Chara*, the duration of the cell cycle is directly related to the rate of the both above named intermitotic processes. The first condition for mitosis, fulfilled in S phase, does not seem to be regulated by light in *Chara*, which results from the stability of the duration time of this phase. Under various illumination conditions, however, the time elapsing to the moment of entering mitosis is not constant for the same generation of the filament. The reaction of the particular generations to the same light conditions also differs.

Continuous light, stimulating mitotic activity, cell growth and the rate of the processes leading to the initiation of mitosis exerts a stronger effect on the antheridial filaments in the early stages of their development, while its influence is weaker at later stages. Darkness, a factor

with marked inhibitory action, releases a similar range of reactions in particular generations of the filaments: a depressive action is noted most distinctly in the period which is included by the first 4 divisions, i.e. in 2-, 4-, and 8-cell generations. Thus, the results obtained seem to indicate that the light factor interferes mainly with G_2 phase, and its stimulating or inhibitory action is proportional to the duration of this phase.

The increment of the cell length under continuous illumination and the reduction of the cell cycle suggest a more intensive dynamics of the cell growth rate in interphase. The effect of darkness is opposite to that of light — although the duration of G_2 phase is considerably protracted, the cell dimensions are markedly reduced.

The physiological depression of the material deprived of light, expressed in a decrease of mitotic activity becomes more pronounced with time. At the first stages of the development of antheridial filament it becomes impossible to follow the wave of radioactive mitoses, and the curve representing the cell cycle of the 32-cell generation is diffuse as compared with that of the control material, thus indicating, in agreement with the concept of Van't Hof and McMillan (1969), an enhanced heterogeneity of the material.

The phenomenon of the increment of heterogeneity of the primarily uniform population under the action of a negative physiological factor, such as the lack of light for the antheridial filaments, is also manifested in a change of the frequency of the particular classes of cell sizes. Culture in darkness reduces in each generation the population of the medium-sized cells, which corresponds in the control material to the stage of transition from S phase to G_2 phase. This must be the consequence of the inhibition of growth in initial and final stages of interphase. The successive appearance of the peaks of mitotic activity in the material exposed to light after a prolonged period of darkness, is probably a manifestation of this process. The first peak of mitotic activity occurring in the 16-, and 32-cell generations after about 4 h, and in the 2-, 4-, and 8-cell generations 25 h after the transfer of plants from darkness to light would represent the populations inhibited in the late period of interphase. The next wave of mitoses occurring for these generations after 15 and 34 h, respectively, would represent the fractions of cells arrested in the growth at an earlier stage of interphase. Thus, the change of the culture conditions, consisting in the elimination of the inhibitory influence and the introduction of the stimulating factor (light), does not have a synchronizing effect on the processes occurring in the antheridial filaments of *Chara*, as it is the case for instance in the autotrophic cultures of *Euglena* (Edmunds and Funch, 1969). On the contrary, the cells of the same generation are divided into two populations varying in time of their reaction to the light stimulus.

The rise of the level of heterogeneity of *Chara* cells may be determined by the mechanisms analogous to the energetic requirements of the root meristem cell populations (Van't Hof, 1968; Van't Hof et al., 1973). Precise establishment of the "control points" in the cell cycle and of the subpopulations composition (Van't Hof, 1974) for the antheridial filaments still remains impossible.

The intensity of the mitotic activity in the control material is correlated with the period of light. The undulating character of this rhythm under continuous illumination or in darkness suggests an endogenous mechanism of the regulation of the mitotic activity. The effectiveness of the factors inducing mitoses in an endogenous diurnal rhythm seems, however, subordinated to the energetic and nutritional requirements of cells, which are associated with the period of the photosynthetic activity of the thallus. As regards the nutritional requirements of the antheridia, darkness must cause in *Chara* a deficit of nutrient components as in the case when antheridia devoid of chlorophyll are detached from the assimilating thallus. The antheridial filaments of such antheridia show a similarly rapid decline of mitotic activity and a considerable decrease of cell dimensions (Kuran, unpubl. information).

Slowing down of the rate of the vital processes in the cells of the antheridial filaments when cultured in darkness and the consequent diminution of the number of mitoses may be a response not only to the physiologically negative state of nutritional deficit, but may also reflect the inhibitory action of several factors. One of these may be a disturbance of administration of the endogenous growth regulators. After a short period of darkness, already, there is a drastic increase of the length of internodes, which is probably the morphological manifestation of a rise in the level of auxin in the thallus. The stimulating action of IAA introduced into the culture medium on growth processes has been observed in *Nitella hookesi*, a closely related species of *Characeae* (Starling et al., 1974). On the other hand, however, the inhibitory influence of an excess of these regulators on growth processes and cell division in the antheridial filaments may also be expected. The reaction of stimulation in the above mentioned *Nitella hookesi* occurs within a relatively narrow range of IAA concentration. The lowered frequency of mitoses at higher auxin concentrations was also observed in numerous other species of algae (Marcenko, 1971). An over-optimal level of auxin synthesized in the apical part of the thallus of *Chara* seems to exert a stronger inhibitory effect in young antheridia, situated on the apical part of the plant, than on the 16-, and 32-cell generations, that is in the antheridia removed further from the presumed source of the regulator.

The essential factor in the control of the growth processes and

mitotic activation is most probably also phytochrome. A different effect of a given light spectrum on a period of time indispensable for the initiation of mitosis has been the object of studies of Wada and Furuya (1972) on the gametophyte of *Adiantum*. Red light may determine various growth reactions in the different-aged cells (Miller and Wright, 1961).

The knowledge of the role of phytochrome in the development of the antheridial filaments would be extremely interesting. The increment of the volume of the antheridium and the succession of the generations of the antheridial filaments are associated with the formation of chromoplasts and gradual saturation of the orange-red colour in the shield cells protecting the interior of the antheridium. Thus, the differentiation of the antheridial filaments occurs under the natural screen limiting the wave-length more and more to the red. Culture of the material in darkness creates, perhaps, conditions which are particularly unfavourable for the development of the younger generations of the cells by depriving them of the physiologically important wider range of light spectrum.

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Wpływ czynnika świetlnego na przebieg cyklu komórkowego w różnych stadiach rozwojowych nici spermatogenicznych *Chara vulgaris* L.

Streszczenie

W kolejnych pokoleniach nici spermatogenicznych *Chara vulgaris* ciągłe działanie światła powoduje wzrost indeksu mitotycznego, natomiast hodowla w ciemności prowadzi do wyraźnego obniżenia liczby mitoz i po dłuższym działaniu do całkowitego ich zaniku.

Światło odwraca wywołany ciemnością efekt depresji mitotycznej: w pokoleniach 16- i 32-komórkowych aktywność podziałowa pojawia się już po 3 godzinach, w pokoleniach 2-, 4- i 8-komórkowych dopiero po 18 godzinach.

W porównaniu z materiałem kontrolnym rozmiary komórek nici spermatogenicznych roślin hodowanych w ciągłym oświetleniu są większe, a po hodowli w ciemności ulegają one zmniejszeniu. Analiza wielkości tych ostatnich sugeruje zahamowanie wzrostu komórek w początkowym i w końcowym okresie interfazy.

Oświetlenie ciągle skracza we wszystkich pokoleniach czas trwania cyklu komórkowego; ciemność powoduje jego znaczne wydłużenie. Czas trwania fazy S jest zbliżony we wszystkich pokoleniach nici spermatogenicznych (ok. 16 godzin) i nie jest modyfikowany warunkami oświetlenia. Czynniki świetlne wydają się więc ingerować głównie w fazie G_2 i jego udział w regulacji cyklu komórkowego jest skorelowany z czasem trwania tej fazy.

Rola światła w kinetyce cyklu komórkowego poszczególnych pokoleń nici spermatogenicznych *Chara* dyskutowana jest w aspekcie zapotrzebowania pokarmowego komórek, regulacji hormonalnej i fitochromu.