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Effect of Irradiance on the Course of RNA Synthesis in the Cell Cycle of *Scenedesmus quadricauda*

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Abstract. In synchronous populations of *Scenedesmus quadricauda* the RNA amount in the cells increases in waves: periods of a high rate of RNA synthesis alternate with periods of a low rate in the course of the cell cycle. Each wave usually leads to the doubling of the RNA amount per cell. In cells growing under normal conditions the waves of RNA synthesis seem to be linked with consecutive rounds of DNA replication. The pattern of RNA synthesis in the course of the cell cycle, however, does not change, if DNA replication is prevented by application of 5-fluorodeoxyuridine. In darkness the rate of RNA synthesis drops to zero and thereafter the RNA amount per cell decreases. In cells which have been induced to cellular division RNA synthesis may become restored in the dark in newly formed daughter cells. The lowering of RNA amount and its new increase during the dark period become more pronounced with increasing irradiance in the previous light period as well as with its increasing length. In the period of protoplast fissions RNA synthesis is arrested even if the cells divide in the light; whether a similar inhibition occurs during mitoses is not clear.

A characteristic feature of chlorococcal algae is their division into more than two, in general into 2^n, daughter cells. The number of daughter cells is controlled by light conditions (MORIMURA 1959, WANKA 1959, 1967, STEENBERGEN 1974).

The sequence of reproductive processes starting with DNA replication and leading to cell division is light-independent. The number of these sequences initiated in one cell cycle is controlled by the specific growth rate of algal cells and, consequently, by irradiance (ŠETLÍK *et al.* 1972).

The growth of the cells is based on a sequence of macromolecular and other syntheses leading to an increase of cell mass (MITCHISON 1971). RNA synthesis can be considered to be one of the first processes in the growth sequence as well as one controlling the overall growth rate.

This paper reports our results on the effect of irradiance and reproductive processes on the rate of RNA synthesis in the cell cycles of the chlorococcal alga *Scenedesmus quadricauda*. Its populations, synchronized by alternating light and dark periods, were exposed to light for varying periods of time and

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at various levels of irradiance. At low irradiance the cells of *S. quadricauda* divide exclusively into four daughter cells (quadruplet cell cycle) at high irradiance into eight (octuplet cell cycle). Consequently, two or three DNA replication rounds and two or three mitoses occur within one cell cycle of *S. quadricauda* (ŠETLÍK *et al.* 1972). Whether one or several growth cycles occur in one cell cycle of *S. quadricauda* is analyzed in the discussion.

MATERIAL AND METHODS

Organism

The chlorococcal alga *Scenedesmus quadricauda* (TURP.) BRÉB. strain Greifswald/15 was obtained from the culture collection kept at the Institute of Experimental Botany, Praha, Czechoslovakia (now at the Institute of Botany, Třeboň, Czechoslovakia).

Culture Conditions

Synchronous populations of *S. quadricauda* were grown in a chemostat with plate-parallel culture vessels (volume 1200 or 2200 cm^3 distance of the glass walls 18 mm) submersed in a water bath at 30 °C and illuminated from one side. Incandescent lamps (500 W — Tesla) served as the light source. The irradiance at the surface of the cultivation cuvettes was 140—180 W m^{-2} PhAR. Different values of the mean irradiance of one cell were established by the variation of culture density. The latter was controlled by adjusting appropriately the dilution rate, which varied between 0.05 h^{-1} and 0.10 h^{-1}. The cultures were synchronized by alternating light and dark periods (14 : 10 h).

Carbon dioxide concentration in the aerating gas mixture was maintained between 1.5 and 3 % (v/v). The rate of the gas stream was about 60 cm min^{-1}. The following nutrient solution was used: (concentration of compounds is given in mg l^{-1}) KNO_3 — 4042, KH_2PO_4 — 340, $MgSO_4$ — 988, EDTA Fe/Na — 18, $CaCl_2.6H_2O$ — 10.96, H_3BO_3 — 3.09, $MnSO_4.4H_2O$ — 1.18, $CoSO_4.7H_2O$ — 1.4, $CuSO_4.5H_2O$ — 1.24, $ZnSO_4.7H_2O$ — 1.43, $(NH_4)_6Mo_7O_{24}.4H_2O$ — 0.88. Continuously diluted cultures were used for experiments. Culture equipment and growth parameters of the cultures are described in more detail by ŠETLÍK *et al.* (1972) and by DOUCHA (1979).

Light conditions in suspensions of varying density at a given surface irradiance were characterized by the mean irradiance ($\bar{I}$). This is defined as $\bar{I} = \frac{I_i - I_t}{\ln I_i/I_t}$, where I_i is the radiant flux density incident on the front wall of the cuvette and I_t is the radiant flux density outgoing from the rear wall of the cuvette. The photosynthetically active radiation was measured by a phytoactinometer proposed and constructed in this laboratory by KUBÍN (1971).

Determination of Induction Curves

The induction of nuclear and cellular division was assessed by a modified version of recording the "potential cell number" originally devised by WANKA (1959). The significance of the term "induction" for various reproduction processes was explained and the method for its determination was described by ŠETLÍK *et al.* (1972).

Cell Counting

The number of cells as well as the number of induced quadruplet and octupled daughter coenobia in darkened samples were counted in the Bürker counting chamber.

Staining of Nuclei

Nuclei were fluorochromed by acridine orange and observed through a fluorescent microscope. Details of the procedure were described elsewhere (ZACHLEDER *et al.* 1974).

Chemicals

All chemicals used for analyses were of analytical grade. DNA and RNA used for calibration assays and 5-fluorodeoxyuridine were products of Serva Heidelberg. Other chemicals were purchased from Lachema, Praha.

Nucleic Acid Assay

WANKA's procedure (WANKA 1962) as modified by LUKAVSKÝ *et al.* (1973) was applied. The algal cells in suspension (10 cm^3) were spinned down, 5 times extracted for 50 min at 20 °C by 0.2N perchloric acid in 50% ethylalcohol, 3 times for 10 min at 70 °C by mixture of ethanol — ether (3 : 1) and washed by ethylalcohol (96%). Nucleic acids in the sediment were hydrolyzed by 0.5N perchloric acid at 60 °C for 5 h. Total concentration of nucleic acids in the extract was measured by UV absorption at 260 nm. For DNA estimation in the extract a colorimetric reaction with diphenylamine was used. The reaction mixture was allowed to stand for 24 h in the dark at 30 °C. Then the absorption at 600 nm was measured. The concentration of RNA was evaluated by subtraction of DNA values from total nucleic acid content.

RESULTS

A. The Effect of Irradiance

Synchronous cultures of *S. quadricauda* were grown at two irradiances chosen so as to provide populations in which the cells divided exclusively either into eight daughter cells (octuplet cell cycle, Fig. 1a) or into four daughter cells (quadruplet cell cycle, Fig. 1c). In both cases the increase in RNA content in the course of the cell cycle proceeds in waves; periods with a high rate of RNA synthesis alternate with periods of a low rate (Fig. 1b). At high irradiance both the number of the waves of RNA synthesis per cycle and the rate of RNA synthesis in the individual steps are higher than at low irradiance.

Each wave of RNA synthesis usually leads to the doubling of RNA amount in the cells (Fig. 2). At a higher irradiance the doubling of RNA amount is sometimes realized in two consecutive steps of RNA synthesis (Fig. 2, curves 1 and 2).

B. The Effect of Darkening

Populations of *S. quadricauda* synchronized by alternating light and dark periods were darkened at various stages of the cell cycle. In all experimental variants the rate of RNA synthesis drops very rapidly upon darkening (Figs. 3, 4, 5, 7). A further increase in RNA content in the dark depends both

on the level of irradiance during the preceding light period and on the length of this period.

Very slow, if any, RNA synthesis was measurable after darkening of cultures grown at low irradiances. At higher irradiances RNA synthesis continued for 1 or 2 h after darkening, however, at a markedly reduced rate (Figs. 4, 5).

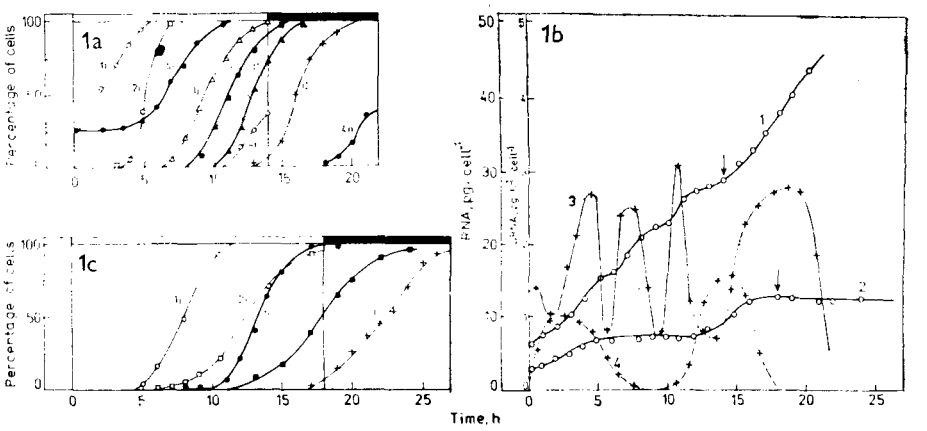

Fig. 1. The course of RNA synthesis (1b) and of some cell cycle events (1a, 1c) in a synchronous population of *Scenedesmus quadricauda* grown in a chemostat at high and low mean irradiance. $I_1 = 140$ W m^{-2}, $T = 30$ °C. Light and dark periods are marked by vertical lines and white and black strips at the top of the panels. Panel 1a ($\bar{I} = 80$ W m^{-2}, $D = 0.1$ h^{-1}) and 1c ($\bar{I} = 60$ W m^{-2}, $D = 0.045$ h^{-1}): 1i, 2i, 3i, 4i — the fraction of the cells which attained the induction of the first, second, third and fourth mitoses, respectively. The inductions of the second and third mitosis coincide with the inductions of quadruplet and octuplet cellular divisions, respectively. The fourth induction of mitosis belongs to the next cell cycle where the corresponding nuclear division is realized (curve 4n). 1n, 2n, 3n, 4n — the fraction of the cells in which the first, second, third and fourth mitoses were terminated. c — the fraction of cells which released their autospores. Panel 1b: 1, 2 — increase in RNA content per cell at high and low irradiance, respectively, 3, 4 — rate of RNA synthesis at high and low irradiance, respectively (obtained by graphical differentiation of curves 1 and 2).

Once RNA synthesis stops in the dark, the RNA content of the cells tends to decrease (see Figs. 3, 4). This decay is very faint with cultures growing in low light and was rarely observed. It becomes pronounced with increasing irradiance as well as with increasing time of the cell cycle at which darkening occurs (see curves *b*, *c*, and *d* in Fig. 3a or Figs. 4a and 5).

A certain time after RNA synthesis stops in the dark it becomes restored again and this new RNA synthesis may compensate for the preceding decrease in RNA amount (Figs. 3a, 4, 5) or even brings about an increase. Its extent increases again with increasing irradiance (Fig. 2) and with the duration of the preceding light period (Figs. 3, 4, 5).

This new RNA synthesis occurs only after all reproductive events were finished and newborn daughter cells released (Figs. 3a, 7). Therefore, this is a synthetic activity of the newborn daughter cells and belongs to the next cell cycle. The quadruplet induction which marks the ability of the cells to divide is also the transition point after which the cells kept in the dark may restore their RNA synthesis at the end of the dark period.

C. The Effect of DNA Amount on the Rate of RNA Synthesis

As with RNA, the DNA content of daughter cells at the end of the dark periods also depends on growth conditions in the previous cycle. It is low if the previous growth rate was low (under low irradiance) and this is the DNA content that corresponds to cells containing one nucleus with the lowest number of genomes. With increasing irradiance (and growth rate) in the previous cycle, daughter cells keep to develop further in the dark. This development may entail another round of DNA replication and, in some cases, also of nuclear division. Uninuclear bigenomic or binuclear daughter cells thus arise and are present at the start of the next cell cycle.

We took advantage of this fact and we prepared daughter cell populations with a low content of DNA (0.2 pg per cell; corresponding to unigenomic cells) and with more than double this amount (0.5 pg per cell; corresponding to a mixture of cells with two and four genomes). These two cultures were grown at the same irradiance. The rate of RNA synthesis and also its amount in the first wave were approximately proportional to the initial DNA amount (Fig. 6). This result indicates that at a given irradiance gene dosage is an important factor codetermining the rate of RNA synthesis.

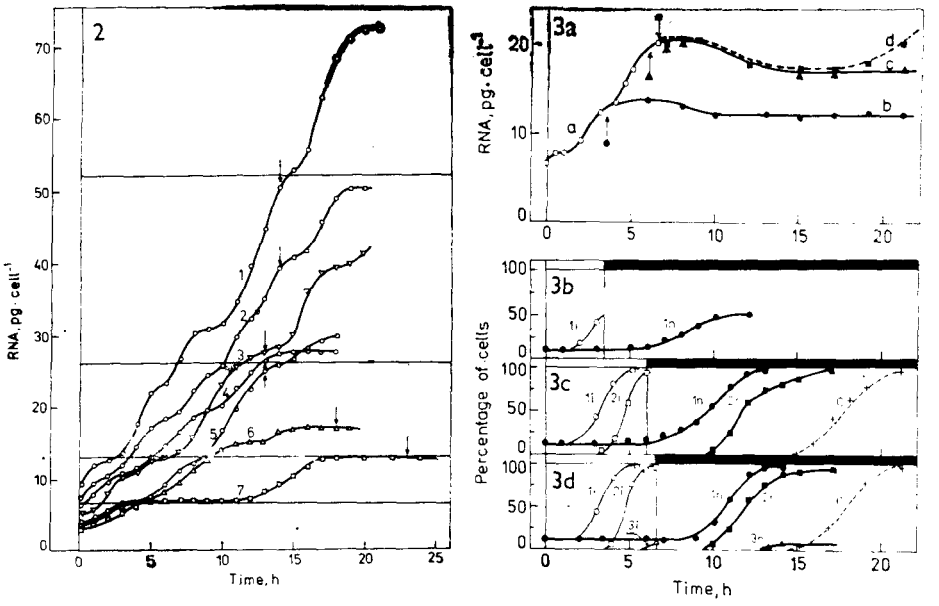

Fig. 2. The course of RNA synthesis in synchronous populations of *Scenedesmus quadricauda* grown in a chemostat at different mean irradiances.
I_i = 140 W m^{-2}, T = 30 °C, values of $\bar{I}$ and D for individual curves: 1 = 105 W m^{-2}, 0.11 h^{-1}, 2 — 96 W m^{-2}, 0.10 h^{-1}, 3 — 80 W m^{-2}, 0.10 h^{-1}, 4 — 70 W m^{-2}, 0.08 h^{-1}, 5 — 65 W m^{-2}, 0.08 h^{-1}, 6 — 60 W m^{-2}, 0.06 h^{-1}, 7 — 56 W m^{-2}, 0.05 h^{-1}. Horizontal lines indicate the levels corresponding to successive doublings of the lowest RNA amount per cell. Vertical arrows mark the ends of light periods.

Fig. 3. The courses of RNA synthesis and of some cell cycle events in synchronous populations of *Scenedesmus quadricauda* grown in a chemostat and placed into dark after 3, 6, and 6.5 h of light. Panel **3a**: increase in RNA content per cell in light (curve *a*) and in darkened cultures (curves *b*, *c*, *d*). The time of darkening is marked by arrows. Corresponding cell cycle characteristics for curves *b*, *c*, *d* are illustrated in panels **3b**, **3c**, **3d**, respectively. For cultivation conditions, meaning of the symbols and labelling of curves in panels 3b, 3c, 3d see legend to Fig. 1a.

As mentioned in the Introduction, in the course of the cell cycle of *S. quadricauda* two or three rounds of DNA replication occur. In fast growing populations (under high irradiance) the first DNA replication starts rather early. The cell operates then for a greater part of the cell cycle with a twofold and

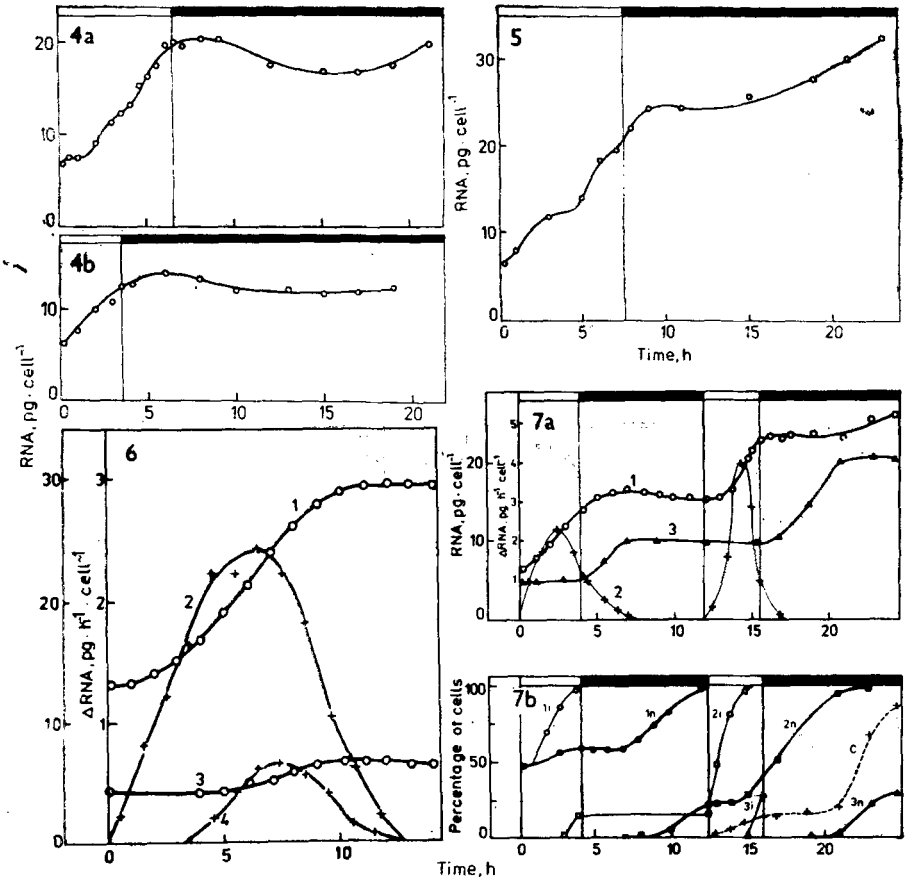

Fig. 4. The course of RNA synthesis in synchronous populations of *Scenedesmus quadricauda* grown in a chemostat and placed into dark after 3.5 h and 6.5 h of light. For cultivation conditions see legend to Fig. 1a.

Fig. 5. The course of RNA synthesis in a synchronous culture of *Scenedesmus quadricauda* grown in a chemostat and kept in the dark after 7 h of light.

For cultivation conditions see legend to Fig. 1a.

Fig. 6. The course of RNA synthesis in the two synchronous populations of *Scenedesmus quadricauda* which differed in DNA content at the start of the light period and were grown at the same irradiance.

$I_i = 140$ W m^{-2}, $\bar{I} = 56$ W m^{-2}, $D = 0.045$ h^{-1}, 1, 3 — increase in RNA content per cell (1 — mean DNA content 0.5 pg per cell, 3 — mean DNA content 0.2 pg per cell). 2, 4 — rate of RNA synthesis (obtained by graphical differentiation of curves 1 and 3, respectively). In the figure only the first wave of RNA synthesis is illustrated.

Fig. 7. The course of RNA synthesis and of some cell cycle events in a synchronous culture of *Scenedesmus quadricauda* grown in a chemostat and with the light period interrupted for 7.5 hours of darkness.

For cultivation conditions, meaning of the symbols and labelling of curves in panel 7b see legend to Fig. 1a. Panel 7a: 1 — increase in RNA content per cell, 2 — rate of RNA synthesis (obtained by graphical differentiation of the curve 1), 3 — increase in DNA content per cell.

later in the cell cycle with a fourfold and an eightfold number of genomes. The rate of RNA synthesis should increase accordingly, with the progress of the cell cycle.

On the other hand, two or three mitoses occur consecutively mostly in the second half of the cell cycle. Consequently, a certain fraction of mitotic cells is always present at that period. If DNA template activity is inhibited during mitosis (and possibly even during DNA replication) the gene dosage effect in later phases of the cell cycle may be masked.

Therefore, we have performed an experiment in which the growth processes (*i.e.* RNA synthesis) and reproductive processes (DNA replication, mitosis) were separated in time. The population of daughter cells with DNA content corresponding to two genomes (about 0.4 pg per cell) was illuminated to produce the first wave of RNA synthesis. Thereafter, the cells were placed into darkness and the DNA replication induced by light as well as the corresponding mitosis took place during the dark period. At the beginning of the next illumination the cells were, therefore, binuclear and contained approximately the double amount of DNA as compared with the start of the experiment (0.8 pg per cell). The rate of RNA synthesis in the following light period was about double the rate in the cells with lower content during the first light period (Fig. 7).

In some cases a higher rate of RNA synthesis was observed later in the cell cycle even concomitantly with reproductive processes (Fig. 1, curve 4, Fig. 9, curve 2, Fig. 10). To examine, whether this increase can be caused by the increased DNA content, the rate of RNA synthesis in a population treated with 5-fluorodeoxyuridine (FUDR) was compared with that in an untreated culture. The drug was applied in concentration 25 μg ml^{-1} at the start of the cycle. DNA synthesis was inhibited and so were also the ensuing reproductive processes (mitoses and protoplast fissions). It is reasonable to assume, however, that the template activity of DNA remained unaffected in FUDR-treated cells. Nevertheless, the rate of RNA synthesis (per cell) did not accelerate with the progress of the cycle, in contrast to the untreated cells (Fig. 8, curves 2 and 3). In other words, the rate of RNA synthesis referred to unit DNA amount in the cell was the same whether DNA content of the cells increased or was kept constant. It is interesting that in the latter case, *i.e.* in FUDR-treated cells, the same periodic variation was observed as is known in untreated cultures (Fig. 8, curves 1 and 3).

D. The Effect of Mitoses and Protoplast Fissions

It follows from the data in section A that the pattern of RNA synthesis changes markedly with irradiance. On the other hand, irrespective of irradiance, RNA synthesis stops or is, at least, slowed down substantially during the period of protoplast fission. Unfortunately, in most experiments protoplast fission occurred just at the beginning of the dark period in synchronized populations. To examine whether under these conditions the rate of RNA synthesis sinks in response to darkening or is decreased by protoplast fission, synchronized populations were grown for one or two cell cycles in continuous light (Figs. 9 and 10, respectively). In Fig. 9 the course of RNA synthesis during dark period in a subculture darkened at the usual time in the cell cycle is also illustrated. The findings (Fig. 9) support the idea that during protoplast fission the rate of RNA synthesis always drops irrespectively of light conditions.

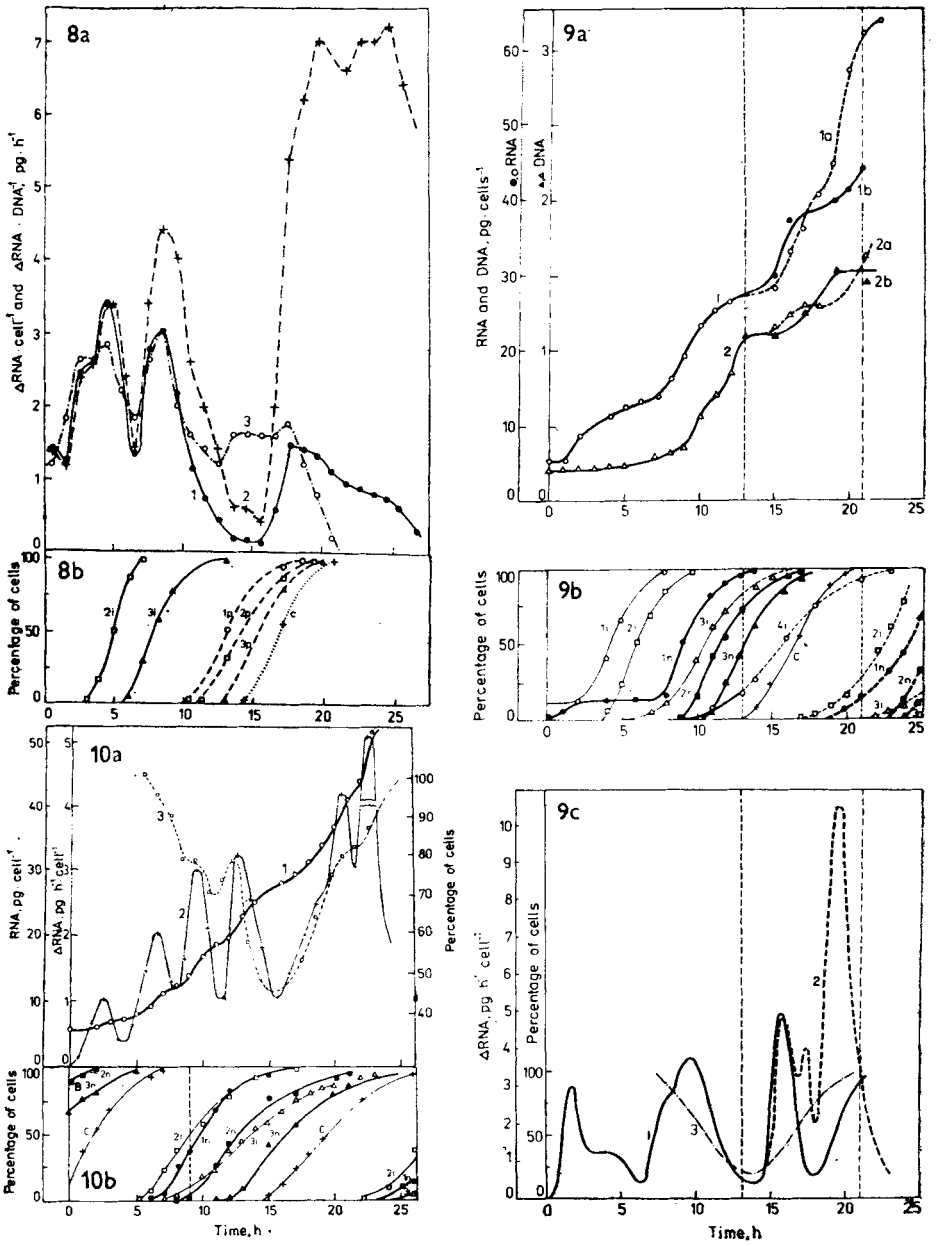

Fig. 8. The rate of RNA synthesis per cell and per unit amount of DNA in an untreated and a 5-fluoro-deoxyuridine treated synchronous population of *Scenedesmus quadricauda*.
I_1 = 170 W m^{-2}, $\bar{I}$ = 80 W m^{-2}, T = 30 °C, periodically diluted. Dark period at the end of the cell cycle was omitted. 5-fluorodeoxyuridine in concentration 25 μg ml^{-1} was applied to one culture at the beginning of the light period. Panel 8a: rate of RNA synthesis per unit DNA amount in the untreated culture (curve 1) and in the FUDR-treated (curve 3) culture (the curve 3 illustrates simultaneously the rate of RNA synthesis per cell), 2 — rate of RNA synthesis per cell in untreated culture. Panel 8b: cell events in the untreated culture 2i, 3i, — the fraction of

The effect of protoplast fissions was relatively easy to observe because consecutive protoplast fissions follow each other, separated by short intervals only and so their curves in the population overlap partially. Consequently, in a synchronous population the majority of the cells can be found at some phase of protoplast fission for a relatively long time period (3 h) before the end of the cell cycle (Fig. 8b). In contrast, the two or three consecutive mitoses occurring in the cell cycle of *S. quadricauda* are well separated in time (Fig. 1) and the mitosis itself lasts only very short (half an hour at maximum) (SULEK 1975). Therefore, only a relatively small fraction of cells pass simultaneously through mitosis, and a possible inhibition of RNA synthesis caused by the latter process will not show up as a pronounced deceleration in the increase of the total RNA amount.

DISCUSSION

In the experiments reported here the quantity actually measured was the "total RNA", *i.e.* the amount of (poly)ribonucleotides extracted from the cells upon hydrolysis with perchloric acid. Thus, the data represent mainly the sum of the rRNA and tRNA species since the mRNAs account for only a minor fraction of the total RNA amount at any time of the cell cycle.

The sum of tRNAs and rRNAs in *Scenedesmus quadricauda* consists of about 15% tRNA and 85% rRNA (BARTOŠ and TETÍK 1975). The syntheses of these two components were found to vary in parallel in *Scenedesmus quadricauda* (BARTOŠ and TETÍK 1975) and also in the volvocal alga *Chlamydomonas geitleri* (TETÍK and NEČAS 1979). Conservation of a constant ratio of tRNA and rRNA in a wide range of growth conditions was also observed in the cell cycle of the blue-green alga *Anacystis nidulans* (MANN and CARR 1973). Therefore, it is assumed that the course of "total" RNA synthesis described in this paper reflects first of all the course of rRNA synthesis.

Under certain growth conditions tRNA and rRNA syntheses can be perhaps separated in time as has been described in *Chlorella fusca* (ENÖCKL 1968). However, even in this case the course of rRNA increase in the cell would

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cells which attained the quadruplet and octuplet induction, respectively, 1p, 2p, 3p — the fraction of cells which divided their protoplasts into two, four, and eight, respectively, c — the fraction of cells which released their autospores.

Fig. 9. The course of RNA and DNA synthesis and of some cell cycle events in synchronous populations of *Scenedesmus quadricauda* grown in a chemostat and kept in continuous light (population a) or darkened at the usual time (population b).

$I_i = 140$ W m^{-2}, $\bar{I} = 75$ W m^{-2}, $T = 30$ °C, $D = 0.1$ h^{-1}. Vertical dashed lines indicate the beginning and the end of dark period in the population b. Panel 9a: 1 — increase in RNA content per cell in population a (1a) and b (1b); 2 — increase in DNA content per cell in population a (2a) and b (2b). Panel 9b: for meaning of symbols and the labelling of curves see legend to Fig. 1. Dashed curves illustrate the course of cell cycle events in population a. Panel 9c: 1, 2 — rate of RNA synthesis in population b and a, respectively, (obtained by graphical differentiation of the curves 1b and 1a, respectively). 3 — percentage of cells in which mitosis or protoplast fission did not occur at a given moment.

Fig. 10. The course of RNA synthesis and of some cell cycle events in a synchronous culture of *Scenedesmus quadricauda* grown in a chemostat in continuous light for two cell cycles.

$I_i = 180$ W m^{-2}, $\bar{I} = 96$ W m^{-2}, $T = 30$ °C, $D = 0.1$ h^{-1}. Vertical dashed line indicates the end of dark period in the control culture. Panel 10a: 1 — increase in RNA content per cell, 2 — rate of RNA synthesis (obtained by graphical differentiation of the curve 1), 3 — percentage of cells in the population in which mitosis or protoplast fission did not occur at a given moment. Panel 10b: For meaning of symbols and the labelling of curves see legend to Fig. 1.

markedly differ from that of "total" RNA only if the tRNA would go through several doublings in a relatively short period.

The periodic variation in the rate of RNA synthesis during the cell cycle of *Scenedesmus quadricauda* has been confirmed under all growth conditions used in the present experiments. It does not seem to be unique for this alga but is apparently typical of all algae which divide into more than two daughter cells, *e.g. Chlamydomonas reinhardtii* (KNUTSEN *et al.* 1974, WILSON and CHIANG 1977, LIEN and KNUTSEN 1979) or *Chlorella pyrenoidosa* (HOPKINS *et al.* 1972). In contrast, with algae which divide into two daughter cells, RNA synthesis seems to proceed in one step only, as described for *Euglena gracilis* (EDMUNDS 1965) and *Navicula fusiformis* (DARLEY *et al.* 1976).

LIEN and KNUTSEN (1979) suggested that the drop in the rate of RNA synthesis coincides with the start of DNA synthesis. From the inspection of Fig. 4 in their paper, however, it is apparent, that RNA synthesis is slowed down some time before the onset of DNA replication. In addition, a faint wave in the rate of RNA synthesis can be also seen earlier in the cell cycle (KNUTSEN *et al.* 1974, LIEN and KNUTSEN 1979). We assume that these two or three waves of RNA synthesis represent the doublings of RNA amount during the cell cycle of *Chlamydomonas reinhardtii*, similarly as it was found in our experiments with *Scenedesmus quadricauda*.

These waves do not seem to be related to DNA replication because at least the first one occurs a long time before the start of DNA replication (LIEN and KNUTSEN 1979). Also our experiments with FUDR-treated cultures seem to indicate that the periodic variation in the rate of RNA synthesis is not related to DNA replications.

An increase in several steps was also found for protein concentration and cell volume in the cell cycle of *Scenedesmus quadricauda* (ŠETLÍK *et al.* 1972, ZACHLEDER *et al.* 1975) and for cell volume in *Chlamydomonas reinhardtii* (MIHARA and HASE 1971). It may be assumed that the increase in RNA and protein content and in cell volume are processes coupled in one growth cycle, which under normal conditions, leads to a doubling of cell growth parameters. If this assumption is valid, several successive growth cycles may occur in the cell cycle of *Scenedesmus quadricauda*.

The present results also show that the rate of the RNA synthesis is strictly controlled by irradiance. The simplest way to explain the regulatory role of light is via the trophic function of photosynthesis. In photosynthetic microorganisms the reduction of nitrate to ammonia (LOSADA 1975/76) as well as its further assimilation to the level of α-amino nitrogen (KIRK and LEECH 1972, MAGALHAES *et al.* 1974) are intimately related to photosynthesis. It was also reported that the rate of amino acid synthesis in algae is proportional to irradiance (KANAZAWA *et al.* 1970).

On the other hand, it has been extensively documented for prokaryotes (MAALØE and KJELDGAARD 1966) and demonstrated also in mammalian cells (MARTIN 1980) that the concentration of amino acids controls the rate of rRNA synthesis in the cell. It is, therefore, possible that the rate of amino acid supply, either directly from the chloroplast or mediated through some cytoplasmic step, may be the transmitting factor in the light control of RNA synthesis.

Our findings manifested that RNA synthesis is blocked during protoplast fission. It was described that during the protoplast fission in the chlorococcal alga *Chlorella fusca* very extensive morphological changes occur (WANKA 1968). Similarly, during protoplast fission of *Scenedesmus quadricauda* cells extensive structural transformations were observed, *e.g.* of the structure of thylakoids (ŠETLÍK *et al.* 1981), shape of nuclei (ZACHLEDER *et al.* 1974), and shape and position of newly formed protoplasts (BŘEZINA *et al.* 1972). During protoplast fission also the binding properties of DNA to the acridine orange change markedly and nuclei are in a diffusely stainable state (ZACHLEDER *et al.* 1974). It may be assumed that the transcription activity of nuclei is probably suppressed during protoplast fission.

During protoplast fission the photosynthetic activity is also deeply inhibited (BERKOVÁ *et al.* 1972). But since RNA synthesis stops in dividing cells both in the light and in the dark the depression of photosynthesis cannot be the principal cause of this inhibition.

Our data do not provide a direct evidence that RNA synthesis stops during mitosis. The rate of RNA synthesis decreases some time before protoplast fission sets in; this could be perhaps attributed to the fraction of cells in which mitosis proceeds. This is all the more probable since in all eukaryotes, except yeast, RNA synthesis is in fact inhibited during mitosis (MITCHISON 1971).

Our results, such as illustrated in Figs. 3, 4, 5, show that the total RNA content of darkened cells decreases. The decay is relatively fast shortly after darkening and slows down gradually; after some 10 to 15% of the RNA amount originally present is degraded, the process comes to a halt. It has been shown by BARTOŠ and TETÍK (1975) that this decrease involves the stable forms of RNA (tRNA, rRNA) as well. Therefore, what we observe as a drop in the total RNA content may be due mainly to these RNA species.

We have not performed any experiments that would allow us to decide whether the degradation of the RNAs proceeds also during the growth of the cells in light and if so, what is its rate. Since, however, the extrapolated rate of RNA degradation, immediately upon darkening seems to be proportional to the rate of RNA synthesis in light, it is most probable that the same applies to the rate of RNA degradation in the light. If it is so, then the curves of RNA dynamics will not change substantially in shape if the observed net rates are corrected for the degradation rates.

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BOOK REVIEW

ARNOLD, L., LEFEVER, R. (ed.): STOCHASTIC NONLINEAR SYSTEMS IN PHYSICS, CHEMISTRY, AND BIOLOGY. Proc. Workshop, Bielefeld, Oct. 1980. — Springer Verlag, Berlin—Heidelberg—New York 1981. 237 pp., 48 figs. Cloth DM 62,—, approx. US $ 29.60.

The book contains twenty one invited papers presented at the interdisciplinary workshop held at the University of Bielefeld. The main aim of this meeting was, to bring physicists, chemists and biologists together with mathematicians who are interested in the theory of stochastic processes. The contributions are grouped in nine parts as follows: 1) From Deterministic to Stochastic Behavior; 2) Approximation of Stochastic Processes; 3) Description of Internal Fluctuations; 4) Long-Term Behavior of Stochastic Systems; 5) External Fluctuations and Noise Induced Transitions; 6) Stochastic Behavior in Model Systems; 7) Space-time Processes and Stochastic Partial Differential Equations; 8) Phase Transitions and Irreversible Thermodynamics; 9) Markov Processes and Time Reversibility.

The papers can be divided into two groups. The first contains four mathematically oriented survey lectures. The problems solved in them are: approximation of discontinuous processes by continuous, asymptotic behavior of several dimension diffusion, qualitative theory of ordinary stochastic differential equation and theory of stochastic partial differential equations.

The first paper shows on some examples a natural approach to approximation theorems for the process given by stochastic differential equation as well as for the process specified by its generator. The other two papers survey the results in the given theory and sketch some problems to be solved. The theory of stochastic partial differential equations is summarized and applied on models of chemical reactions in the last paper.

The second group is less homogeneous as the contributions are oriented to specific topics of research. Those devoted to biological questions are directed to population genetics and neuronal behavior. The theory of noise induced transitions is applied to the model of genic selection and the Hodgkin-Huxley model for sodium and potassium activation in nerve membrane. How to simulate a set of continuous stochastic processes describing phenomena studied in population genetics is suggested in paper concerning the application of Ito's stochastic integrals. The application of Poisson processes in biology is reviewed on the models of population growth and namely on the Stein's model of spontaneous neuronal activity.

The book presents a progress in application of modern mathematical theory in both the traditional and non-traditional fields, but relatively deep knowledge of this mathematical theory is necessary to understand it.

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