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Combination of the Mutation Process with the Sensitization and Repair Processes Leading to Increased Frequencies of Mutations in Algal Populations

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Abstract. The possibility of using a combination of the mutation process with the induction of the repair processes has been studied to increase the mutation frequencies in algal populations after UV-treatment. From this study it follows that the repair process induced by visible light is much more effective than the dark repair processes in the chlorococcal algae used. In these algae, visible light perhaps does not induce only those repair processes which affect their DNA, but probably also some recovery ones which affect their damaged structures and physiological functions. A suitable combination of the sensitization of algal cells by a DNA-base analogue before UV-treatment and the induction of the light repair and recovery processes resulted in a rather high increase of viable mutations in chlorococcal algae. These findings may be useful in the breeding of chlorococcal algae, which have no possibility of hybridization (except somatic).

The increased occurrence of various heritable changes in the characteristics of chlorococcal algae makes it possible to select new types of them to suit well the solution of numerous theoretical and practical problems, *e.g.* mass cultivation for the production of algal biomass or its components. In the populations of chlorococcal algae as in our strain *Scenedesmus quadricauda*, very unfavourable relations occur between the cells which are inactivated or permanently changed after mutagen treatment (NEČAS 1974, 1975, 1976a, LI *et al.* 1967, *et al.*). We, therefore, proposed to induce the repair mechanisms into the affected cells to save them from a lethal or sublethal state (NEČAS 1974, 1976a, 1976b). Part of the cells may be mutationally changed, another part may mutate due to an erroneous repair of the damaged DNA (*e.g.* error-prone repair). The existence of the error-prone repair was already proved in some organisms (*e.g.* WITKIN 1975). However, it is unknown so far in the chlorococcal algae we used.

For the repair and recovery of the algal cells damaged by UV-light, the repair induced by visible light proved itself to be most effective (TAUBE 1970, HALLDAL and TAUBE 1972, NEČAS 1974, 1976a, 1976b). We assumed in some previous papers that some parameters considered as indicators of the genetic damages are also the indicators of the physiological damages in algal cells

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(NEČAS 1974, 1975, 1976a). It seems that the repair processes induced by visible light do not act upon the damages of DNA only; probably some recoveries of the structural and functional damages are also put into action.

A detailed analysis of the mutation process and the repair process in chlorococcal algae will demand much more effort than they have been given up to now. We hope that this paper and the previous ones prove sufficiently the suitability of combining the sensitization and induction of the repair processes with UV-mutagenesis. In this way, the frequencies of the viable mutations increase significantly in the algal populations treated by UV-light.

Material and Methods

Three strains of chlorococcal algae were compared: *Chlorella kessleri* strain LARG-1, *Scenedesmus quadricauda* strain GREIFSWALD/15 and *Scenedesmus obliquus* strain LHOTSKÝ 1966/7. All these strains are kept in our algal collection in a bacteria-free state. They are reinoculated regularly so as to keep them in good physiological condition for the experiments.

Before the beginning of the experiments, the cells were adapted for four to five cell cycles in a liquid medium to the conditions under which the experiments were run: irradiation at 20 $W.m^{-2}$ PhAR, temperature at 28 to 30 °C, minimum medium according to NEČAS (1971). The adapted culture was diluted to 10^5 cells per 1 ml of the medium. The diluted cultures grew in two vessels (one for the control and one for the sensitization by 5-BdU) in a water bath. Bacterial contamination was prevented by a cotton stopper, which enabled the flow of CO_2 into the vessels. 5-BdU was added to the culture intended for sensitization in such a quantity as to reach the resulting concentration of 100 $\mu g\ ml^{-1}$. Both cultures grew further for approximately one cell cycle (24 h) under the same conditions. After that the sensitized culture was separated, washed once with distilled water and resuspended in the same fresh medium. Half of each culture (the control and the sensitized one) were irradiated in a 1 mm thick layer by UV-light of a low pressure mercury lamp at a dose of 38 Ws (3.16 W m^{-2} for two minutes from a height of 45 cm). In such a way, we obtained four parts of the original cell population differing in the above mentioned treatment: control, addition of 5-BdU, UV-light irradiation, 5-BdU and UV-light. All the treatments of the same cell population were inoculated in Petri dishes on an agar medium (6 on a minimum one and 6 on a complete one — NEČAS 1971) in a very dim light. All the inoculated dishes were left in darkness. Three dishes on the minimum medium were transferred to light after 6 h and three dishes with the same medium after 24 h. Three dishes with the complete medium were transferred to light after 24 h and three dishes with the same medium were left permanently in darkness. This arrangement of the experiment proved satisfactory in previous experiments (NEČAS 1974, 1976a, 1976b). The algae on an agar medium grew in a cultivation shelf with several floors under regulated conditions (temperature 30 °C, irradiance 15 W m^{-2} PhAR).

The following parameters were recorded in the course of the experiments: frequency of the cells that divided into the lowest number of autospores in the first cell cycle after treatment, length of the lag phase (according to the

Abbreviations used: DNA = deoxyribonucleic acid; 5-BdU = 5-bromodeoxyuridine; UV = = ultraviolet light; PhAR = photosynthetically active radiation.

frequency of the non-dividing cells after 72 h), frequency of the non-survivals after 7 days, frequency of the permanent changes visible on the growing cell colonies (delayed death, morphological changes, pigmentation changes). All these parameters are given in the figures. Each of the values given is the average of three replicate determinations; the range of variability is shown by the bars when the whole population was not uniformly affected. Several more detailed descriptions of the recorded parameters are contained in previous papers (NEČAS 1974, 1975, 1976a, especially 1977).

Results

Decreased Number of Autospores in the First Cell Cycle after Treatment

Numerous mutagens, if applied at higher doses, inhibit the course of the nuclear cycles in the treated cells. Their lower number in the course of the cell cycle after treatment results in a decreased number of autospores. As was shown in some earlier papers (NEČAS 1969, ŠETLÍK *et al.* 1972, SULEK 1972, 1975), the physiological state of the cells in the cycle before treatment decides on the value of this parameter. Therefore, the interaction of a mutagen including all the factors that determine the course of the nuclear cycle is a very complex one. It is impossible to achieve a clear and convincing pattern in a non-synchronized population.

The effect of the sensitization of cells manifested itself more convincingly only in *Chlorella* (Fig. 1 — A 1 and D 1). Even in the preceding study (NEČAS 1976b), the dependence of this parameter on the concentration of 5-BdU in a precultivation medium before UV-treatment was little pronounced. The narrow range of the values of the replicate determinations in the whole experiment proved the accuracy of the results presented. The repair and recovery processes did not influence this parameter significantly (Fig. 1 — A×B, C×D). The sensitive regulation of the course of nuclear cycles in combination of the sensitization of the cells by 5-BdU before UV-treatment with the induction of the repair and recovery processes by visible light after UV-treatment did not seem to be satisfactory. It cannot be compared with the sensitivity of its regulation by light intensity (NEČAS 1969, ŠETLÍK *et al.* 1972).

Length of the Lag Phase

The prolongation of the lag phase is also a usual response of algal cells to higher doses of mutagens. All the three algal strains displayed a rather high sensitivity expressed by sensitization effect of 5-BdU in this parameter (Fig. 2). Especially the lag phase of the cells on the minimum medium was pronouncedly prolonged (Fig. 2 — A, B). In the paper (NEČAS 1976b), the dependence of this prolongation on the 5-BdU concentration in a precultivation medium is not so marked. The repair and recovery mechanisms (KUZIN 1975) did not suffice to compensate the prolongation of the lag phase caused by the sensitizer (obviously only those mechanisms which were induced by visible light), neither did the transfer of dishes for the first time to light (Fig. 2 A). In the sensitized cells not only the strain differences but also those between the groups of the dishes with both types of the medium were obliterated to a certain degree. It seems that it would be rather difficult to regulate sensitively enough the response manifested by the length

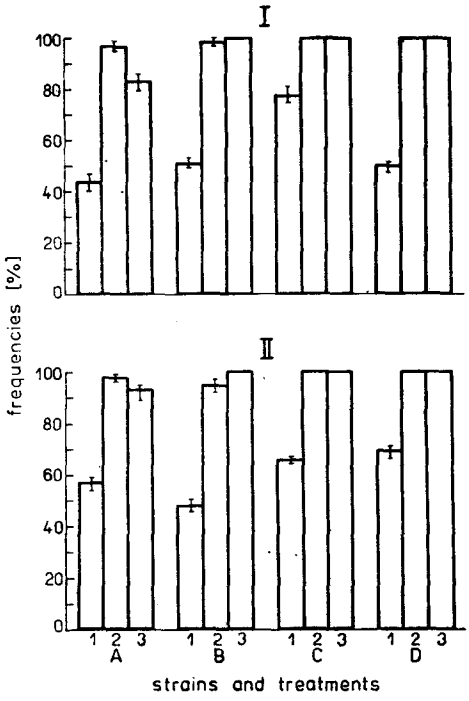

Fig. 1

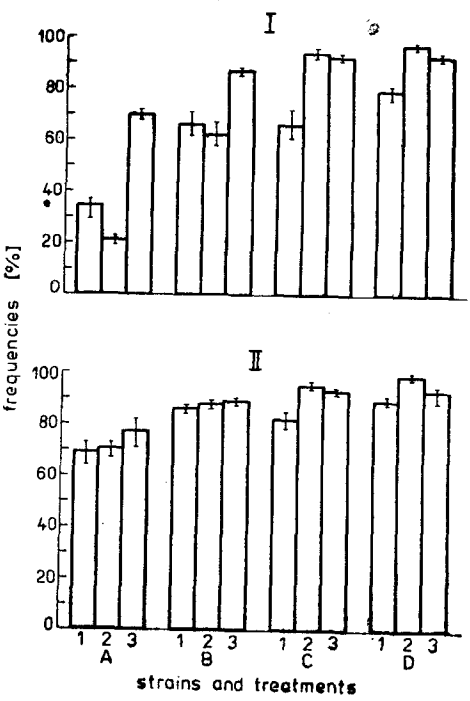

Fig. 2

Fig. 1. Frequencies of the cells that divided into four autospores during the first cell division after treatment. Explanations valid for all Figs. I = irradiation by UV-light without sensitization. — II = irradiation by UV-light after 5-BdU-sensitization. — A = 6 h of darkness after treatment (minimum medium). — B = 24 h of darkness after treatment (minimum medium). — C = 24 h of darkness after treatment (complete medium). — D = in permanent darkness after treatment (complete medium). — 1 = *Chlorella kessleri* strain LARG-1. — 2 = *Scenedesmus quadricauda* strain GREIFSWALD/15. — 3 = *Scenedesmus obliquus* strain LHOTSKÝ 1966/7.

Fig. 2. Length of the lag phase expressed as the frequencies of the cells that did not divide before 72 h.

of the lag phase of algal cells to the UV-treatment by sensitization and the induction of the repair and recovery processes by means of visible light.

Survival

This parameter revealed very sensitively the response of the algal cells to UV-treatment especially after sensitization. This response differed significantly in the algal strains (Fig. 3). The most sensitive response to UV-light in either the non-sensitized or the sensitized state was recorded in *Scenedesmus obliquus*. The greatest difference between the sensitized and non-sensitized cells in response to UV-irradiation was noted in *Scenedesmus quadricauda* on a minimum agar medium. In *Chlorella*, the complete medium seemed to be a saving factor. Part A in Fig. 3 proves convincingly that the repair and recovery mechanisms induced by visible light may save a fairly large part of the population (of either sensitized or non-sensitized cells). Part B in Fig. 3 proves, similarly to the corresponding results in previous papers (NEČAS 1974, 1976a, 1976b), that a certain part of the cell population may be saved from

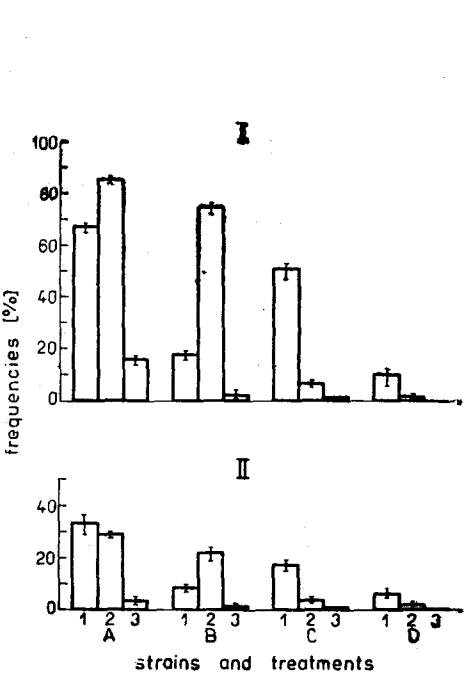

Fig. 3

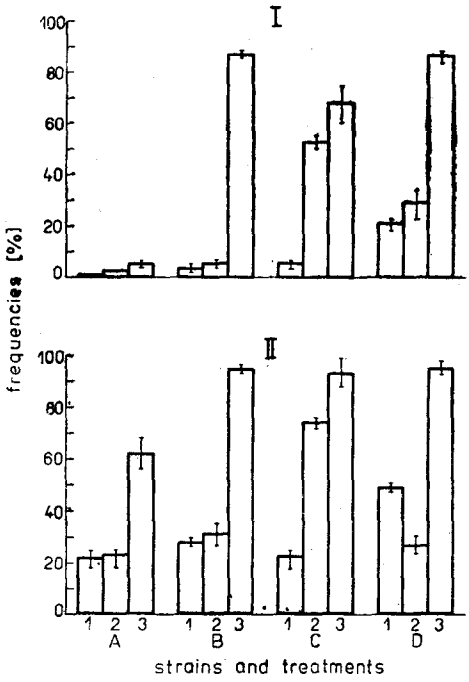

Fig. 4

Fig. 3. Frequencies of the surviving cells (at least one cell division after 7 d).
Fig. 4. Frequencies of the cells that divided only once after the treatment, whereas all the produced autospores died.

death caused by UV-irradiation, if the repair and recovery processes are induced by visible light, even after 24 h of darkness following treatment. This was shown very clearly in *Scenedesmus quadricauda* on a minimum medium (Fig. 3 — B 2). Lethal damages are very high in algae and blue-green algae after UV-treatment in comparison with the frequencies of the viable mutations (*e.g.* BAALEN VAN 1968, BAALEN VAN and O'DONNELL 1972, KEMP and WENTWORTH 1971, KEMP and MALLOY 1975). The dark repair and recovery systems are obviously only little effective or are absent altogether in the algae under study (compare part D in Fig. 3 with the other three parts). This is in agreement with some other authors (*e.g.* KEMP 1972, KEMP *et al.* 1972, KEMP and MALLOY 1973). The dark repair system in *Chlamydomonas reinhardtii* was described by DAVIES (1967a, 1967b) and DAVIES and LEVIN (1968).

Lethal Effect Delayed by One Cell Cycle

In this parameter, it was possible to see the distinct differences between the treatments (A, B, C, D) as well as between the strains (1, 2, 3) in Fig. 4. This is in agreement with the clear dependence of this parameter on the 5-BdU concentration in the precultivation medium before UV-treatment (NEČAS 1976b). A higher sensitivity of *Scenedesmus obliquus* to UV-light in both the sensitized and non-sensitized state was again proved. Part A in

Fig. 4 would prove the efficiency of the repair and recovery systems very convincingly, if one could consider the decreased values of this parameter as an unambiguous manifestation. It is impossible to exclude the fact that part of them may result from an incomplete repair and recovery of the lethal state. The great difference between parts B and C in Fig. 4 concerning *Scenedesmus quadricauda* may be explained in two ways. Either the repair and recovery effects are much greater on a minimum medium or the lethal effect is delayed by one cell cycle in a great number of cells that would die without division on a minimum medium. To what extent some minimal repair and recovery may enable the cells to survive still by one cell cycle including the cell division is very difficult to decide. The difference between parts C and D in Fig. 4 has to be taken into consideration, if this suggestion is to be judged.

If all the parts of the experiment are compared, this parameter also shows that there is a good possibility of shifting the whole cell population towards a higher survival percentage when the sensitization of the cells before the UV-treatment and the following induction of the repair and recovery systems are suitably combined. Then, some cells which would not survive had their death delayed by one cell cycle or some less damaged or more repaired and recovered cells would survive and produce viable progenies.

Lethal Effect Delayed by Two Cell Cycles

The frequencies of these cases are much lower in the populations of the three algal strains if we compare them with the preceding parameter and they correspond to the frequencies of two types of recorded permanent changes visible on cell colonies; therefore they are included in Fig. 5. Here, too, the sensitization effect manifests itself quite distinctly. The effect of the repair and recovery systems induced by visible light was revealed most pronouncedly in the sensitized and non-sensitized cells of *Scenedesmus obliquus* (compare parts A 2 and B 2 in Fig. 5). The values of this parameter were higher on a complete medium in all the three strains of algae.

Even here, the effect of the repair and recovery systems could manifest itself in either a decrease or an increase of the values recorded. This is the same as in the preceding parameter. An insufficient repair and recovery of the lethal state, or the cells the death of which was delayed even by one cell cycle, may result in an increase of the cells whose death of whole progenies was delayed by two cell cycles. Their sufficient repair and recovery leads to a decrease of the values in this parameter.

The possible causes of the occurrence of the lethal states and the cells whose death was delayed by one or two cell cycles were analyzed in a previous paper (NEČAS 1977).

Pigmentation Changes

This type of permanent change is relatively the most uniform and suits well the conclusions on the combination of the sensitization, mutation and repair processes. The effect of sensitization follows from the comparison of the results obtained in the sensitized and non-sensitized parts of the same original population (Fig. 5 — I×II). A favourable effect of the combination of the mutation, repair and recovery processes is clearly shown in parts A and B in Fig. 5., above all in *Scenedesmus obliquus* (3). The comparison of the results obtained in the three strains points to the necessity of preparing the

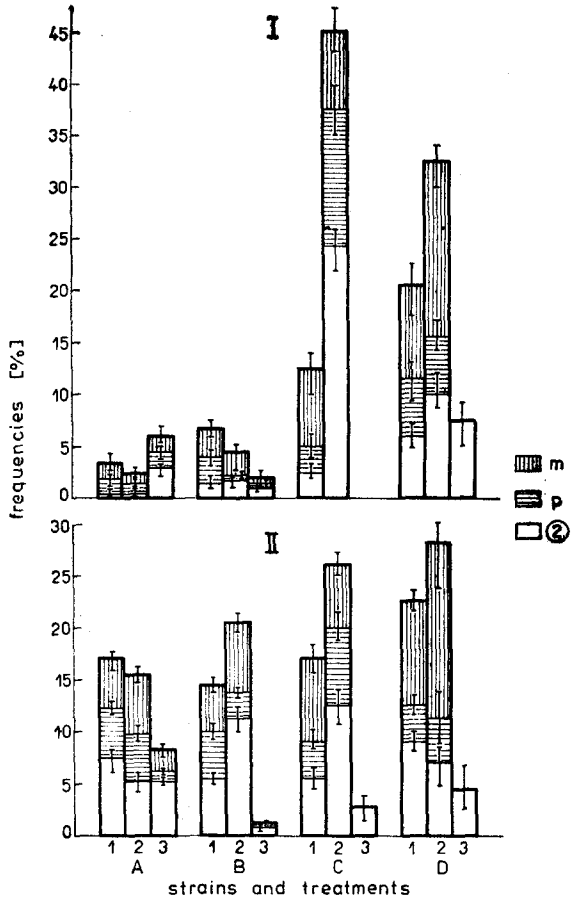

Fig. 5. Frequencies of the cells, the grown cell colonies of which displayed the permanent changes recorded.
2 = all the autospore progenies died after the completion of the second cell cycle.
p = permanent pigmentation changes.
m = permanent morphological changes visible on the growing cell colonies.

cell population into a suitable physiological state. This may be different for different strains. Mutations in the sensitivity to UV-light are also known in algae and in blue-green algae (DAVIES 1967b, ROSEN and EBERSOLD 1972, ZHEVNER and SHESTAKOV 1972). Probably, the synchronous populations affected in a most sensitive state would be the most suitable material for the mutation experiments. However, the synchronization of algal cultures for genetical purposes is rather a difficult way of their preparation. This is documented by the fact that studies of this kind are very rare so far. The analysis of the causes of such difficulties was carried out by SULEK (1972, 1975) for *Scenedesmus quadricauda.*

Permanent Changes Visible on the Shape of Algal Cell Colonies

The types included in the group of permanent changes of this kind and the possible causes of their occurrence were described in a previous paper (NEČAS 1977). Even this parameter shows clearly the sensitization effect of 5-BdU, especially in the parts of the original population inoculated on a minimum medium (Fig. 5 — A, B). The most suitable combination of the mutation process and the repair and recovery processes induced by visible light may be seen in *Scenedesmus quadricauda.* The recorded frequencies of this type of

change (Fig. 5) prove the conclusion made already in the pigmentation changes. However, neither sensitization nor the effect of the repair and recovery systems were convincing enough in the parts of the treated population inoculated on a complete medium.

Discussion

I have already pointed out the possibility of increasing the frequencies of viable mutations in the algal population treated by a mutagen if the mutation process and the induced repair and recovery processes are suitably combined (NEČAS 1974, 1976a, 1976b). The same was mentioned earlier by some other authors (GIESE 1968, BRIDGES and MUNSON 1969, WITKIN 1969, 1975, and others).

A new cultivation equipment constructed in our laboratory (NEČAS unpubl.) sensitively regulated for algae that were inoculated on the surface of a solidified medium enabled us to restrict the variability of the results obtained in the replications of the experiments. The differences between the treatments in an experiment became significant in a greater number of cases and the expressed conclusions, therefore, became still more convincing.

The physiological parameters and all the others recorded in this work again show the advantage of recording all the effects determinable in the cells after treatment by UV-light (see also KUZIN 1975); especially, if some permanent changes visible on algal cell colonies are difficult to prove as mutation changes in all cases (NEČAS 1977). It seems that even the repair effects induced in the cells by visible light do not include only the repair of a genetic information in the molecules of DNA. However, it is necessary to consider quite different mechanisms which are little known so far but differ from those repairing DNA. In many cases, the repair and recovery make it possible to save the cells with induced mutations. This proves also the existence of UV-sensitive types defective in the repair and recovery of the damages caused by UV-light which have lately been described in many organisms (*e.g.* FABRE 1971, PARKER and HORSLEY 1972, GUIALIS and DEERING 1976).

Recently, the error-prone repair was described as one of the causes of the occurrence of mutations resulting from the erroneous repair of DNA that was damaged in an induced mutation process (WITKIN 1975). Neither this nor the previous papers allow such a precise analysis, which would be necessary if we wanted to describe all the processes in detail. However, it is possible to state that the repair and recovery processes induced by visible light are more effective than the dark-repair processes in the chlorococcal algae studied. The existence of the dark-repair could not be proved in these algae either in present paper or in several previous ones.

To achieve an optimal ratio of the surviving cells and viable mutations in a population of algae, we must find a suitable relation among the combined processes of sensitization, mutation and repair. This certainly will be different in different algal species or strains. Even in the cell population of the same species, the degree of synchrony and the distribution of the physiological state of the cells may be decisive (NEČAS 1976b). On considering only the above mentioned factors, we are convinced of the difficulties connected with such a task. Optimum conditions are required for all the succeeding processes in the prevailing part of the given algal cell population.

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BOOK REVIEW

TRIBE, M. A., ERAUT, M. R., SNOOK, R. K.: **Photosynthesis.** Basic Biology Course. Unit 3: Regulation Within Cells. Book 6. — Cambridge University Press, Cambridge, London, New York, Melbourne 1975. 77 S. £ 2.40. Filmstreifen £ 3.50, Cassette £ 3.80 (für Buch 6 und 8 zusammen).

In der Reihe der biologischen Lehrbücher, die vom „Inter University Biology Teaching" project team an der Universität Sussex herausgegeben werden und die in erster Linie zum Selbststudium bestimmt sind, kann natürlich ein Buch über die Photosynthese, diesen so wichtigen Vorgang auf der Erde, nicht fehlen.

Das Lehrbuch wurde als Frage- und Antwort-Programm ausgearbeitet, dass den Studenten zur ununterbrochenen aktiven Mitarbeit am Lehrprozess zwingt. Die einzelnen Fragen und Antworten sind durch verschiedene Typen von Strichen abgetrennt und nach jeder Frage folgt sofort die richtige Antwort. Der Student ist mit einer Deck- oder Maskierungskarte (am Ende des Buches im Anhang zu finden) ausgestattet und soll beim Studium folgendermassen vorgehen: die Frage lesen, die Antwort mit der Deckarte zudecken, die Frage in einem Heft schriftlich beantworten und die Antwort mit der richtigen Beantwortung im Text vergleichen. Bei Übereinstimmen, d.h. richtig beantworteter Frage kann im Text weiter fortgeschritten werden, bei falscher Antwort soll die Passage nochmals durchgelesen werden und die Beantwortung der Frage schriftlich wiederholt werden.

Im ersten Teil des Buches werden die Energiegewinnung in den Chloroplasten der Pflanzen aus Sonnenlicht und die Transformierung in chemische Energie, also die Grundvorgänge der Photosynthese, einleitend erläutert, der Unterschied zwischen autotrophen und heterotrophen Organismen, die Aufgabe des Chlorophylls, die Begriffe Absorptionsspektrum und Redoxpotential erklärt. Es folgt ein Abschnitt über die Hillreaktion. Dieser Vorgang wird an Hand von 16 Buntdiapositiven und des auf einer Tonbandcassette festgehaltenen Kommentars (in englischer Sprache) durchgearbeitet. Der Filmstreifen und die Cassette werden vom Cambridge University Press auf Wunsch mitgeliefert und es wird dann natürlich vorausgesetzt, dass der Student mit einem Diabetrachter oder Diaprojektor und einem Cassettentonbandgerät ausgerüstet ist. Die Passage von der Chloroplastenisolierung bis Messung der Sauerstoffproduktion wird von Zeit zu Zeit unterbrochen und der Student muss 23 Kontrollfragen, die im Text des Lehrbuches stehen, beantworten. Der nächste Abschnitt des Lehrkurses behandelt die Umwandlung der Lichtenergie in chemische Energie, die zwei Photosysteme der Photosynthese. Weiter folgt ein Teil über die lichtabhängigen und nichtlichtabhängigen Reaktionen der Photosynthese, über die Kohlenstoffdioxid-Reduktion mittels NADPH und ATP, also die Sekundärvorgänge der Photosynthese. Die „Struktur der Chloroplasten mit Rücksicht auf deren Funktion" macht den Studenten mir der räumlichen Situierung der photosynthetischen Einheit bekannt. Zuletzt behandelt ein Abschnitt noch die Energiegewinnung und -speicherung in tierischen Zellen oder Pflanzenzellen ohne Chlorophyll. In der Form eines Anhanges enthält das Lehrbuch Erklärungen zu einigen speziellen Fragen, einen Komplex von Kontrollfragen zum behandelten Thema, ein Fachwörterbuch, empfohlene Literatur und die Deckarte. Es ist reich illustriert (Schemata, Abbildungen, Photographien) und tadellos gedruckt.

Abschliessend möchte ich sagen, das dieses Lehrbuch bestimmt sehr zu begrüssen ist und dass hier eine Art und Weise gefunden wurde auch im Selbststudium den komplizierten Vorgang der Photosynthese darzulegen, verständlich zu machen. Ich habe aber den Eindruck, dass hier die Photosynthese als Ganzes doch etwas zu sehr nur auf die Primärreaktionen und auf die Hillreaktion reduziert wurde und dass eine Erweiterung des Lehrbuches in Richtung anderer Messmethoden (z.B. CO_2-Aufnahme), CO_2-Transport, C3, C4 und CAM-Photosynthese, und überhaupt in Richtung Physiologie der Photosynthese zu empfehlen wäre. Als grossen Vorteil des Buches sehe ich die Verarbeitung des Textes auf Grund von "up to date" experimentellen Ergebnissen, sodass ein modernes Lehrbuch entstanden ist.

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