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REVERSIBLE UNCOUPLING OF ENERGY TRANSFER BETWEEN PHYCOBILINS AND CHLOROPHYLL IN *ANACYSTIS NIDULANS*

LIGHT STIMULATION OF COLD-INDUCED PHYCOBILISOME DETACHMENT

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Summary

Phycobilin fluorescence of *Anacystis nidulans* grown at 28°C increases substantially upon cooling below 10°C. A maximal increase is found around —5°C and amounts to 300%, with almost complete reversibility upon re-warming. Illumination with actinic light leads to considerable stimulation of the cold-induced phycobilin fluorescence increase. Analysis of the light stimulation phenomenon reveals: (1) Actinic illumination shifts the fluorescence-temperature characteristic by about 3°C upwards on the *T*-axis. At temperatures below 5°C the light stimulating effect becomes smaller again and fluorescence-temperature characteristics measured at high and low light intensity converge around —5°C. (2) In the 13—8°C region a large (up to 100%) light-induced phycobilin fluorescence increase is observed, while only negligible changes occur in the dark. (3) 3-(3,4-Dichlorophenyl)-1,1-dimethyl urea (DCMU) as well as uncouplers inhibit the light stimulation, which hence depends on coupled electron transport.

In agreement with previous work (Schreiber, U. (1979) FEBS Lett. 107, 4—9) it is concluded that illumination enhances cold-induced phycobilisome detachment by increasing the net negative charge at the outer surface of the thylakoid membrane. The possible role of a fluid → ordered transition of membrane lipids (Murata, N. and Fork, D.C. (1975) Plant Physiol. 56, 791—796) is discussed.

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Abbreviations: DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethyl urea; Chl *a*, chlorophyll *a*; Chl *b*, chlorophyll *b*; CCCP, carbonyl cyanide 3-chlorophenylhydrazone.

Introduction

Photosynthesis in blue-green algae is very similar to that in green plants as far as the principal mechanisms are concerned (see e.g. review by Krogmann [1]). Important differences between blue-green algae and green plants are found, however, in the organization of the photosynthetic apparatus. In blue-green algae the photosynthetic membranes are not organized within an organelle and the main light-harvesting pigment complex contains phycobiliproteins instead of Chl *b*. The phycobilisomes are not integrated within the thylakoid membrane as the chlorophyll *b*-protein complex in green plants, but rather loosely attached to the membrane surface [2]. Under normal, physiological conditions energy transfer between the phycobilisomes and Chl *a* is very efficient [3,4]. This energy transfer is, however, severely disturbed by hydrostatic pressure [5] and at temperatures below 10°C [6—8]. Thus it is possible to manipulate the degree of phycobilisome attachment to the pigment-protein complexes situated within the thylakoid membrane. The phycobilin fluorescence yield can serve as a convenient, intrinsic indicator for the efficiency of energy transfer towards Chl *a*.

The present study deals with the discovery that the cold-induced uncoupling of energy transfer between phycobilins and Chl *a* is considerably stimulated by light. An analysis of this light stimulation suggests that the formation of a transthylakoid proton gradient, coupled to photosynthetic electron transport, is required for the effect. In agreement with recent results on ionic factors effecting the cold-induced phycobilisome detachment [8] it is proposed that the light-induced proton translocation from the outside to the inside of the thylakoids leads to an increase of the membrane surface charge, which favors detachment. The analogy between light-induced, cation-related Chl *a* fluorescence changes and the newly discovered light-induced phycobilin fluorescence changes is discussed.

Materials and Methods

Anacystis nidulans was grown at 28°C in the C medium of Kratz and Myers [9], supplemented with 0.85 g $NaHCO_3$ per liter. The algae were supplied with air enriched with 5% CO_2, and continuously illuminated with daylight fluorescent light (about 0.5 mW/cm^2). If not stated otherwise the experiments were carried out with samples which were dark-adapted for at least 2 h in the aerated culture tube. Samples were transferred in the dark from the culture tube into the measuring cuvette about 5 min before start of a measurement. The algae culture was daily diluted with fresh medium to keep a Chl *a* concentration of approx. 8 μg/ml, as determined by the method of Arnon [10,11]. The 627/678 nm absorbance ratio, which is characteristic for the relative content of phycobilin pigments and chlorophyll [12], corrected for scattering, was 1.7.

Cold-induced fluorescence changes were measured in a system which allowed rapid cooling (e.g. from 25 to 5°C within 2 s) or slow cooling (at about 0.7 K/min) as described previously [8]. Sample thickness was 0.5 mm, giving 0.4 μg/cm^2 of chlorophyll per area exposed to the measuring beam. Samples did not

freeze even at the lowest temperatures applied in this study. Phycobilin fluorescence was excited with 560 nm light selected either with a monochromator (2 nm half-bandwidth) or with an interference filter (Balzer B-40, 8 nm half-bandwidth). Corning CS 4-96 filters were added to remove stray red light in the excitation light. Phycobilin fluorescence was measured around 640 nm, with a Balzer B-40 interference filter, half-bandwidth 11 nm, a Schott AL 640 interference filter, half-bandwidth 20 nm and a Schott RG 630 cut-off filter in front of the photomultiplier. The measurements at very low excitation light intensity ($I = 0.1$ to $I = 1$, corresponding to 0.1 to 1 $\mu W/cm^2$) were carried out with a 2500 Hz chopped measuring beam. By use of a frequency and phase sensitive lock-in implifier (Brookdeal Electronics, Type 411) only the modulated signal was detected.

Results and Interpretation

Cold-induced partial detachment of phycobilisomes

Fig. 1 depicts the main features of the cold-induced increase of phycobilin fluorescence in *Anacystis*. Cooling is performed in two different ways: (a) Rapidly within about 2 s, yielding a temperature-jump fluorescence induction curve (*T*-jump curve); (b) slowly by about 0.7 K/min, giving a fluorescence-temperature curve. Fluorescence is excited with low intensity 560 nm light which is almost exclusively absorbed by the phycobilins, and which is weak enough as not to cause a Chl *a* fluorescence induction phenomenon. Fluorescence is measured at 640 nm, although the phycobilin emission peak is at 655 nm, to minimize spurious contribution of Chl *a* fluorescence. Upon rapid cooling from 25°C to −5°C an almost 3-fold increase of fluorescence is induced. This increase is reversed when the sample is rapidly re-warmed to 25°C. These fluorescence changes are much slower than the time required for the change of temperature which is about 2 s. Thus they represent with good approximation the time course of the structural changes within the pigment

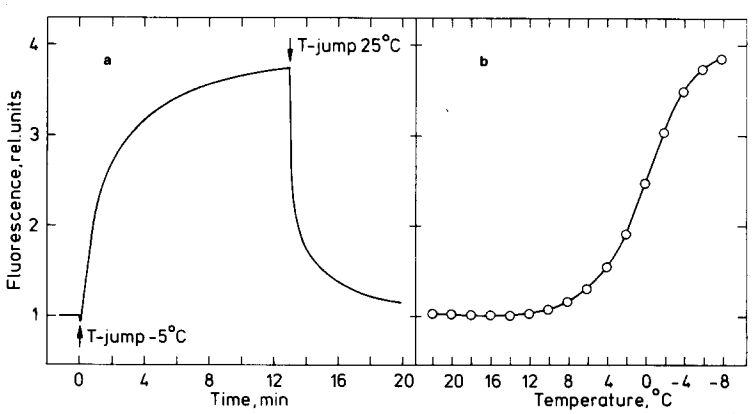

Fig. 1. Temperature-dependent changes of phycobilin fluorescence around 640 nm. Excitation, 560 nm (1 $\mu W/cm^2$). (a) Fluorescence changes induced by rapid cooling or rapid re-warming. 95% of the 30°C temperature jump occurred in 2 s. (b) Fluorescence increase induced by slow cooling at about 0.7 K/min. One relative ordinate unit is equivalent to the fluorescence at 25°C of a dark-adapted sample, which is not affected by the weak excitation beam.

system induced by a temperature change. The almost complete reversibility of the cold-induced changes suggests that cooling during 10 min does not lead to gross structural damage in *Anacystis* grown at 28°C. Upon slow cooling (Fig. 1b), the resulting fluorescence-temperature curve reveals that a major increase of phycobilin fluorescence only occurs at temperatures below 10°C. Phycobilin fluorescence yield is most sensitive to temperature changes in the +2 to −2°C region.

On the basis of a low-temperature spectrofluorimetric study, we have concluded [7] that the cold-induced increase of phycocyanin fluorescence correlates with a partial uncoupling of energy transfer between the phycobilins and Chl *a*. This change leads to a 'functional detachment' of the phycobilisome from the chlorophyll pigment-protein complexes within the thylakoid membrane. Such detachment may result from some cold-induced change within the membrane by which the distance between the phycobilisomes and the chlorophyll-protein complexes is increased [8]. According to the Förster theory of resonance energy transfer [13], the efficiency of transfer decreases rapidly with the distance between pigment molecules.

Stimulation of cold-induced detachment by light

In the experiment of Fig. 1 the cold-induced increase of phycobilin fluorescence was monitored with a weak measuring beam, with negligible actinic effectiveness. Fig. 2 shows that superposition of an actinic background light causes substantial stimulation of phycobilin fluorescence if applied at low temperature, while almost no stimulation is found at room temperature. In this experiment a weak, modulated measuring beam is used, while a 100 times stronger, continuous background light is applied. Only the modulated fluorescence excited by the weak beam is recorded. The fluorescence increase induced by the background light consists in a small rapid step followed by a much slower and larger sigmoidal rise. When the background light is switched

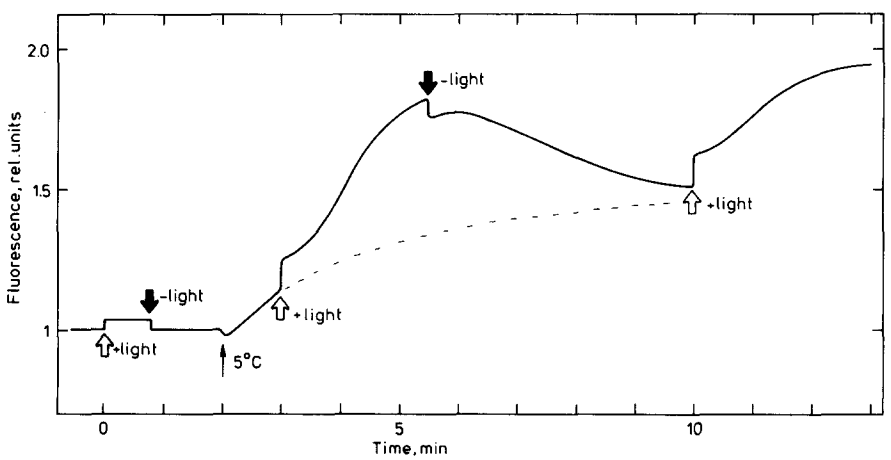

Fig. 2. Stimulation of cold-induced phycobilin fluorescence increase by actinic illumination. Only fluorescence excited by modulated measuring beam (560 nm; 5 $\mu W/cm^2$) is recorded. Where indicated by arrows, continuous light (560 nm; 500 $\mu W/cm^2$) is switched on and off, and the sample is rapidly cooled from 25 to 5°C. The dotted line represents the fluorescence increase in the dark.

off there is a small, rapid decay which after a lag-phase is followed by a slow decay, which leads to the same fluorescence level as observed without an actinic illumination in the *T*-jump curve. The second application of background light gives again stimulation of phycobilin fluorescence, essentially as before.

These data suggest that the cold-induced phycobilisome detachment is stimulated by actinic light. The same actinic light does not lead to any appreciable detachment at room temperature. The extra detachment occurring in the presence of actinic light is reversed slowly upon removal of this light. The slow kinetics of this reversal could be limited by the disappearance of some 'stimulating factor' produced in the light or by the rate of re-attachment at the given temperature. At room temperature any stimulating factor accumulated in strong light must disappear relatively rapidly: No stimulation of a *T*-jump fluorescence increase was observed with actinic preillumination ceasing approx. 2 s before a *T*-jump to 5°C (not shown).

Fig. 3 shows *T*-jump curves for rapid cooling from 25 to 5°C at different light intensities. Samples were preilluminated for 5 min before the *T*-jump curves were measured at the same, indicated light intensities. At measuring light intensities below 1 $\mu W/cm^2$ the cold-induced fluorescence increase is identical to the one occurring in the dark.

The relative extent of the light stimulation effect depends on the applied temperature. Fig. 4 compares fluorescence-temperature curves recorded at actinic and non-actinic measuring light intensities. There is only very weak light stimulation of phycobilin fluorescence at room temperature, as already

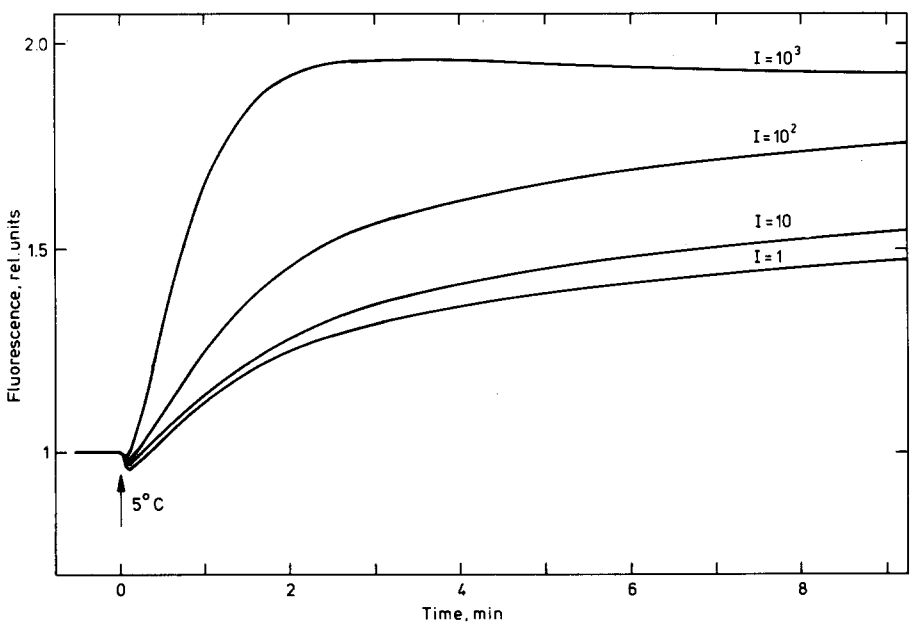

Fig. 3. Light intensity dependency of the cold-induced phycobilin fluorescence increase. Samples were illuminated for 5 min at the indicated light intensities (560 nm; $I = 1$ corresponding to 1 $\mu W/cm^2$) at 25°C before being rapidly cooled to 5°C. The curve for $I = 1$ was identical to a curve recorded at $I = 0.1$. One relative ordinate unit corresponds to the fluorescence yield at 25°C at the given light intensity.

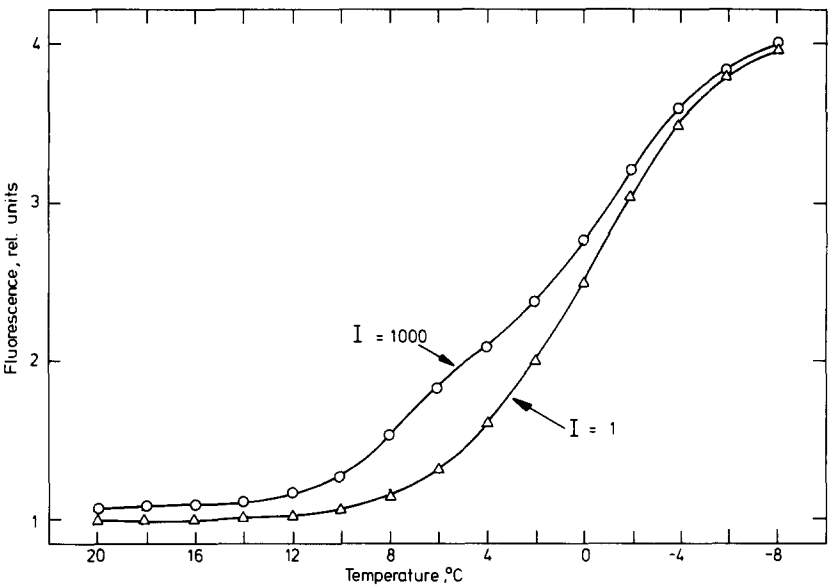

Fig. 4. Comparison of the fluorescence-temperature characteristics at actinic and non-actinic light intensities. Samples were illuminated for 10 min at 25°C before being slowly cooled at 0.7 K/min. Other conditions as in Fig. 3.

noticed in Fig. 2. Stimulation is largest between 10 and 0°C, and becomes minimal at −5°C. The same behaviour is apparent from a comparison of *T*-jump curves recorded at actinic and non-actinic light intensities in dependency of the applied temperature (not shown). At 10°C there is only a very small slow fluorescence rise at low light intensity, but already about 40% fluorescence rise at high light intensity. At 5°C the extent of the light-induced fluorescence yield increase is maximal, amounting to about 90% of the fluorescence yield in low light. At all temperatures the relative stimulation by light decreases with longer times. At −5°C the *T*-jump induction curves are very similar at high and low light intensity, except for the initial rate following the *T*-jump, which is distinctly higher in the high light sample. These data demonstrate that the simultaneous application of high intensity light and temperatures around 10°C produces a clear increase of phycobilin fluorescence, while only negligible effects are found with high intensity light at room temperature, or at 10°C with low intensity light. In this sense the effects of illumination and cooling around 10°C are synergistic in causing the uncoupling of energy transfer from the phycobilins to Chl *a*.

The phenomenon of light-induced phycobilin fluorescence changes

From the data presented so far it can be predicted, that with the appropriate choice of temperature, i.e. around 10°C, it should be possible to observe a relatively large light-induced phycobilin fluorescence induction phenomenon. In Fig. 5 light-induced phycobilin fluorescence changes are shown in dependence of temperature. Phenomenologically the induction kinetics bear a certain resemblance to Chl *a* fluorescence induction (Kautsky effect) [14—16]. There is a rapid, small spike at about 1 s after onset of illumination which

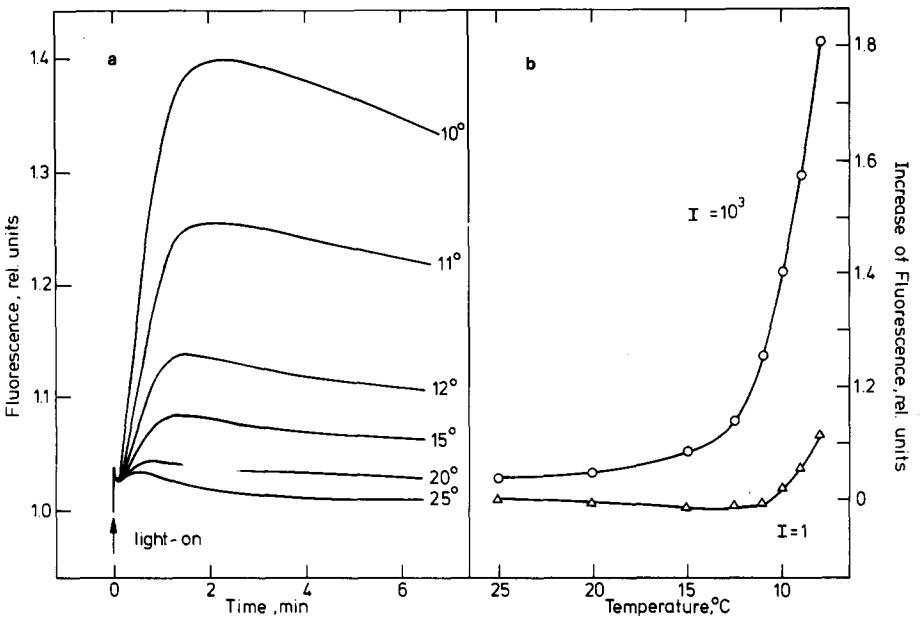

Fig. 5. (a) Light-induced phycobilin fluorescence induction kinetics in dependence of temperature. Samples were dark-adapted for at least 2 h at 28°C in the aerated culture tube before being transferred into the measuring cuvette and cooled to the indicated temperatures. After 2 min, light induction curves were recorded at the given temperatures. The curves are vertically shifted such that initial fluorescence yield values coincide (one relative ordinate unit at 25°C). For relative changes of initial fluorescence values, see Fig. 5b. The amplitude of the rapid, small spike is not identical for the different curves (not resolved in this figure) and, as presented here, represents primarily the 25°C and 20°C curves, $I = 10^3$. (b) Plot of phycobilin fluorescence increase versus temperature. In the $I = 10^3$ curve the amplitude of the main transient in the curves of Fig. 5a is plotted. The $I = 1$ curve represents the phycobilin fluorescence change induced during the 2 min the samples were kept at the indicated temperatures in the dark before light induction was measured. One relative ordinate unit corresponds to the phycobilin fluorescence yield of a dark-adapted sample at 25°C.

corresponds to the rapid Chl *a* fluorescence changes. More detailed analysis of this spike reveals a fine structure apparently identical to the O-I-D-P-S transients in Chl *a* fluorescence (not shown). The emission spectrum of this small, rapid transient represents true phycobilin fluorescence changes and not spurious Chl *a* fluorescence contribution (unpublished data). Most likely these small, rapid phycobilin fluorescence changes reflect the low efficiency reverse energy transfer from the Chl *a* pigment bed into the phycobilisome, as previously observed in DCMU-poisoned *Anacystis* by other investigators [17,18]. The dominant feature of the light-induced phycobilin fluorescence changes is a second, slower peak the amplitude of which is extremely sensitive to temperature. In Fig. 5b this peak amplitude is plotted versus temperature, showing a steep rise at temperatures below 13°C. For comparison Fig. 5b also shows on the same scale the corresponding changes of fluorescence yield at non-actinic light intensity, as measured 2 min after a *T*-jump from 25°C to the indicated temperature. In this case the 'critical temperature' for fluorescence stimulation is around 10°C.

Chemical inhibition of light-stimulated detachment

The light-induced phycobilin fluorescence changes observed at 10°C are inhibited by addition of electron transport inhibitors as well as by uncouplers. In Fig. 6 the effect of DCMU is demonstrated. In this experiment the cold-induced phycobilin fluorescence increase is recorded at high light intensity, where in the absence of additions substantial stimulation is observed. Half-maximal inhibition of light stimulation occurs at $5 \cdot 10^{-8}$ M DCMU. The inhibitor effect is saturated at $3 \cdot 10^{-6}$ M. At this concentration the cold-induced fluorescence rise becomes independent of light intensity. Addition of diaminodurene leads to restoration of light stimulation in the presence of DCMU. The cold-induced fluorescence increase recorded in the presence of diaminodurene + DCMU is almost identical to the control curve, except for a somewhat longer lag-phase at the beginning. At non-actinic light intensities neither DCMU nor diaminodurene had any effect on the cold-induced fluorescence increase.

In Fig. 7 the effect of uncouplers on the light-stimulated, cold-induced fluorescence rise is depicted. Methylamine, NH_4Cl and CCCP inhibit the light stimulation of the cold-induced fluorescence rise. Half-maximal inhibition of light stimulation is observed with about $4 \cdot 10^{-4}$ M methylamine. Interestingly there is even a distinct suppression below the level reached at non-actinic light intensities. And, contrary to the effect of DCMU, these uncouplers also affect the cold-induced fluorescence rise measured at low light intensity.

The data in Figs. 6 and 7 suggest that the light-induced increase of phycobilin fluorescence observed at low temperatures depends on coupled electron transport. Electron transport is inhibited by DCMU and partly restored when an artificial electron donor as diaminodurene is added. Presence of uncouplers prevents the light-driven formation of a transthylakoid proton gradient. Thus the 'stimulating factor' produced in the light could be the transthylakoid proton gradient or any state which is induced by the presence of such a gradient. The fact that uncoupers also affect the cold-induced fluorescence increase in the

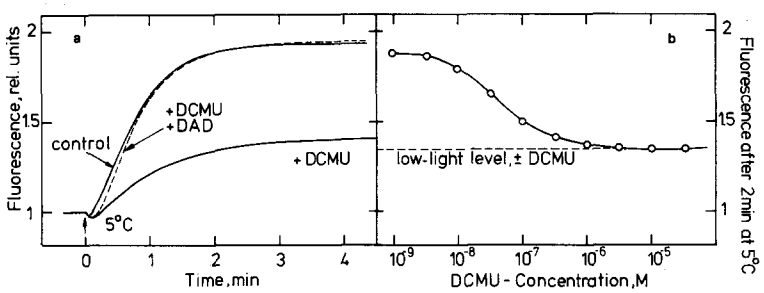

Fig. 6. (a) Increase of phycobilin fluorescence induced by rapid cooling from 25 to 5°C. Inhibition of light stimulation by DCMU and restoration by diaminodurene (DAD). Conditions as described for Fig. 3. Light intensity, $I = 10^3$ (corresponding to 1 mW/cm^2). The curve is the presence of DCMU alone is identical to a curve measured at $I = 1$ with or without DCMU present. DCMU concentration, 10^{-5} M. DAD concentration, $2 \cdot 10^{-4}$ M. The substances were added with minimal amounts of methanol, resulting in a methanol concentration of 0.3% in the sample for DCMU + DAD. (b) Plot of the phycobilin fluorescence yield reached 2 min after rapid cooling from 25 to 5°C at actinic light intensity ($I = 10^3$) in dependence of DCMU concentration. The fluorescence yield reached after 2 min with the same cold treatment at non-actinic light intensity ($I = 1$) is not affected by DCMU and indicated as 'low-light level',

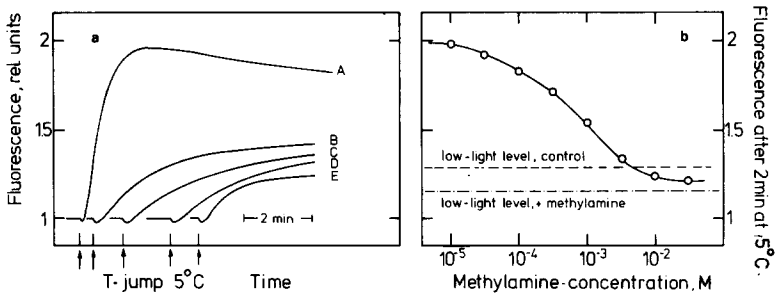

Fig. 7. (a) Inhibition of light stimulation by uncouplers. Conditions as described for Fig. 3. Where indicated by arrows samples were rapidly cooled from 25 to 5°C. Curve A, control at $I = 10^3$. Curve B, control at $I = 1$. Curve C, presence of 20 mM methylamine-HCl, $I = 10^3$. Curve D, presence of 20 mM NH_4Cl, $I = 10^3$. Curve E, presence of $2 \cdot 10^{-5}$ M CCCP, $I = 10^3$. (b) Plot of phycobilin fluorescence yield reached 2 min after rapid cooling from 25 to 5°C at actinic light intensity ($I = 10^3$) in dependence of methylamine-HCl concentration. The fluorescence yields reached after 2 min with the same cold treatment at non-actinic light intensity (I = 1) in the presence and absence of 20 mM methylamine-HCl are indicated by the 'low-light level' lines.

dark, seems to indicate that also in the dark there is some of this 'stimulating factor' present.

Discussion and Conclusions

The data presented in this study demonstrate that, contrary to the widespread opinion based on experiments at room temperature, the phycobilins can undergo relatively large light-induced fluorescence yield changes. Large light-induced phycobilin fluorescence changes are observed, if the algae are at temperatures around 10—8°C. At these temperatures light induces 50—100% phycobilin fluorescence changes which are comparable in size to corresponding Chl *a* fluorescence changes in *Anacystis* (see e.g. Refs. 15 and 16). Although phenomenologically the data in Figs. 2 and 5 clearly represent a light-induced phenomenon, an analysis of this phenomenon leads to the conclusion that it may be more appropriately referred to as 'light stimulation of a cold-induced fluorescence change'. As shown above (see Fig. 4) and in previous work [7,8], cold treatment at sufficiently low temperature alone can induce a maximal fluorescence change. The effect of high intensity light is to shift the threshold temperature at which a fluorescence increase is induced to higher values (see e.g. Figs. 4 and 5). Thus, by shifting the fluorescence-temperature characteristic by about 3°C on the *T*-axis, illumination allows a cold-induced change, which in darkness will only occur at 3°C lower temperatures.

A light induced modification of the phycobilisome-thylakoid membrane attachment has been discussed before by Harnischfeger and Codd [19]. These authors investigated the effect of preillumination at room temperature on fluorescence emission spectra at liquid nitrogen temperature. In some blue-green algae, including *Anacystis nidulans*, the spectra suggested a light-induced increase of attachment, while with other blue-green algae a decrease of attachment was indicated. An increase of attachment in *Anacystic* appears to contradict our finding of stimulated phycobilin fluorescence. However, as pointed out above, our data relate specifically to a light-stimulation of cold-induced detachment. At room temperature no light-induced phycobilin fluorecence

increase and hence no detachment is apparent from our data. It remains to be investigated, to what extent the freezing of the cells in liquid nitrogen may have induced changes of membrane conformation in the study of Harnischfeger and Codd [19].

In a previous report it has been proposed that a high negative charge at the surface of the thylakoid membrane will stimulate the cold-induced phycobilin fluorescence increase [8]. This proposal was made on the basis of the observation that the cold-induced phycobilin fluorescence increase is stimulated at high pH and in the presence of high monovalent cation concentrations, and is suppressed at low pH and in the presence of high divalent cation concentrations. The same interpretation can also be applied to the light stimulation effect: There is light-driven translocation of protons from the exterior into the interior of the thylakoids. The removal of protons from the outer surface is buffered by the dissociation of acidic groups at membrane proteins or phospholipids. This dissociation leads to an increase of the negative surface charge. In this sense it can be readily explained that illumination gives a similar stimulation effect as a high pH or presence of high monovalent cation concentrations in the dark [8]. The observation that uncouplers also suppress the cold-induced phycobilin fluorescence increase in the dark (see Fig. 7) may suggest that in *Anacystis* a substantial proton gradient is maintained in darkness.

Assuming that the cold-induced phycobilin fluorescence increase reflects phycobilisome detachment, and adopting the hypothesis that this detachment is stimulated by the membrane surface charge, the question remains what is the mechanism of this detachment. How does cold treatment lead to a detachment, and how can the membrane surface charge stimulate this process? As has been argued before [8], the experimental facts favor a model in which the fluid → ordered transition of the physical phase of the membrane is indirectly involved. From the work of Murata and coworkers [6,20] it is known that in *Anacystis*, grown at 28°C, the fluidity change occurs around 13°C. This happens to be close to the threshold temperature at which cold-induced phycobilisome detachment sets in (see e.g. Figs. 4 and 5). However, the data do not support a simple model in which the fluidity change directly leads to phycobilisome detachment. The decisive argument is that an increased surface charge will shift the fluid → ordered transition to lower temperatures [21]. Hence an increased surface charge enhances fluidity, and consequently cold-induced phycobilisome detachment is stimulated if the membrane is still in a fluid rather than in a fluid-crystalline state. Therefore, one has to assume two separate cold-induced processes, one which causes an increase in the distance between the phycobilisome and the chlorophyll-protein complexes and another one involving the fluid → ordered transition. It can be visualized that in the ordered state any particle movement is mechanically somewhat hindered. This hindrance seems to be sufficiently strong to prevent a phycobilisome detachment around 10°C. At lower temperatures, however, the driving force for detachment becomes increasingly strong and overrules the hindering force. By increasing the negative surface charge illumination shifts the fluid → ordered transition to a lower temperature, removing the hindering force at 10°C and thus allowing phycobilisome detachment at this temperature.

The kinetics of the light-induced phycobilin fluorescence changes depicted

in Fig. 5 are phenomenologically very similar to certain slow Chl *a* fluorescence changes, which have been the subject of numerous investigations (for a review see ref. 22). There also seem to be some analogies in the mechanisms involved. Both slow phycobilin and slow Chl *a* fluorescence changes are uncoupler-sensitive [15,16], both are affected by monovalent and divalent cations in antagonistic ways [8,24,25] and for the interpretation of both phenomena hypotheses have been put forward which involve a role of the membrane surface charge [8,24,25] and a variable degree of attachment between the major light-harvesting complex and the reaction center complexes [6—8,26]. Further work will be required to separate real and coincidental analogies. It can be expected that any real analogies will hep to understand the regulation of energy transfer properties in the blue-green as well as in the green system. A distinct advantage offered by the blue-green system is the specific fluorescence emission from the main light-harvesting complex at physiological temperatures.

Acknowledgements

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