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PHOTOCHEMICAL ASPECTS OF PHOTOSYNTHESIS IN BLUE-GREEN ALGAE

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SUMMARY

The mechanism of the photochemical aspects of photosynthesis in blue-green algae has been outlined in this paper. Many of the crucial conclusions about plant photosynthesis were first made with blue-green algae, and later confirmed in other green plants. Although there are differences, the photosynthesis of blue-green is very similar to that of other green plants.

Blue-green algae contain two pigment systems. The pigment system I is composed of a large proportion of chlorophyll *a*, and a small proportion of phycocyanins. On the other hand, pigment system II has more phycocyanin than chlorophyll *a*. The short wave forms of Chl *a* (Chl *a* 670 and Chl *a* 680) are present in both the systems, but the system I is enriched in the long wave forms of Chl *a* (Chl *a* 695, etc). Partial success with the physical separation of the two systems has been obtained in some laboratories. Light quanta absorbed by molecules in the two pigment systems are transferred to their respective "energy traps" or reaction centers, P700 or P680–690. Evidence is presented in this paper for the energy transfer from phycocyanin to Chl *a* under widely different conditions, for the variability in the energy transfer, and for the dependence of such transfer on temperature (in the 4-77° K range).

At the reaction centers, two separate oxidation reduction reactions occur but they involve different reaction partners. The net effect of these reactions is an "uphill" electron transfer from H_2O to CO_2. During this transfer, several known (plastoquinones, cytochromes, plastocyanin, ferredoxin, and $NADP^+$) and "unknown" ("Z", "Q" and "X") electron transfer intermediates are involved. Finally, the end products are molecular oxygen, reduced $NADP^+$, and ATP. The O_2 is evolved, and reduced $NADP^+$ and ATP are used in the reduction of CO_2 to carbohydrate.

INTRODUCTION

BLUE-GREEN algae (*Cyanophyta*) occupy a unique position in the plant kingdom. Like photosynthetic (and other) bacteria they are prokaryotes (Lang, 1968); in them, the photosynthetic, the respiratory, and the nuclear apparatus are *not* organized into distinct organelles. But, unlike photosynthetic bacteria, they evolve oxygen during photosynthesis.

In plant photosynthesis (Rabinowitch and Govindjee, 1965), there is transfer of electrons from H_2O to CO_2. and this transfer requires two light reactions (Text-Fig. 1). One reaction (arbitrarily called "II") boosts the electrons (or H-atoms) from the oxidation-reduction level of H_2O to that of certain cytochromes, and the other (called "I") transfers electrons from the reduced cytochromes to the pyridine nucleotide $NADP^+$ (nicotinamide adenine dinucleotide phosphate). Somewhere along the electron pathway from H_2O to $NADP^+$, a fraction of the stored energy is utilized to synthesize ATP (adenosine triphosphate). With sufficient reduced $NADP^+$ (NADPH) and ATP available, enzymatic reduction of CO_2 to the carbohydrate [CH_2O] level becomes possible.

The act of photosynthesis starts with the absorption of light quanta by the "bulk" of the pigments, then there is energy transfer to active reaction centers (or energy traps) and finally excitation energy is converted into chemical energy at these centres.

Light Absorption

In blue-green algae, there are three major types of pigments: chlorophyll *a* (Chl *a*),

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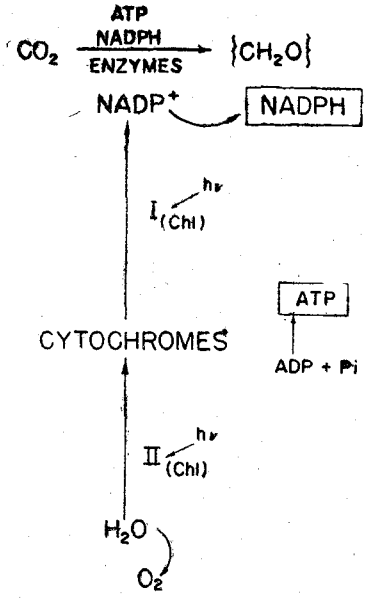
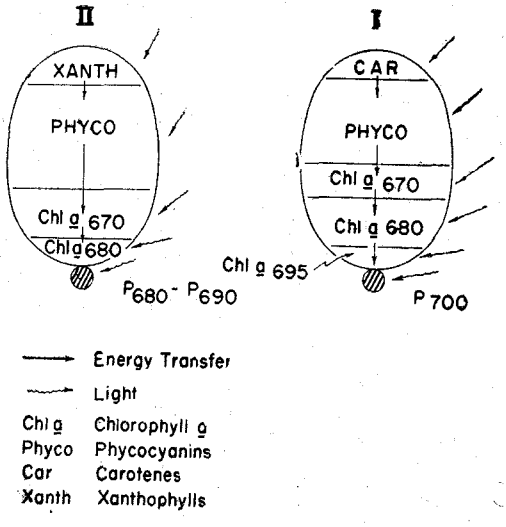
phycocyanins and carotenoids (carotenes and xanthophylls). These pigments are distributed unequally in the two pigment systems that sensitize the two light reactions (Govindjee *et al.*, 1967) (Text-Fig. 2). The system I contains a large proportion of Chl *a*, a small proportion of phycocyanins, and the carotenes, whereas system II contains a small proportion of Chl *a*, a large proportion of phycocyanins and the xanthophylls. Thus, excitation in phycocyanin would lead to preferential abosrption in system II, and that in Chl *a* to system I. This feature makes these organisms very suitable for the study of the biophysical aspects of photosynthesis (Amesz and Duysens, 1962; Duysens, 1952; Emerson and Rabinowitch, 1960;



TEXT-FIG. 1. Transfer of electrons (or hydrogen atoms) from water to carbon dioxide involving two light reactions. ADP, adenosine diphosphate; Pi, inorganic phosphate; ATP, adenosine triphosphate; $NADP^+$, nicotinamide adenine dinucleotide phosphate; NADPH, reduced $NADP^+$: I and II, light reactions; (CH_2O) carbohydrate moiety; $h\nu$, light quanta.



TEXT-FIG. 2. A working model for the composition of the two pigment systems in blue-green algae. P680-P690, reaction center of system II; P700, reaction center of system I.

Govindjee and Rabinowitch, 1960 *b*; Jones and Myers, 1964; Kok and Gott, 1960; Papageorgiou and Govindjee, 1967 *a*, *b*, 1968).

However, another complexity must be added to the above-mentioned composition of the two pigment systems as chlorophyll *a* does not exist as a single homogeneous species *in vivo*. It exists in several spectroscopically distinguishable forms labelled Chl *a* 670, Chl *a* 680, Chl *a* 695, etc, according to their absorption maxima in the red end of the spectrum (Cederstrand *et al.*, 1966; French, 1971). Both the Chl *a* 670 and Chl *a* 680 seem to be present in both the pigment systems, but there is more of these two Chl *a* forms in system I than in system II of blue-green algae; the long-wave form Chl *a* 695 is, however, present exclusively in system I (Govindjee *et al.*, 1967).

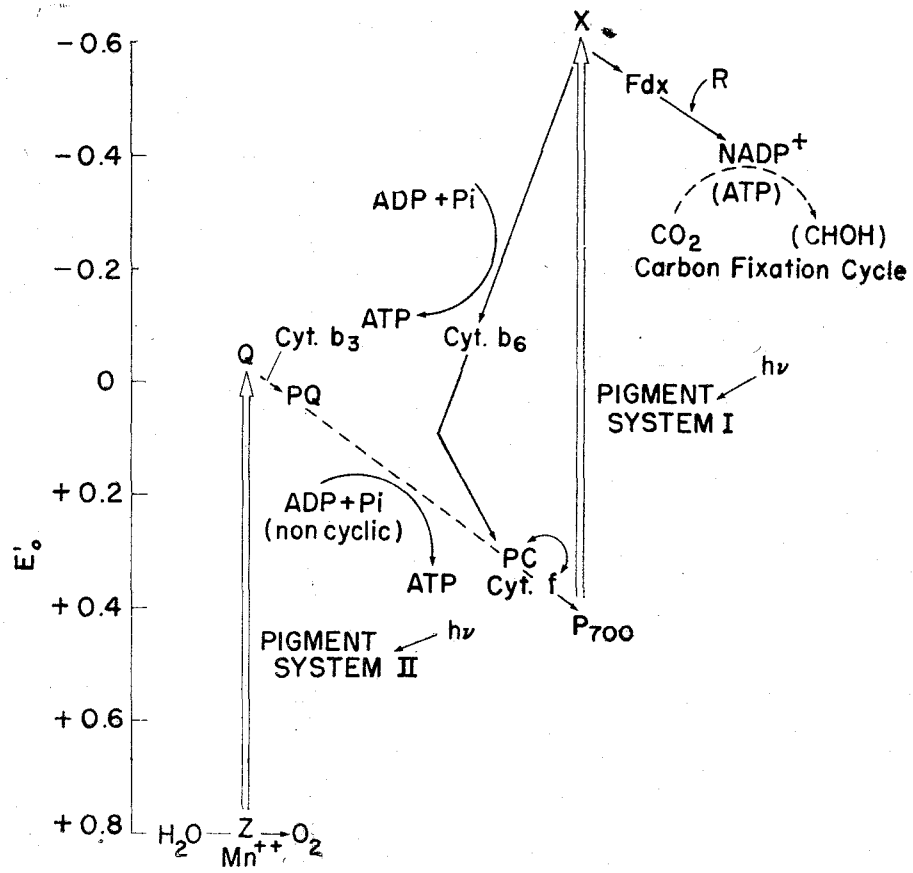
Energy Transfer

Light energy absorbed by pigments in the system II is transferred by a "resonance mechanism" to the energy trap of system II. This trap has been labelled P680–690 because one of its absorption bands is at 680–690 nm. It was recognized only recently by Döring *et al.* (1968, 1969) and Govindjee *et al.* (1970) in the green alga *Chlorella*, and in chloroplasts of several higher plants. But no data on P680–690 are available in the blue-green algae. However, its existence has been suggested from the presence of a new fluorescence band at 696 nm at very low temperatures in blue-green algae (Bergeron, 1963; Govindjee, 1963), in red algae (Krey and Govindjee, 1964, 1966) and in chloroplasts (Govindjee, 1966; Govindjee and Yang, 1966). We believe that P680–690 must be present in all photosynthetic systems. Just as in the system II, light energy absorbed by pigments in the system I is transferred to the energy trap of system I labelled P700 (Kok and Gott, 1960). The P700 has been shown to be a Chl *a* complex having one of its absorption maxima at 700 nm. The energy transfers in systems I and II, mentioned above, are very efficient.

Electron Transport and the Production of Reducing Power

We will now discuss chemical products of the primary reactions at the energy traps and show how they are related to the production of reduced $NADP^+$ and ATP needed for the fixation of CO_2. For this, we require a more extensive picture than given in Fig. 1 (*see* Govindjee, 1967; Govindjee and Robinowitch, 1965; Hind and Olson, 1968; Levine, 1969). As a consequence of a light reaction at P700, a cytochrome of *c* type (perhaps Cyt *c* 554 in blue-green algae) is oxidized, and another intermediate labelled X is reduced (Text-Fig. 3). (The X may be equivalent to a compound labelled P430—see Hiyama and Ke, 1971). During this oxidation-reduction reaction, the light energy is converted into chemical energy. The reduced X transfers its electrons (or H-atoms) to $NADP^+$ *via* three enzymes: cytochrome reducing substance (CRS), ferredoxin, and ferredoxin-$NADP^+$ reductase. At the energy trap II, an unknown H-donor labelled "Z" is oxidized and another unknown intermediate "Q" is reduced. Here again, light energy is converted into chemical energy. The oxidized Z somehow reacts with H_2O to evolve O_2, and Z is restored (*see* Forbush *et al*; 1971; Joliot *et al*; 1971; Mar and Govindjee, 1972). The reduced Q transfers its electrons (or H-atoms) *via* a series of intermediates to Cyt *c* 554 oxidized by system I; these intermediates are plastoquinone (PQ), cytochrome *b* 559 and a copper protein plastocyanin (PC). The exact order of these intermediates is not clear. In particular, controversy exists regarding the order of Cyt *c* or *f* in green algae and plastocyanin. But, most investigatorsbelieve that plastocyanin comes after Cyt *c* in the chain.

The net result of the series of reactions (I and II) is the transfer of electrons from H_2O to $NADP^+$. This is then how NADPH (the reduced $NADP^+$) is produced. But, we also need the other important compound ATP. It is generally accepted that it is produced in two ways. The first one, the *non-cyclic phosphorylation*, is coupled with the electron transfer from the reduced Q (perhaps equivalent to a compound *c* 550—for a description of the latter *see* Arnon *et al.*, 1971) to cytochrome *c*. This electron transfer is "downhill" energy-wise just as in mitochondrial respiration, and enough energy is available for the conversion of ADP (Adenosine diphosphate) and Pi (inorganic phosphate) to make ATP when a pair of electrons move from cytochrome *b* 559 or PQ to cytochrome *c*. The second, the *cyclic phosphorylation*, is coupled with the back reaction of system I. For example, reduced X, instead of transferring electrons to $NADP^+$, may transfer them to plastocyanin in the electron transport chain. This back flow of electrons may occur *via* another intermediate—



TEXT-FIG. 3. A detailed scheme for the transfer of electrons (or Hydrogen atoms) from water to carbon dioxide (modified Hill and Bendall scheme). Z, electron donor of system II; Q, (C=550), electron acceptor of system I; cyt., cytochrome; X, (=P430), primary electron acceptor of system I; Fdx, ferredoxin; R, Fdx-NADP reductase; other symbols have the same meaning as in Fig. 1 except that (CHOH) =(CH_2O) of Fig. 1; Eo', oxidation reduction potential at pH 7·0. Cytochrome reducing substance (CRS) should be after X, cyt *f* should read cyt C554, and cyt b_3 as cyt 559.

cytochrome b_6. There is plenty of energy available, and the reaction could be coupled with phosphorylation. However, this back flow of electrons should not run all the time, otherwise it would disallow $NADP^+$ reduction. Anyhow, with sufficient NADPH, and ATP, the Calvin-Benson Cycle for the fixation of CO_2 into carbohydrates can be completed. This is then how photosynthesis is suggested to occur in chlorophyll *a* containing organisms[2] [*see* recent books (Clayton, 1965; Fogg, 1968; Heath, 1969; Kamen, 1963; Rabinowitch and Govindjee, 1969) for a more complete discussion].

In this paper, we shall discuss some of the evidence for the above picture as obtained from experiments with the blue-green algae. First, we shall discuss the composition and properties of the pigment systems, and then the light reactions and the electron transport pathways. No attempt will be made to give an exhaustive review. But, we will emphasize the work done in our laboratory.

THE PIGMENT SYSTEMS AND PRIMARY EVENTS

In order for light energy to be effective in any photochemical reaction, it must be first absorbed. As noted in the introduction, blue-green algae contain chlorophyll *a*, carote-

[2] For alternate formulations, *see* (*a*) Govindjee, J. C. Munday, Jr. and G. Papageorgiou, 1966. Fluorescence studies with Algae: changes with time. In J. M. Olson (editor): *Energy Conversion by the Photosynthetic Apparatus*, Brookhaven National Laboratory, Upton, N.Y., pp. 434–445 (*see* Fig. 5); and (*b*) D. B. Knaff and D. I. Aronn. 1969. A concept of three light reactions in photosynthesis by green plants, *Proc. Nat. Acad. Sci., U.S.*, **64**: 715–722 (*see* Fig. 7).

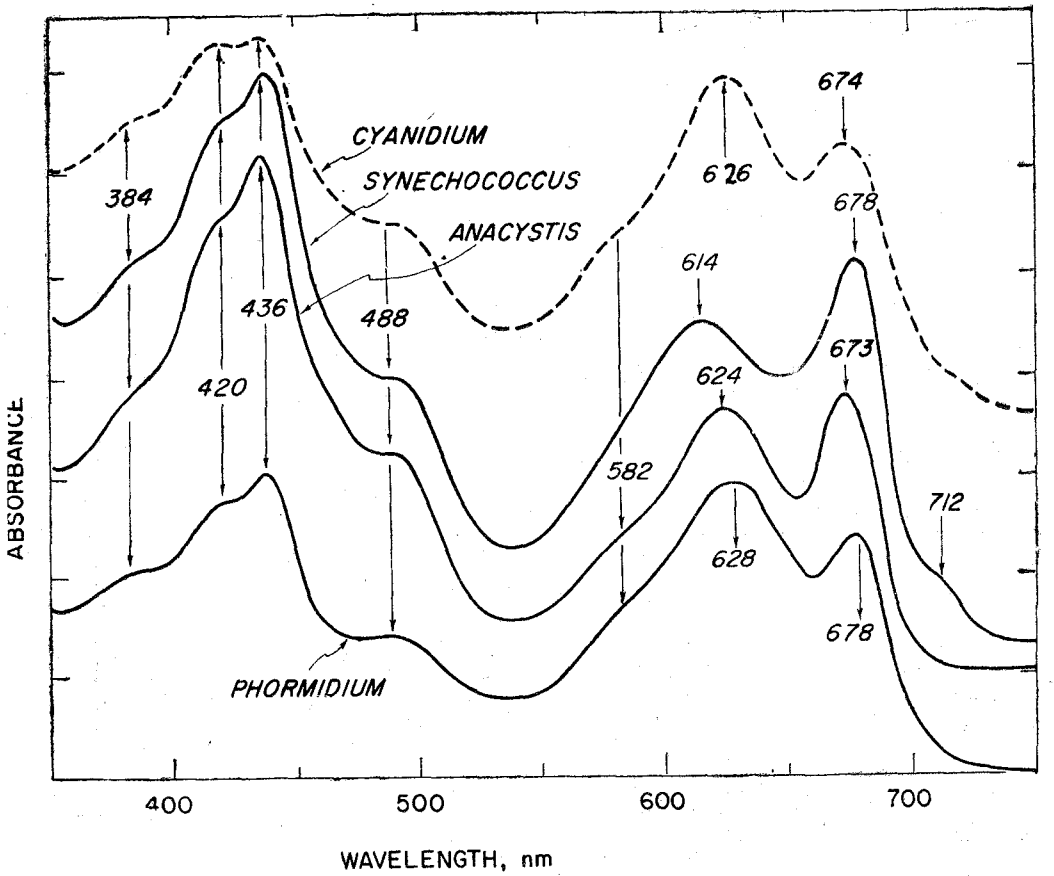
noids[3] and phycocyanins. However, several blue-green algae (e.g., *Anabaena* and *Caramium*) contain also phycoerythrins (*see* O'hocha, 1960). Also, some algae that are not classed under *Cyanophyta* are known to contain phycocyanins—examples are an acidophilic alga *Cyanidium*, and several cryptomonads.

Now, let us see how one finds out, what pigments are present in an organism. For this, one measures the absorption spectrum, *i.e.*, absorbance as a function of wavelength.

Absorption Spectra

Measurements of absorption spectra of algal suspensions are usually made with spectrophotometers equipped with integrating spheres. When suspensions are placed in cuvettes inside such spheres, the transmitted light as well as that scattered by the suspension is collected and read as transmitted or non-absorded light. Without the sphere, spectrophotometers would read the scattered light as absorbed light giving distorted absorption spectra. Using a Bausch and Lomb spectrophotometer (Spectronic 505) equipped with an integrating sphere, we measured the absorption spectra of several blue-green algae (*Anacystis*, *Phormidium*, and a thermophilic *Synechococcus* that grows at 65° C) and of *Cyanidium* (Text-Fig. 4). There are obvious differences among these algae, but they all show bands for chlorophyll *a* at 420 nm, at 434–437 nm and at 673–678 nm, for phycocyanin at 614–628 nm, and at about 580 nm and for carotenoids at about 488 nm. At room temperature, other bands due to carotenoids and due to allophycocyanin are

[3] The carotenoids found in blue-green algae are: β carotene, zeaxanthin echinenome, myxoxanthophyll, oscilloxanthin, flavacin, aphanicin, aphanizophyll, cryptoxanthin and a hydroxylated keto carotenoid (*see* Herzberg and Jensen, 1966 a, 1966 b).

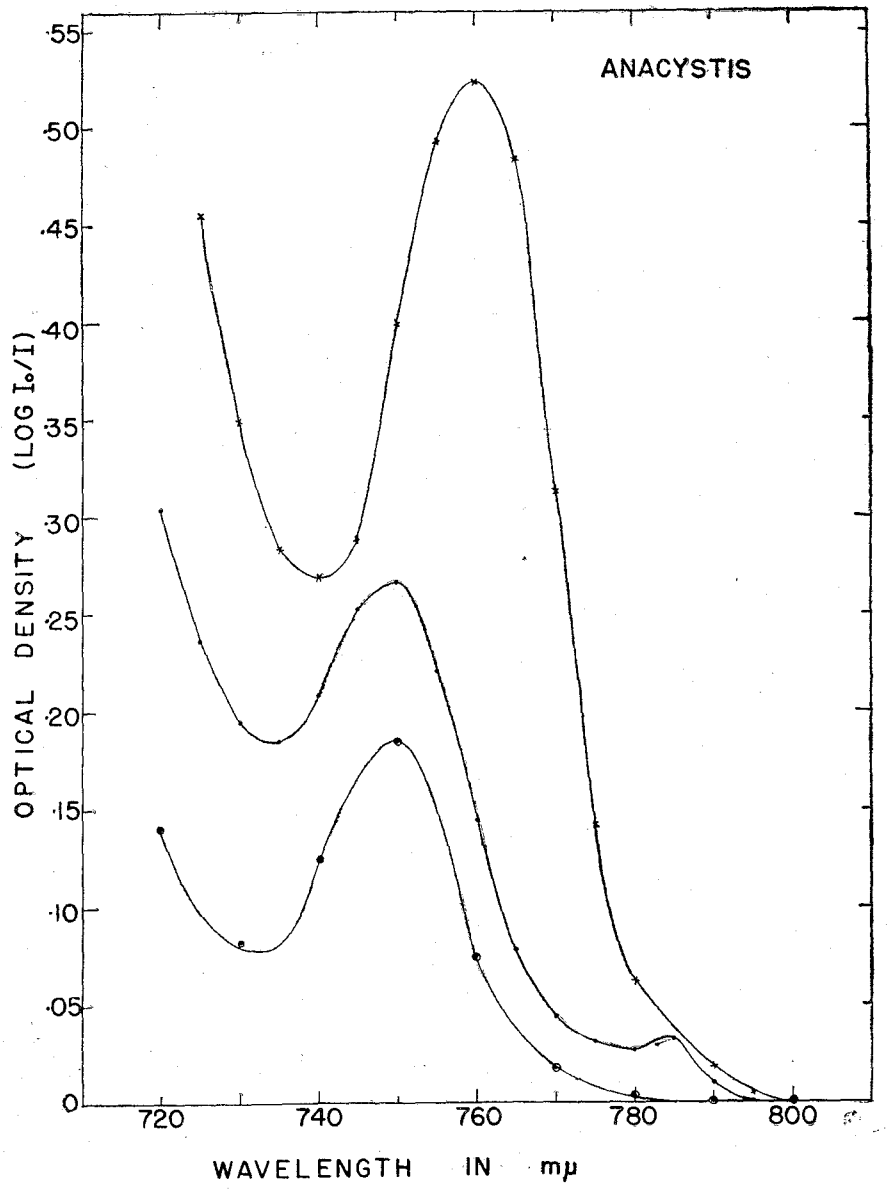


TEXT-FIG. 4. Absorption spectra of several blue-green algae (solid curves) and of *Cyanidium* (dashed curve). The base line for the different algae were shifted on the ordinate scale; nm = nanometer.

not resolved because of strong overlap with chlorophyll *a*.

The different forms of Chl *a*—as noted in the introduction—are present in blue-green algae. A longer wave form of Chl *a* (bands around 710–720 nm) is only seen in *Synechococcus*. A still longer wave form absorbing at 750 nm is present in *Anacystis* (Gassner, 1962; Govindjee, 1963; Govindjee *et al.*, 1961) (Text-Fig. 5). No functional role for P750 has been found (Govindjee *et al.*, 1960). Recently, Fischer and Metzner (1969) have suggested that P750 may be an open-chain tetrapyrrol pigment—perhaps related to bile pigments or phytochrome.

The red absorption band (at 673–678 nm) is composed of, at least, two Chl *a* forms (Chl *a* 670 and Chl *a* 680) as revealed by the analysis of the main band into gaussian components (Cederstrand *et al.*, 1966). However,



TEXT-FIG. 5. Absorption spectra of three dense suspensions of *Anacystis nidulans* showing a new band at about 750 mμ (millimicron = nanometer, nm) (Govindjee *et al.*, 1961).

the existence of Chl *a* 670 and Chl *a* 680 is more clearly observed when the absorption spectra are measured in the 4 to 77° K range (Text-Fig. 6) (Cho and Govindjee, 1971).

Examination of the absorption spectra at 4–77° K also reveals details pertinent to pigments other than Chl *a*. For example, the caretenoid band is resolved into bands at 465 nm and at 502 nm, the main phycocyanin band into two peaks at 625 and 634 nm, and the allophycocyanin band at 650 nm. Thus, there is evidence for the existence of different forms of Chl *a*, various carotenoids, phycocyanin(s), and allophycocyanin in the blue-green algae.

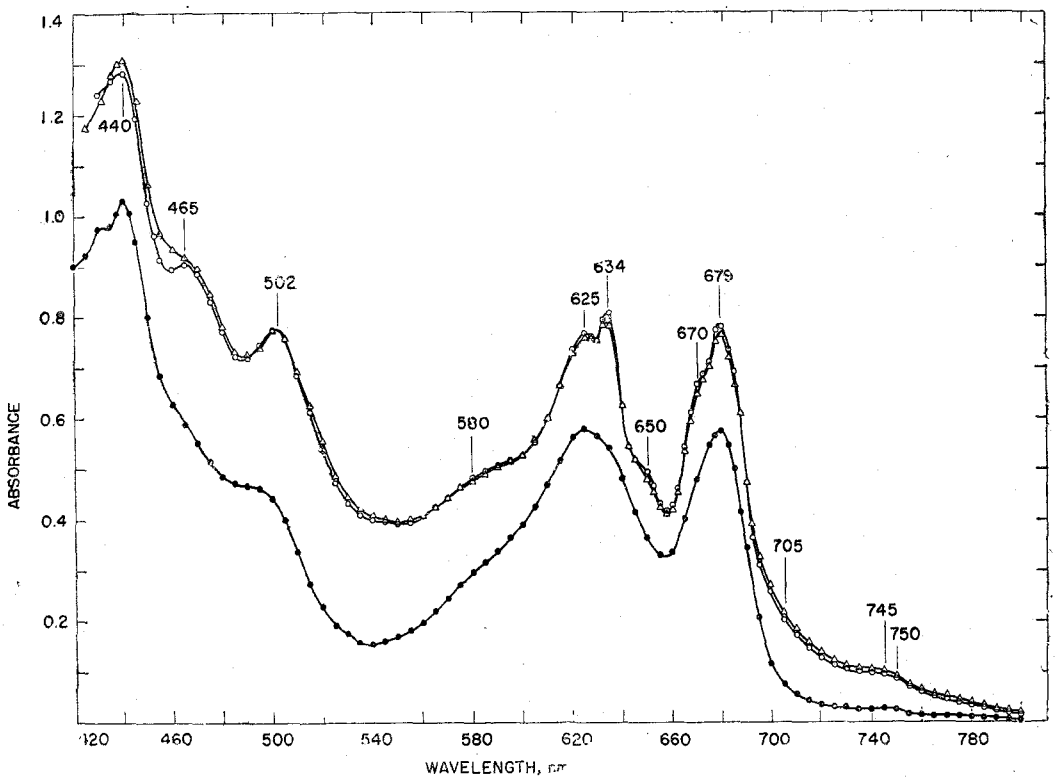
The concentrations and the ratios of these pigments, however, do not remain constant. They vary depending upon the light intensity and wavelength of light used during growth (Fujita and Hattori, 1962; Ghosh and Govindjee, 1966; Halldal, 1958; Jones and Myers, 1965; Zhevner *et al.*, 1965). In strong (2×10^6 ergs cm^{-2} sec^{-1}) orange light, absorbed preferentially by phycocyanin, the ratio of phycocyanin to Chl *a* is reduced (Text-Fig. 7). And, in strong red light, absorbed by Chl *a*, the same ratio is increased. These experiments show the ability of blue-green algae to "adapt" to the wavelength and intensity of light that falls on them.

In spite of these variations, and the multiplicity of pigments present in the blue-green algae, the nature of the primary events remains the same.

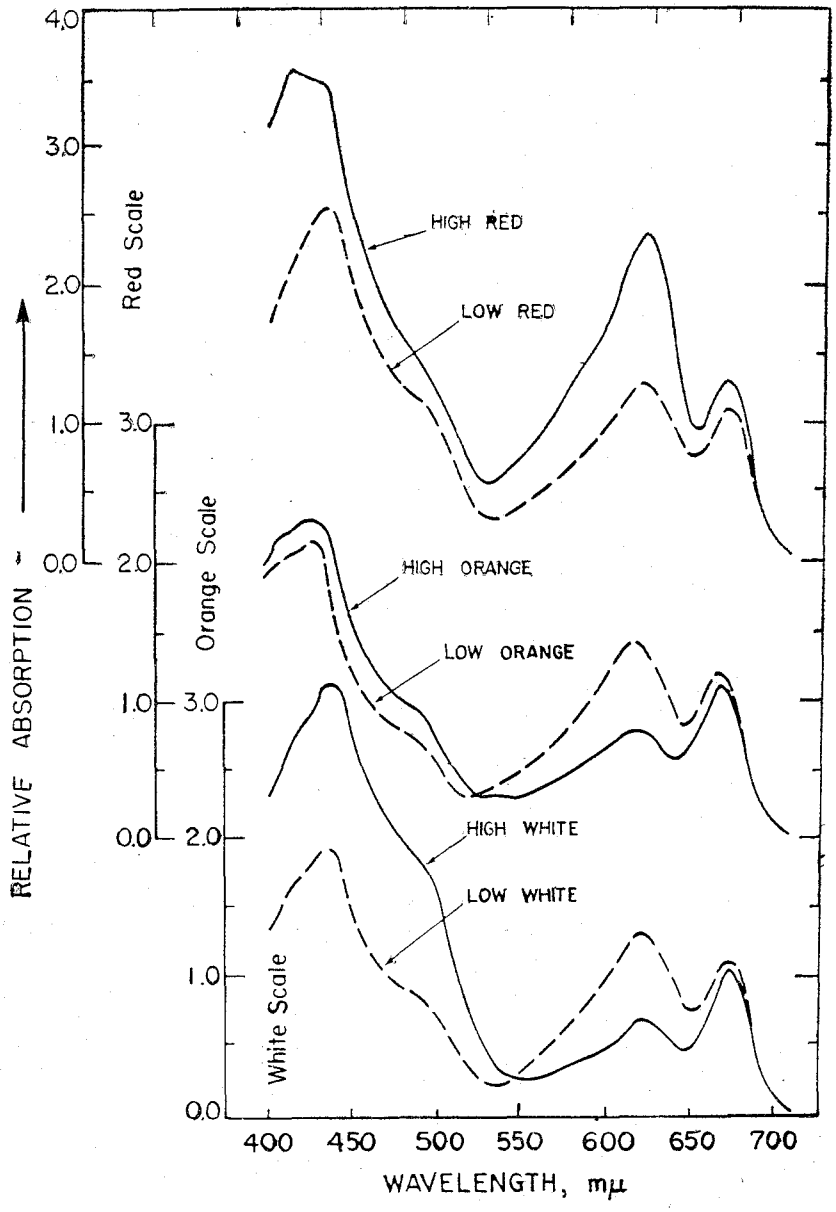
Primary Events

The primary events to be discussed here are the production of the excited states, their de-excitation, and energy transfer.

Excited states.—The first act of photosynthesis is the absorption of light by one of the several pigments described above. The phenomenon of light absorption is extremely fast; it is over in 10^{-15} seconds. A molecule upon abosrption of light is in an excited state; it has a new electronic configuration. It has an excess of energy, namely that of the light quantum it absorbed. Such



TEXT-FIG. 6. Absorption spectra of *Anacystis nidulans* at low temperatures (4° K: open cricles; 77° K: open triangles). The room temperature spectrum is shown for comparison (solid dots) (Cho and Govindjee, 1971).



TEXT-FIG. 7. Absorption spectra of different cultures of *Anacystis nidulans* grown in lights of different intensity and color. Spectra of cells grown in high light intensities are shown with solid lines and those in low light intensities with broken lines (Ghosh and Govindjee, 1966).

molecules are very unstable, and their lifetimes are very short.

The lifetime (τ) of the excited states are calculated from the rate of de-excitation of the excited molecules by light emission (fluorescence), but we will not go into the details here. The τ for Chl *a* in blue-green algae has been measured to range from 0·5 to 1·4 nanoseconds (Brody and Rabinowitch, 1957; Mar *et al.*, 1972; Murty and Rabinowitch, 1965; Singhal and Rabinowitch, 1969; Tomita and Robinowitch, 1962). Since the emission spectrum (light emitted as a function of wavelength) in blue-green algae is complex

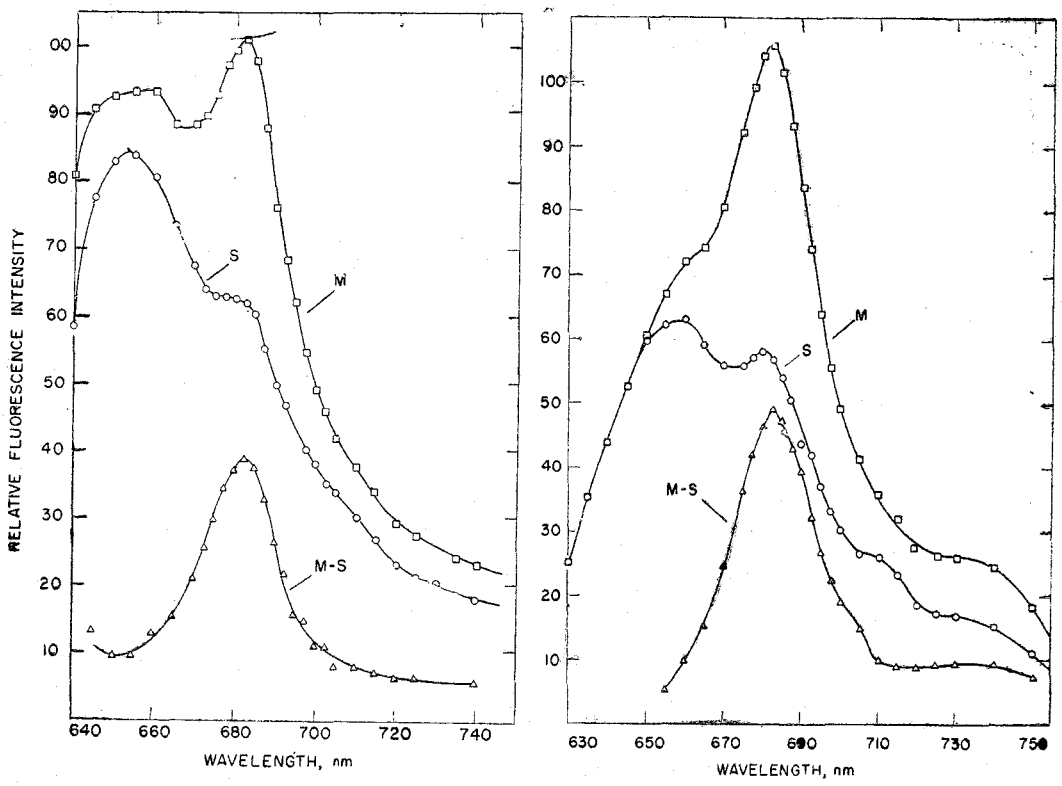
(*see* below) experiments should be made on τ by varying the wavelength range of observation. [The method of measurement has been described elsewhere (Merkelo *et al.*, 1969).] If there was only one pigment responsible for fluorescence, only one value of τ should be obtained. Different values of τ would suggest a heterogeneity of fluorescence in blue-green algae. The value of $\sim 1{\cdot}0$ n sec for τ clearly indicates that the excited states involved are short-lived singlet states, and are not long-lived triplet states. This short lifetime (of $\sim 1{\cdot}0$ n sec) sets a limit on the speed of primary photo-chemistry. The latter must be very rapid so as to effectively compete with fluorescence.

Before we discuss the photochemical reactions we will first provide evidence for the transfer of energy within the pigment system.

Energy transfer.—When a quantum of light is absorbed by a pigment molecule, the energy does not stay in that molecule that initially absorbed it; instead, it is transferred to other molecules. But, how does one prove it. Let us assume we have two types of molecules—one capable of donating energy (donor) and the other capable of accepting energy (acceptor). Let us further assume that they have different absorption and fluorescence spectra. If we excite the donor molecules, and the fluorescence from acceptor molecules is observed, we have proven the existence of energy transfer. This technique of *sensitized fluorescence* has been used to prove energy transfer from phycocyanin to Chl *a* in blue-green algae. There are two methods. First, light of a wavelength preferentially absorbed by phycocyanin is used to excite the algal suspension, and the light emission from it is measured as a function of wavelength (fluorescence spectra). Since phycocyanin, and chlorophyll have distinct emission spectra, it will not be difficult to establish if chlorophyll *a* fluorescence was present. Second, we can measure the intensity of chlorophyll *a* fluorescence upon excitation of the algal suspension with different wavelengths of light (excitation spectra of Chl *a* fluorescence). If we find peaks in the spectra corresponding to absorption by phycocyanin, we can say that phycocyanin transfers energy to chlorophyll *a*. From the measurements of such excitation spectra of Chl *a* fluorescence, and of fluorescence spectra, Duysens (1952) concluded that there was efficient (80–90%) energy transfer from phycocyanin to chlorophyll *a*, but relatively inefficient (15–20%) transfer from the carotenoids to chlorophyll *a*. However, these values of efficiencies are known to change if the ratios of phycocyanin to chlorophyll *a* are changed by growing algae under light of different intensity and wavelength (Ghosh and Govindjee, 1966). Let us now look at some of the experimental data, and the complexities involved with them.

Upon excitation of phycocyanin (560 nm), both phycocyanin and Chl *a* fluorescence bands are observed; the former has a peak at 653 nm, and the latter at 680–685 nm (Duysens, 1952; Papageorgiou and Govindjee, 1967 *b*). This shows that the energy transfer from phycocyanin to Chl *a* is efficient but is not 100%. If all the energy absorbed by phycocyanin was transferred to Chl *a*, phycocyanin fluorescence should have been completely quenched. Not only that this transfer is not 100%, it may also vary with the time of illumination. When the fluorescence spectrum after 10 minutes of 560 nm illumination is compared (Papageorgiou and Govindjee, 1967 *b*, 1968) with that after 3 seconds, the latter has a higher ratio of Chl *a* fluorescence to phycocyanin fluorescence (Text-Fig. 8). This may have been taken to indicate that the efficiency of energy transfer from phycocyanin to Chl *a* decreased with time of illumination. But, there was no decrease in the phycocyanin fluorescence indicating that the above interpretation is wrong. It was suggested that the increase in the Chl *a* fluorescence after 10 minutes of illumination means that the quantum yield of Chl *a* fluorescence increases, and, furthermore, these changes may be related to the "configurational" changes of the chloroplast lamellae because an uncoupler of phosphorylation FCCP (carbonylcyanide *p*-trifluoro methoxy phenylhydrazone), that is known to (indirectly) affect that light-induced "configurational" changes, also affects the time course of the fluorescence of Chl *a* in blue-green algae. (For a review of this phenomenon, see Govindjee and Papageorgiou, 1971).

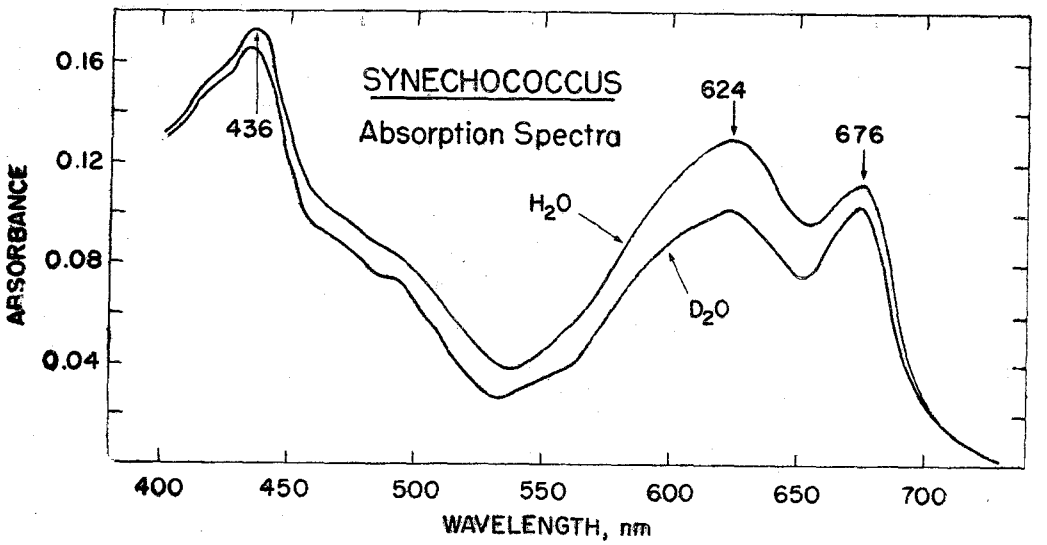
On the other hand, there is strong evidence—mentioned above—that the efficiency of the energy transfer from phycocyanin to chlorophyll *a* indeed varies if the blue-green algae are grown under different wavelengths. It was suggested (Ghosh and Govindjee, 1966), that the decrease in the efficiency of energy transfer from phycocyanin to the highly fluorescent chlorophyll *a* of pigment system II (Chl *a* II) may be accompanied by transfer to the weakly fluorescent chlorophyll *a* of pigment system I (Chl *a* I). If this is true,



TEXT-FIG. 8. Emission (fluorescence) spectra of normal (left) and poisoned (right) *Anacystis nidulans* at 3 sec (S) and 10 min (M) of light exposure; M–S, the difference spectrum. Excitation $\lambda = 590$ nm (Papageorgiou and Govindjee, 1968).

we should observe a higher ratio of 710–740 nm (Chl *a* I) to the 682 nm (Chl *a* II) fluorescence because pigment system I is enriched in the former. With this in mind, we analysed the data of Govindjee, A. K. Ghosh, H. Crespi and J. J. Katz (unpublished).

Synechococcus was grown in regular culture medium (H_2O), and in deuterated medium (D_2O). Absorption spectra showed no difference in the types of chlorophyll *a* present, and in the ratio of chlorophyll *a* to the carotenoids. However, the ratio of phycocyanin to chlorophyll *a* was slightly lower in D_2O cells than in H_2O cells (Text-Fig. 9). Upon excitation with 600 nm light (absorbed primarily in phycocyanin) the phycocyanin emission increased with respect to Chl *a* fluorescence at 682 nm, but the ratio of long wave Chl *a* fluorescence (710–740 nm) to the short wave Chl *a* fluorescence (682 nm) also increased in D_2O than in H_2O cells. The emission spectra of H_2O and D_2O cells, normalized at 682 nm, is shown in Text-Fig. 10. These data may indicate that a decrease in energy transfer from phycocyanin to Chl *a* of system II (Chl *a* II) is accompanied by an increase in energy transfer to Chl *a* I. However, it does not allow us to judge whether this increase in energy transfer to Chl *a* I is due to an increase in transfer from Chl *a* II to Chl *a* I or to increased transfer directly from phycocyanin to Chl *a* I. Text-Fig. 11 shows the emission spectra obtained by exciting *Synechococcus* with 430 nm (absorbed primarily in Chl *a*). Here again, we observe a higher ratio of long-wave to short-wave Chl *a* fluorescence in D_2O than is H_2O cells suggesting that either (1) there is more long wave Chl *a* forms present, or (2) indeed there is increased energy transfer from Chl *a* II to Chl *a* I. The absorption spectra (Text-Fig. 9) and the excitation spectra (Text-Fig. 12) rule out the first possibility. Thus, we believe the above results can best be explained by postulating an increased transfer from Chl *a* II to Chl *a* I. However, we must remember



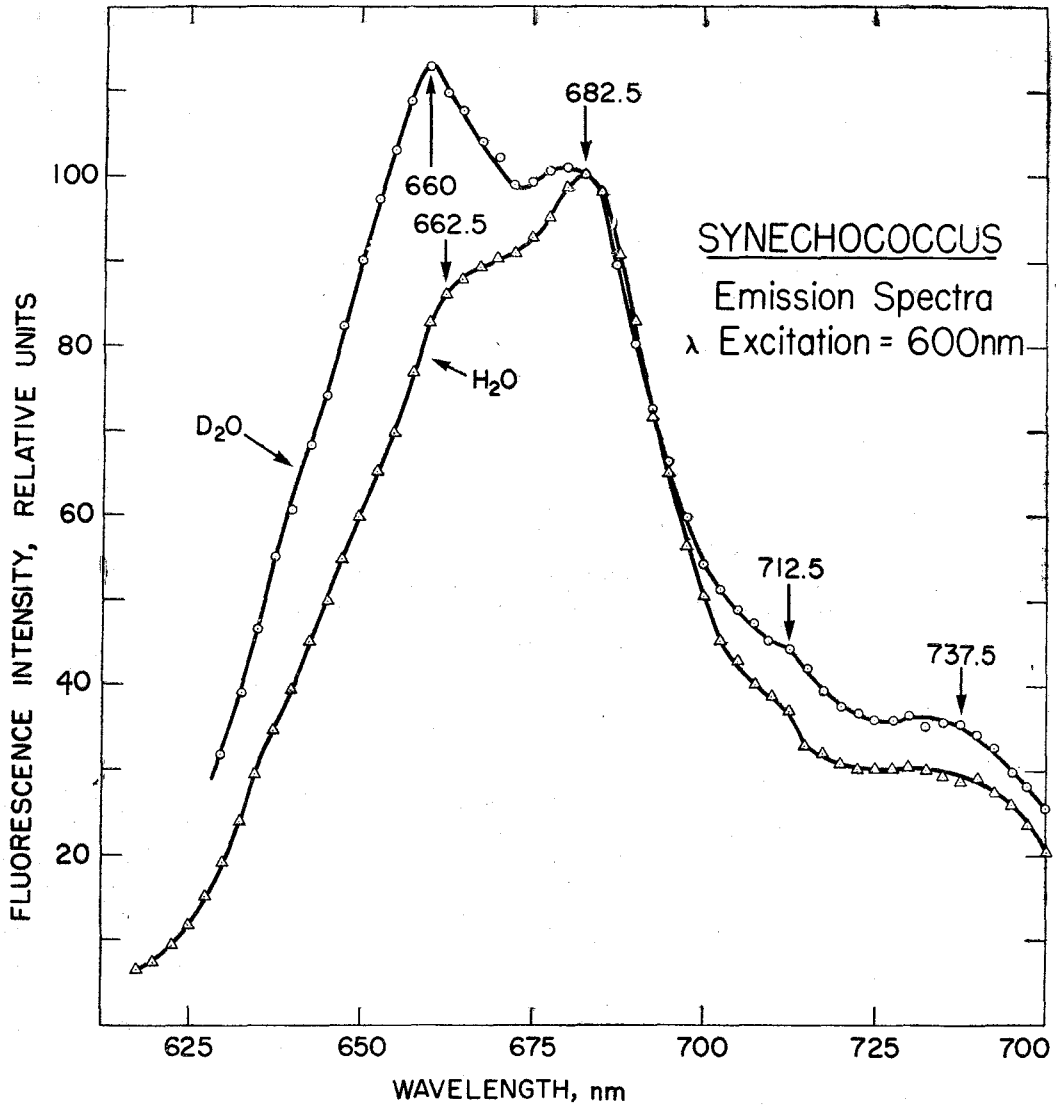
TEXT-FIG. 9. Absorption spectra of deuterated (D_2O) and normal (H_2O) *Synechococcus* (Govindjee, A. K., Ghosh, H. Crespi and J. J. Katz, unpublished observations).

that these conclusions are tentative because the possibility exists that the intrinsic fluorescence yield of the long wave Chl *a* may be higher in D_2O than in H_2O cells. But, is this so? We believe that this is unlikely because the excitation spectra of fluorescence do not show an increased band due to long wave form of Chl *a* in the 690–700 nm region. (In spite of this observation, the conclusion must still be made with caution because the concentration of these long wave forms of Chl *a* is extremely small, and possible errors cannot be completely ignored.)

More detailed information has been recently obtained (Cho and Govindjee, 1971) concerning the energy transfer, and the composition of pigment systems in *Anacystis nidulans* from measurements at low temperatures (4 to 77° K). The two aspects are so "intertwined" that we shall discuss them together. We have already seen that the absorption spectra at low temperatures were better resolved than those at room temperature. The same is true for the fluorescence spectra, and the excitation spectra of Chl *a* fluorescence. At 77° K, there are three emission bands for Chl *a* at 685 nm (F 685), at 696 nm (F 695) and at 712 nm (F 710) (Bergeron, 1963; Bergeron and Olson, 1967; Godheer, 1968; Govindjee, 1963; Mohanty *et al.*, 1972; Murata *et al.*, 1966; Shimony *et al.*, 1967). The experimental results on the fluorescence spectra of blue-green algae (Cho and Govindjee, 1971) in the 4-77 °K range follow (Text-Figs. 13 and 14).

When 560 nm light is used for excitation, most of the energy is absorbed by phycocyanin; and, fluorescence from phycocyanin as well as several forms of Chl *a* is observed confirming energy transfer from phycocyanin to Chl *a* at these low temperatures. However, when 435 nm light is shined on the algae, most of the energy is absorbed by Chl *a*, and only fluorescence from Chl *a* is observed. But, the ratio of the long wave fluorescence band at 712 nm to that at 685 nm and 695 nm is higher when Chl *a* is directly excited than when phycocyanin is excited. This confirms that system I (*see* Introduction), that contains most of Chl *a*, is enriched in the long wave form of Chl *a*.

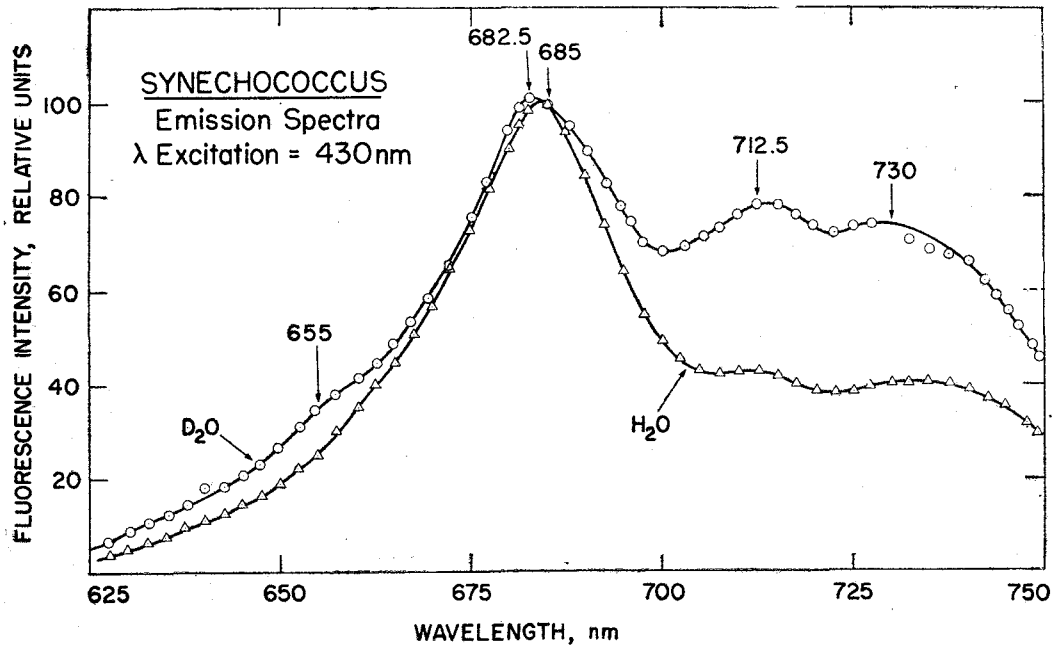
Let us look at some other complexities of the pigment systems. As noted above, there are three emission bands (F 685, F 695 and F 710) at 4–77° K. If these bands are from one and the same pigment system, the excitation spectra for the three bands should be identical. However, if there are more than one pigment system, we expect to see differences. Our results (Text-Figs. 15–17) indicate that the excitation spectra for F 685 and F 695 are different from that of F 710: the ratio of 637 nm (phycocyanin) to 440 nm (Chl *a* band is significantly lower in the spectra for F 710,



TEXT-FIG. 10. Emission spectra of deuterated (D_2O) and normal (H_2O) *Synechococcus*. λ excitation, 600 nm; curves normalized at 682·5 nm (Govindjee, Ghosh, Crespi and Katz, unpublished).

This result is consistent with the conclusions obtained from the fluorescence spectra that the long wave fluorescence (~ 710 nm) belongs preferentially to system I. Another important feature to be noted, from the exictation spectra for F 685, F 695 and F 710, is the presence of bands due to both Chl *a* 670 and Chl *a* 678—a clear confirmation of their presence in both the pigment systems (I and II) in blue-green algae.

Now, let us return to a further discussion of the energy transfer from phycocyanin to Chl *a*. As noted earlier, the existence of such a transfer can be proven by the presence of phycocyanin bands in the excitation spectra of Chl *a* fluorescence. This is indeed the case as we see bands at 580, 623 and 637 nm due to phycocyanin and at 650 nm due to allophycocyanin in the excitation spectra of Chl *a* fluorescence (Text-Figs. 15–17). If we now calculate the efficiency of energy transfer from the available data (absorption, excitation spectra of Chl *a* fluorescence, and emission spectra) we find that this efficiency for

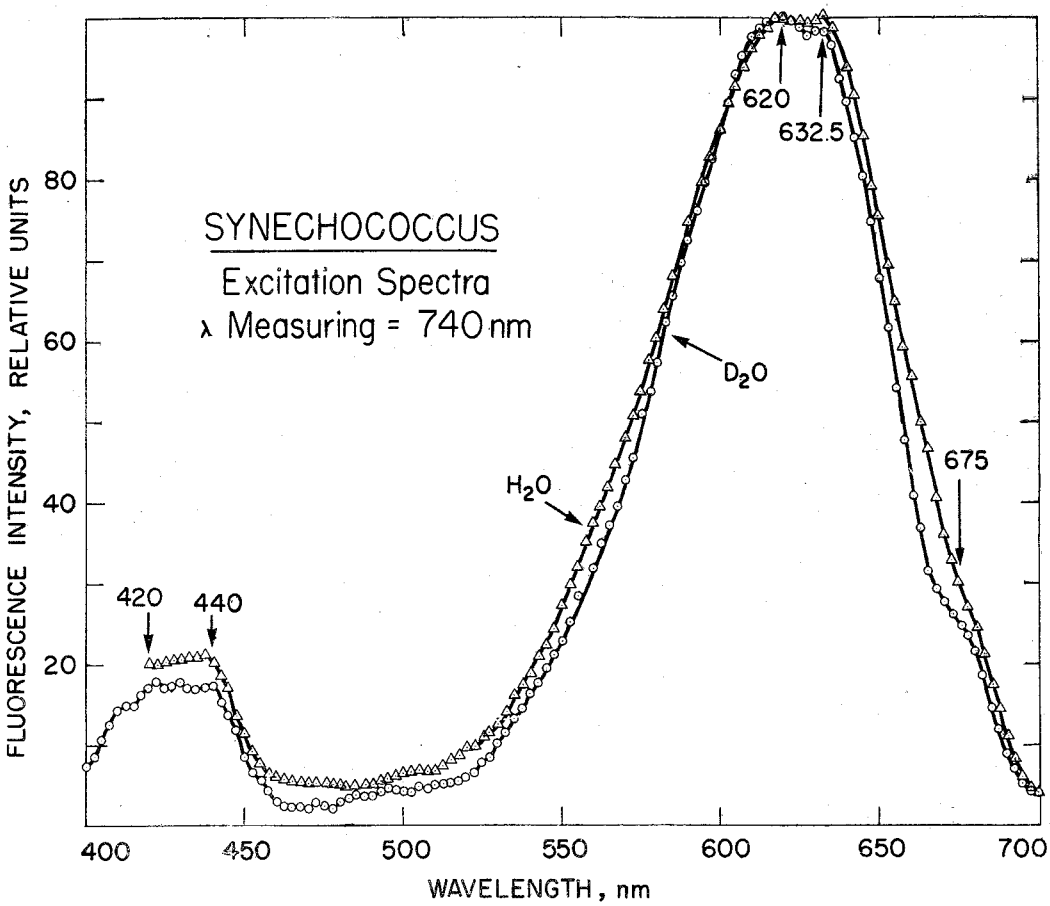


TEXT-FIG. 11. Emission spectra of deuterated (D_2O) and normal (H_2O) *Synechococcus*. λ excitation, 430 nm; curves normalized at 685 nm (Govindjee, Ghosh, Crespi and Katz, unpublished).

phycocyanin to Chl *a* at 4° K is only 80% of that at 77° K. Thus, we now have an additional information about the energy transfer: there is temperature dependence. Moreover, the transfer time (total, not pair-wise) from phycocyanin to Chl *a* is about 0·3 nanoseconds (Tomita and Rabinowitch, 1962). These data appear to be consistent with a model of energy transfer that is labelled "slow". [The term "slow" is used because it is slow in comparison to the "vibrational relaxation" (*see* Chaps. 10 and 12 in Rabinowitch and Govindjee, 1969) which is of the order of 10^{-12} sec.] In such "slow" transfers, there is "vibrational relaxation" in the donor molecule, and then energy transfer. Since the vibration levels depend upon the temperature of the system, the absorption, and/or the fluorescence spectra change with temperature. It has been shown (*see* Förster, 1960) that the rate of transfer by the "slow" mechanism depends upon several factors including the "overlap" of the emission spectra of the donor molecule, and the absorption spectra of the acceptor molecule. If temperature changes this "overlap" region, there will be an effect of temperature on the transfer rate. A change in transfer rate could affect the transfer efficiency. Thus our observed temperature dependence of energy transfer may be taken to mean that a "slow" transfer (Förster's resonance transfer) mechanism operates in blue-green algae.

So far, we have only talked about the energy transfer from phycocyanin to chlorophyll *a*. There is also energy transfer among phycocyanin, and among Chl *a* molecules. This cannot be shown by the technique of *sensitized fluorescence* because the donor and acceptor molecules are identical. However, if polarized light is used to excite pigments, only the molecules whose "dipoles" are aligned in the appropriate direction would absorb this light. If there is energy transfer to other molecules whose dipoles are arranged randomly in all directions, there will be an almost complete depolarization of fluorescence. Such a depolarization of fluorescence has indeed been observed, but no detailed work with blue-green algae is available.

Having provided evidence for the transfer of energy from one pigment molecule to the other, we are now ready to look at the "extent" of this transfer. It occurs in units of about 300 chlorophyll molecules, and the energy is ultimately trapped in a reaction center in each unit.

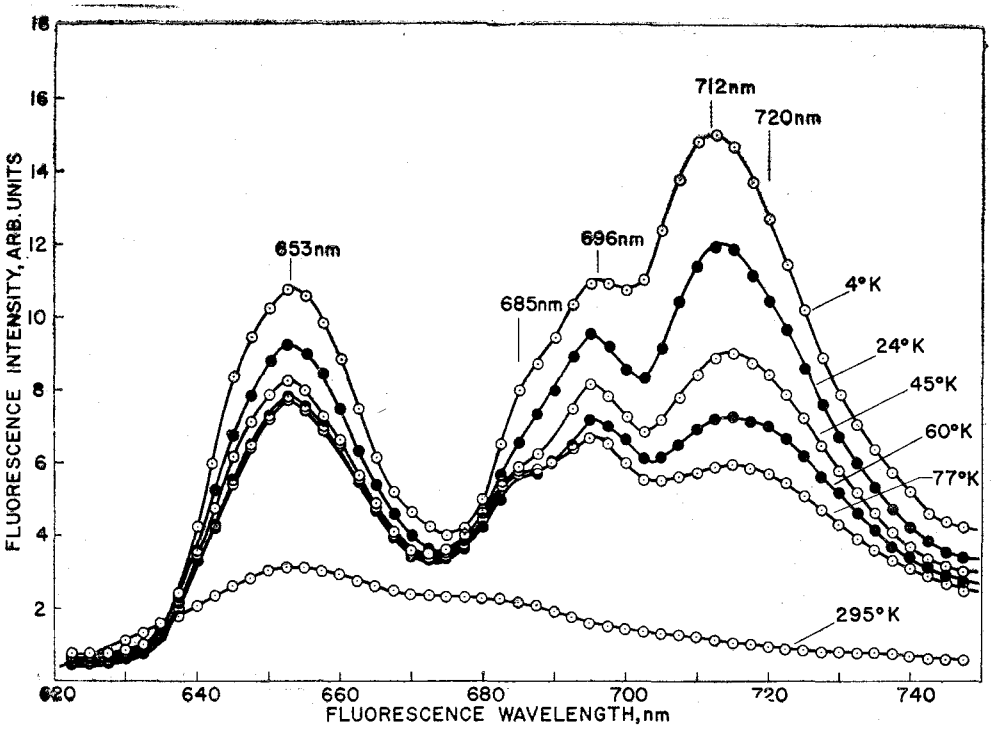


TEXT-FIG. 12. Excitation spectra of chlorophyll *a* fluorescence in *Synechococcus*. λ measuring, 740 nm; curves normalized at 620 nm (Govindjee, Ghosh, Crespi and Katz, unpublished).

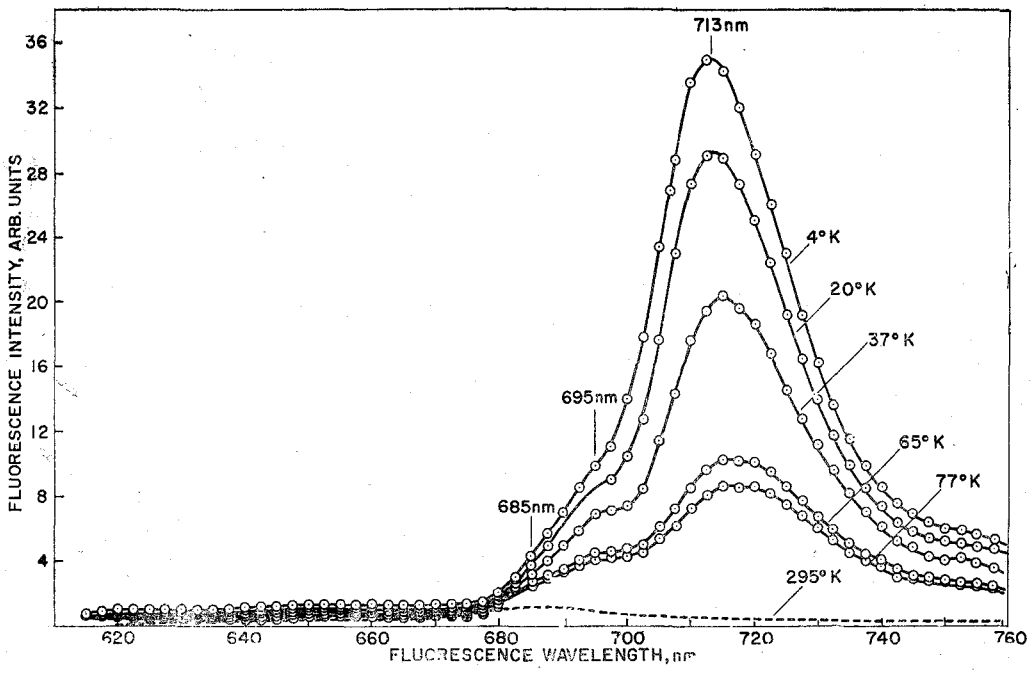
Photosynthetic Units

The classical experiments of Emerson and Arnold (1932 *a*, *b*) with saturating and brief light flashes showed the existence of photosynthetic units in the green alga *Chlorella*; these units were composed of 2,500 chlorophyll molecules per molecule of O_2 evolved. We know that for the evolution of one O_2 molecule 4 electrons (or 4 H-atoms) are transferred, in two steps, from H_2O to CO_2. Thus, 8 primary reactions are involved. Emerson's photosynthetic unit (PSU) could then be divided by 8 to yield units of 300 Chl molecules each. Since there are two light reactions, there are two types of energy traps, as discussed in the introduction: P700 for system I, and P680–690 for system II. (The composition of the two types of PSU in blue-green algae are not clearly understood as most Chl *a* is present in system I.) Thus, energy absorbed in each photosynthetic unit is transferred to its trap that also acts as the reaction center. At these centers the two primary oxidation-reduction reactions of photosynthesis occur.

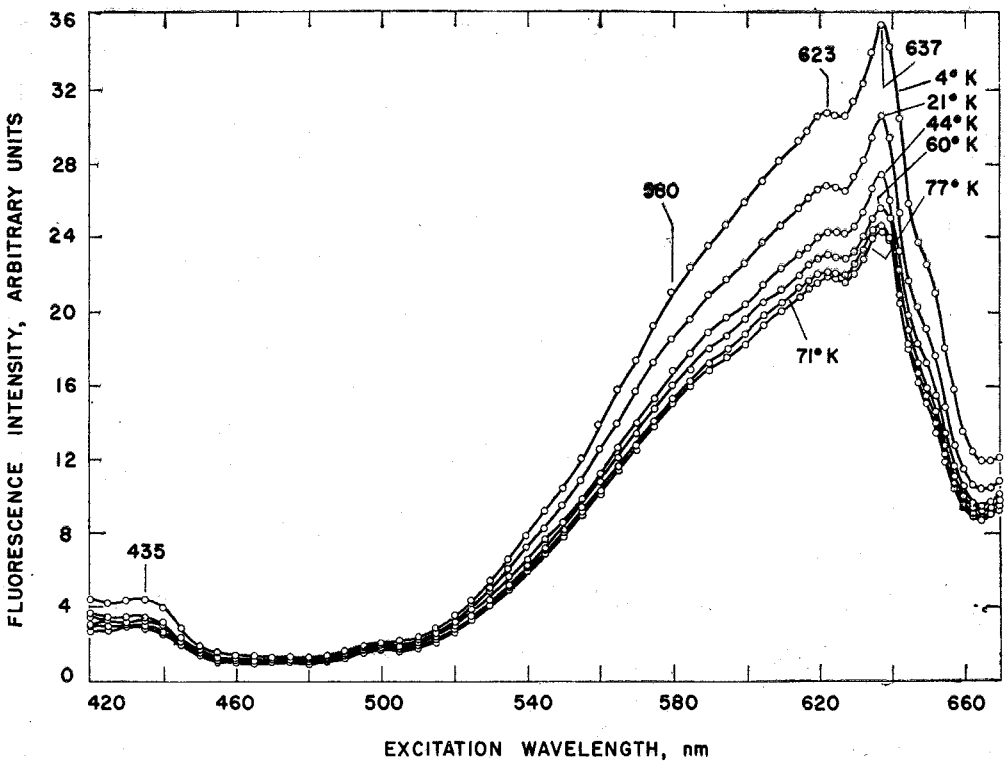
For photosynthesis to be efficient, the products of the primary reactions must be physically separated so that they don't react back. This may be accomplished if the oxidation of the primary reductant and the reduction of the primary oxidant occur on the two sides of the lamella on which photosynthetic units are embedded. Electron micrographs of chloroplast lamellae have suggested (Arntzen *et al.*, 1969) that the pigment system I is on the outer side of the lamella, and the system II on the inner side of the lamella. However,



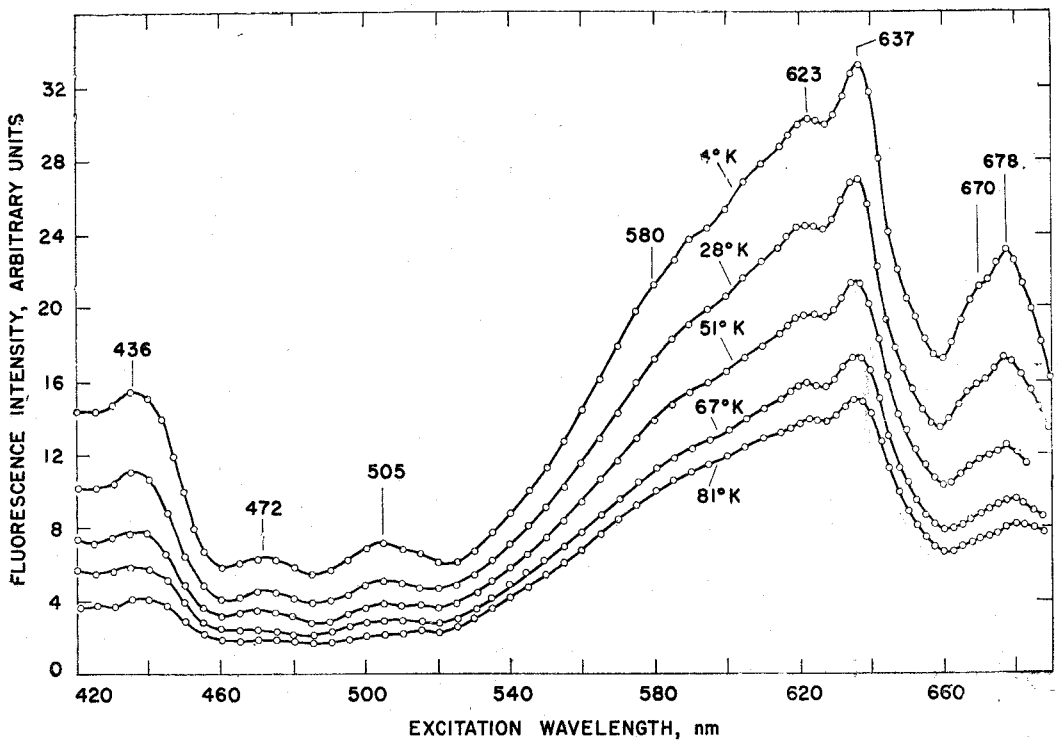
TEXT-FIG. 13. Emission spectra of *Anacystis nidulans* as a function of temperature (4 to 77° K); the room emperature spectrum (295° K) is shown for comparison λ excitation, 560 nm (Cho and Govindjee, 1971).



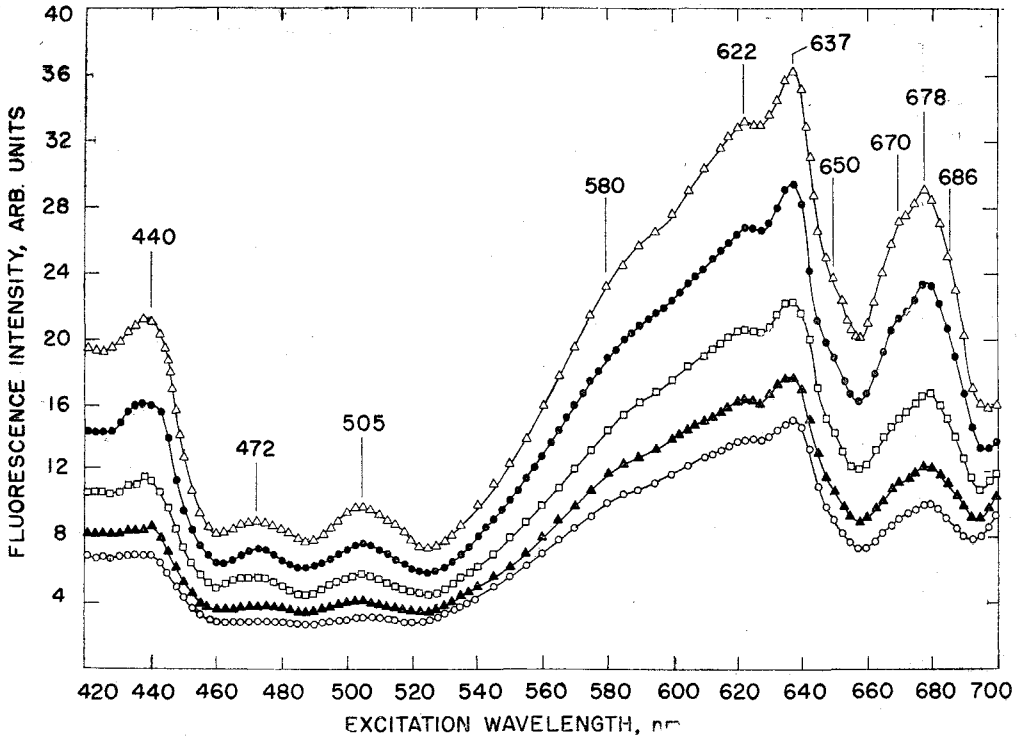
TEXT-FIG. 14. Emission spectra of *Anacystis nidulans* as a function of temperature (4 to 77° K); the room temperature spectrum (295° K) is shown for comparison. λ excitation, 435 nm (Cho and Govindjee, 1971).



TEXT-FIG. 15. Excitation spectra for chlorophyll fluorescence measured at 687 nm in *Anacystis nidulans* as a function of temperature (4 to 77° K) (Cho and Govindjee, 1971).



TEXT-FIG. 16. Excitation spectra for chlorophyll fluorescence measured at 698 nm in *Anacystis nidulans* as a function of temperature (4 to 77° K) (Cho and Govindjee, 1971).



TEXT-FIG. 17. Excitation spectra for chlorophyll fluorescence measured at 715 nm in *Anacystis nidulans* as a function of a temperature (4 to 77° K). Open triangles 4° K; solid dots, 31° K; open squares, 53° K; solid triangles, 68° K; open circles, 79° K (Cho and Govindjee, 1971).

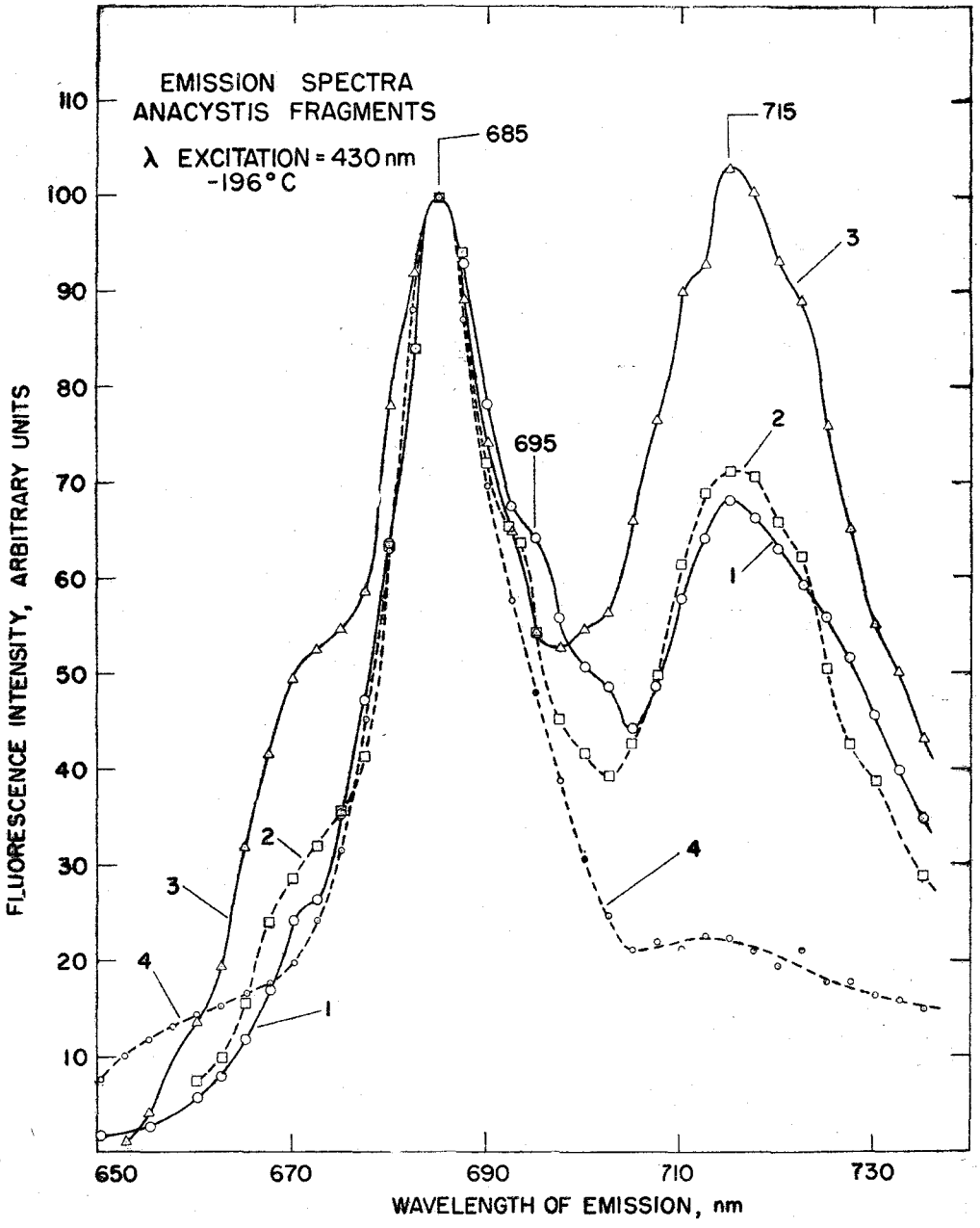
the picture in the red and blue-green algae is not so obvious because phycobilin containing particles (the phycobilisomes)—that should be in the system II—are attached on the outer side of the lamellae (Gantt and Conti, 1966).

Attempts (Ogawa and Vernon, 1969; Shimony *et al.*, 1967) to physically separate the two types of photosynthetic units (or the two pigment systems) in the blue-green algae have not been as successful as in green plants (Anderson and Boardman, 1966; see a recent review by Boardman, 1970). Shimony *et al.* (1967) obtained fractions (Text-Fig. 18) enriched in Chlorophyll *a* of system II, and of system I. Ogawa and Vernon (1970) have recently isolated a fraction from *Anabaena variabilis* that is enriched in the reaction center chlorophyll P700 (about 3 P700/100 Chl). This fraction is capable of $NADP^+$ reduction if appropriate H-donors are supplied. Active system II particles still remain to be isolated from blue-green algae. But, there is ample evidence for the existence of two types of photosynthetic units and reaction centers *in vivo*. We now turn to some other photochemical aspects of photosynthesis.

QUANTUM YIELD AND EMERSON ENHANCEMENT EFFECT

Quantum Yield

We learned in the introduction that there are two light reactions in photosynthesis. Let us look at the earliest suggestion about it from the data on the quantum requirement for O_2 evolution. Photosynthesis requires the transfer of 4 electrons from H_2O to CO_2 for the evolution of one molecule of O_2. If this transfer is aided by two light reactions in series, then we have eight primary reactions. For these reactions, we need at least 8 quanta of light because Einstein's law of photochemical equivalence requires one quantum of absorbed light per photochemical transformation. Indeed Emerson and Lewis (1942) found a minimum requirement of 11–12 quanta for the evolution



TEXT-FIG. 18. Emission spectra of *Anacystis* particles at 77° K (= − 196° C) prepared after treatment with digitonin and differential centrifugation. λ excitation, 430 nm. Fraction 1: at 1,200 × g for 10 minutes; fraction 2: 10,000 × g for 30 minutes; fraction 3: 50,000 × g for 60 minutes; fraction 4: last supernatant. Note the different ratios of 715 nm fluorescence to 685 nm fluorescence in fractions 2 and 3 (Shimony, Spencer and Govindjee, 1967).

of one O_2 molecule in the blue-green alga *Chroococcus*. This was confirmed (Govindjee, 1960) in the *Anacystis nidulans*. Thus, these data are consistent with the hypothesis of two light reactions.

If the light reactions leading to photosynthesis are indeed efficient, the other processes (*e.g.*, fluorescence) that drain the absorbed light energy must be very inefficient. This is also observed as the quantum yield of fluorescence (the number of quanta emitted per quanta absorbed) in blue-green algae is very low (0·2 to 2%) (Latimer *et al.*, 1957; Szalay *et al.*, 1967).

Since the two pigment systems, that sensitize the two light reactions, are known to absorb light of different wavelengths, the efficiency of the overall process must decrease in ths region where only one of the two systems absorbs the light. This is indeed the case.

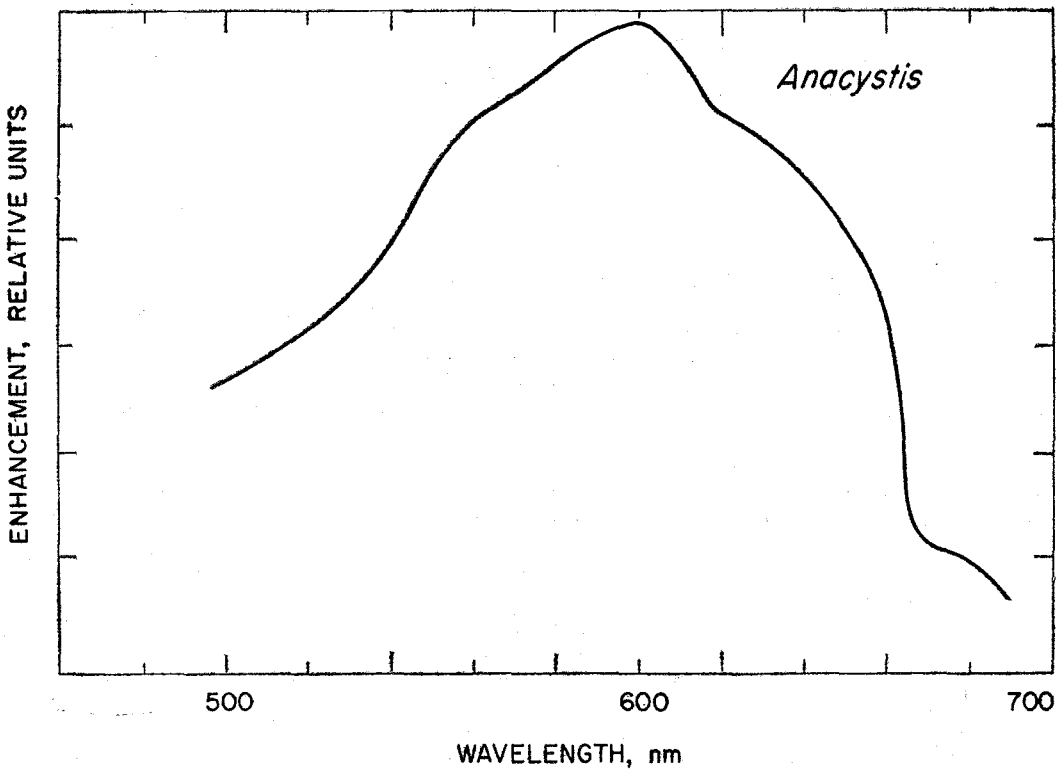
The Emerson Enhancement Effect

The first evidence for the operation of two light reactions came from the discovery by Emerson *et al.* (Emerson, 1956; Emerson *et al.*, 1957; Emerson and Rabinowitch, 1960) of a synergistic effect of two wavelengths of light on the photosynthesis of algae: when light of a certain wavelength (that is absorbed primarily by accessory pigments) is combined with far red light (absorbed primarily by Chl *a*), the production of O_2 in the combined beams is greater than the sum of the production in the two beams given separately. This phenomenon has been termed the Emerson Enhancement Effect and has been confirmed in several systems (Govindjee, and Bazzaz, 1967; Govindjee and Govindjee, 1965; Govindjee and Rabinowitch, 1960 *a*; Govindjee, R. *et al.*, 1964). It is usually calculated as:

$$E = \frac{RO_2 \text{ (combined beams) } \textit{minus } RO_2 \text{ (short wave beam)}}{RO_2 \text{ (long wave beam)}}$$

Using manometric techniques, Emerson and Lewis (1942) discovered that the quantum yield (the inverse of quantum requirement, *i.e.*, the number of O_2 molecules evolved per quantum absorbed) of photosynthesis declines when light is primarily absorbed by Chl *a*. This decline in the red end of the spectrum is referred to as the "red drop". This "drop" was shown to begin at 680 nm in the green alga *Chlorella* (Bedell and Govindjee, 1966; Govindjee, 1960; Emerson and Lewis, 1943), at 650 nm in the red alga *Porphyridium* (Brody and Emerson, 1959) and at 680 nm in *Anacystis* (Govindjee, 1960). Several considerations (*see* Das *et al.*, 1968; Govindjee, R. *et al.*, 1968; Hoch and Owens, 1963; Szalay *et al.*, 1967 *a*) lead us to believe that the "red drop" in blue-green algae begins at about 640 nm, and not at 680 nm as measured by manometry. In blue-green algae, the inhibition of O_2 up-take by low intensity red and far red light (Hoch and Owens, 1963) tends to give false O_2 evolution in this region causing an apparent shift in the location of the "red drop". The existence of the decline in the quantum yield of O_2 evolution, beyond 640 nm in the blue-green algae, is consistent with the hypothesis of two pigment systems sensitizing two light reactions. Of course, this is not a proof as light energy absorbed in the long wave absorbing pigment system could have been *inactive*. where RO_2 is the rate of O_2 evolution. On the basis of this effect, Emerson (personal communication to Govindjee, 1957–58) had proposed two light reactions in photosynthesis.

Action spectra of the Emerson effect.— The question was: what are the pigments involved in the two light reactions ? For this purpose, the action spectra of the Emerson effect were measured in *Anacystis* (Emerson and Rabinowitch, 1960; Govindjee and Rabinowitch, 1960 *b*). During these measurements, different wavelengths of light were combined with far red light (720 nm), and "E" (*see* equation) was plotted as a function of the different wavelengths. This spectrum showed a distinct peak due to phycocyanin (Text-Fig. 19). On this basis, one could suggest that one light reaction is sensitized by chlorophyll *a*, and the other by phycocyanin. However, the conclusion that accessory pigments alone can sensitize a reaction is hard to accept, as we have seen (*see* above) that light absorbed by phycocyanin is transferred to chlorophyll *a* with high efficiency. In 1960 it was suggested (Govindjee and Rabinowitch, 1960 *a, b*) on the basis of the presence of a peak at 670 nm in the action spectrum of Emerson enhancement effect in the green alga *Chlorella* and in a diatom *Navicula*, that for complete photosynthesis the two main forms of chlorophyll *a*, Chl *a* 670 (a form that preferentially receives energy from accessory



TEXT-FIG. 19. Action apectra of the Emerson enhancement effect in *Anacystis nidulans*. Light action of the far red light alone was 8·5 μl. O_2/hour, and the ratio of far red to supplementary light actions was about 1:1 (Govindjee and Rabinowitch, 1960).

pigments) and Chl *a* 680, need to be simultaneously excited. This was a more satisfactory picture, since the high efficiency of energy transfer from accessory pigments to chlorophyll *a* is taken into account. However, in the blue-green algae it was very difficult to find the Chl *a* 670 peak in the action spectrum of the Emerson effect (Govindjee and Rabinowitch, 1960 *b*). Duysens (1963) pointed out that the action spectrum of Emerson effect shows not the spectrum of one of the two pigment systems, but the difference between the two pigment systems. We now know that both Chl *a* 670 and Chl *a* 680 are present in both systems in all organisms. In *Chlorella* and *Navicula* system II is enriched in Chl *a* 670; therefore, we get peaks due to it in the action spectrum of the Emerson effect. However, in blue-green algae a larger proportion of both Chl *a* 670 and Chl *a* 680 is in pigment system I, and system II contains a very small amount of these Chl *a* forms. These smaller amounts of Chl *a* in system II are enough to explain the energy transfer from phycocyanin to chlorophyll *a* but not enough to give a peak in the action spectrum of the Emerson effect. Also, there is more phycocyanin in system II than in system I. This agrees with the conclusions made above. Detailed measurements by Jones and Myers (1964) have confirmed the composition of the two pigment systems mentioned above; there is four times more phycocyanin than Chl *a* in system II, and about equal ratio of phycocyanin and Chl *a* in system I.

THE ELECTRON TRANSPORT INTERMEDIATES

The mechanism of two light reactions and of electron transport in blue-green algae are essentially similar to that in higher plants (*see* introduction, and Fork and Amesz, 1969; Hind and Olsen, 1968; Holm-Hansen, 1968; Levine, 1969). The electron transport and photophosphorylation pathways of higher plants and green algae include the participa-

tion of several electron carriers. Some of these intermediates have been chemically characterized and others have been deduced mainly from the kinetic studies on oxygen evolution and fluorescence. We would catalogue below some of the participants in the electron transport with special reference to blue-green algae (Text-Fig. 3).

1·Z, Mn and O_2 Evolution

Excitation of system II reaction center P680–P690 is assumed to reduce the primary electron acceptor Q (or C550) and oxidize the primary electron donor Z. The primary light reaction of system II can be written as:

$$Z\ \text{Chl}\ a_{II}Q + h\nu_{II} \rightarrow Z^{-}\ \text{Chl}\ a_{II}Q^{-},$$

where Chl a_{II} is P680–P690. Thus light reaction II makes Z^{+} and Q^{-}. One Z^{+} is not enough to evolve O_2 from H_2O. Joliot *et al.* (1969) and Kok *et al.* (1970) have demonstrated that to evolve one O_2 molecule, 4 equivalents of Z^{+} are needed. By a series of complex reactions (Joliot *et al.*, 1969; Kok *et al.*, 1970; Mar and Govindjee, 1970), Z^{+} reacts with H_2O to evolve O_2:

$$4Z^{+} + 2H_2O \rightarrow 4Z + 4H^{+} + O_2 \uparrow$$

It is in this reaction that Mn plays an important role. Whether Mn is a component of Z (or not) is not yet known. Cheniae and Martin (1969, 1970) have shown that 6–12 atoms of Mn are associated with each O_2 evolving unit in *Anacystis nidulans*. (See a recent review by Cheniae, 1970).

The Q

Far-red light (system I) causes a decrease in fluorescence excited by system II light (Govindjee *et al.*, 1960; Mohanty *et al.* 1970; Munday and Govindjee, 1969). Duysens and Sweers (1963) suggested that system I light "produces" a quencher of fluorescence Q, and system II light reduces Q to QH, the latter being a non-quencher. The presence and the fate of "Q" was established by Duysens and Sweers (1963) in *Anacystis nidulans*. (For references to work on fluorescence in bacteria, *see* deKlerk *et al.*, 1969). There are speculations that Q may be a type of quinone (Govindjee, R. *et al.*, 1970; Kohl and Wood, 1969; Witt *et al.*, 1969) but there is, as yet, no definite evidence about its chemical identity. As noted earlier, it has been suggested that Q may be identical to C550 (Butler, personal communication). It occurs in a concentration of ~1/100 chlorophyll molecules and its oxidation-reduction potential at pH 7·0 is −35 mV in spinach chloroplasts. It is believed that reduced Q transfers its electron to plastoquinone and DCMU stops photosynthesis by blocking this electron transfer (Duysens and Sweers, 1963).

Amesz (1964) and Klingenberg *et al.* (1962) provided evidence for the participation of plastoquinones in the electron transport of photosynthesis of blue-green algae by difference absorption spectroscopy. Amesz has shown that only a few per cent of the total plastoquinones present are active as electron carrier. In *Anacystis*, 620 nm light (absorbed by phycocyanin) reduces plastoquinone, and 680 nm light (absorbed by Chl *a*) oxidizes it. Further evidence came from the biochemical investigations by Lightbody and Krogmann (1966). In cell-free preparations of *Anabaena*, they have shown that plastoquinone is required for the Hill reaction (reduction of 2, 6-dichlorophenol indophenol).

Plastocyanin

Levine (1969), on the basis of his experiments with *Chlamydomonas* mutants, has concluded that the sequence of electron transfer involving plastocyanin is:

$$\text{cytochrome}\ f \rightarrow \text{plastocyanin} \rightarrow \text{P700}.$$

As stated in the introduction, there is controversy regarding this sequence. Lightbody and Krogmann (1967) have purified plastocyanin from *Anabaena*. They have shown that this compound is required for system I reactions in cell-free preparations. However, cytochrome *c* isolated from the same alga can replace plastocyanin in these reactions. Thus, the role of plastocyanin in blue-green algae is not clear.

Cytochromes

Amesz and Duysens (1962) showed that a cytochrome of *c* type was an electron carrier between the two light reactions because they found that light absorbed in Chl *a* (system I) oxidized it, and in phycocyanin (system II) reduced it. This antagonistic effect of light of two different wavelengths is one of the best evidences for the operation of

two light reactions in series presented in Text-Fig. 3.

Fujita and Myers (1967) have made a kinetic analysis of light induced cytochrome *c* reactions in *Anabaena* lamella fragments. Holton and Myers (1967 *a*, *b*) have isolated and characterized three types of cytochrome *c* from lyophilized *Anacystis*: Cyt *c* 554, Cyt *c* 549 and Cyt *c* 552. The Cyt *c* 554 is very similar to cytochrome *f* isolated from green algae. The oxidation-reduction potential at pH 7·0 of Cyt *c* 554 is +350 mV.

Biggins (1967) has observed that extensively washed membranes of *Phormidium* retain cytochrome b_6 and Cyt *c* 554. This has been taken to mean that Cyt b_6 is an integral part of the photosynthetic lamellae. Biggins has also shown that Cyt b_6 and another unknown soluble intermediate is involved in the cyclic phosphorylation of blue-green algae.

The P700

Kok and Gott (1960) established the key role of P700 in the scheme of photosynthesis of blue-green algae. They found that system I light oxidizes P700 and system II reduces it. The primary light reaction I is:

$$X + P700 + h\nu_1 \rightarrow P700^+ + X^-.$$

The P700 has not been isolated in a pure state. (However, *see* Dietrich and Thornber, 1971). It appears to be tightly bound to the chloroplast lamellae. It is present in a concentration of 1/400 chlorophyll molecules, and its oxidation-reduction potential, at pH 7·0, is +430 mV.

The oxidized P700 oxidizes Cyt *c* 554, and the latter is " indirectly " reduced by system II.

Cytochrome c *Reducing Substance, Ferredoxin and NADP*$^+$

A cytochrome *c* reducing substance (CRS) was characterized by Fujita and co-workers (Fujita and Murano, 1967; Fujita and Myers, 1967). They found that it can be reduced in light, and the reduced CRS can reduce a cytochrome *c*. Unlike higher plants, this reaction does not require ferredoxin. There is a likelihood that this CRS may be FRS (ferredoxin reducing substance of higher plants). Honeycutt and Krogmann (1970) have observed a photoreduction of O_2 to H_2O_2 in *Anabaena* when reduced trichlorophenol indophenol is used as an H-donor. This reaction does not need any externally added acceptor besides O_2, and is inhibited by an antibody against FRS. This suggests that an oxygen reducing substance exists in blue-green algae that is identical to FRS. This substance may be the same as CRS. These compounds, perhaps, follow the " X " of blue-green algae. The role of another group of compounds the pteridines (Hatfield *et al.*, 1961; Maclean *et al.*, 1966; Fuller and Nugent, 1969) needs to be further investigated before definite conclusion regarding the nature of intermediates after " X " is made.

The transfer of electrons from reduced X to NADP$^+$ is mediated by CRS, ferredoxin and ferredoxin-NADP$^+$ reductase (a flavoprotein enzyme). Recently, Yamanaka *et al.* (1969) have obtained ferredoxin in a purified state from *Anacystics*. Bothe (1970) observed that in lyophilized *Anacystis* externally added ferredoxin catalyzes cyclic photophosphorylation. He found that one requires six to eight times more ferredoxin to saturate cyclic phosphorylation than to saturate NADP$^+$ reduction.

Susor and Krogmann (1966) have isolated ferredoxin-NADP$^+$ reductase from *Anabaena*. This enzyme seems to be loosely bound to the photosynthetic lamellae. In contrast, this enzyme is known to be very tightly bound to the lamellae in spinach chloroplasts. But, the enzymes from these two sources are similar in their absorption spectra, and in their Michaelis-Menton constant.

Black *et al.* (1963) have demonstrated the reduction of NADP$^+$ in fragments of blue-green algae. Amesz (1964) has shown that NADP$^+$ reduction occurs in intact cells of *Anacystis*. And Susor and Krogmann (1966) have demonstrated NADP$^+$ photo-reduction with cell-free preparations of *Anabaena variabilis*. (For a detailed description of the preparation of the components of the blue-green algae, *see* various articles in San Pietro, 1971).

Phosphorylation

Bedell (1972) has recently shown that intact blue-green algae (*Anacystis nidulans*, and a thermophilic strain of *Synechococcus lividus* show a greater ratio of cyclic to non-cyclic photophosphorylation than green algae (*e.g.*, *Chlorella*). In addition, the ratio of the ATP levels in light to that in darkness was higher in blue-green than in green algae. (For references to earlier literature, *see* Bedell (1972) and van Rensen, 1971).

CO_2 Fixation

CO_2 is incorporated into blue-green algae by the carboxylation of ribulose-diphosphate (Kindall and Gibbs, 1963; Norris *et al.*, 1955), but some CO_2 fixation may occur *via* other mechanisms (Evans *et al.*, 1966; Holm-Hansen and Brown, 1963). The end products of the photochemical reactions of photosynthesis, the reduced $NADP^+$, and ATP, are then used to provide the reducing power to convert fixed CO_2 into carbohydrates.

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