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DECREASE IN THE DEGREE OF POLARIZATION OF CHLOROPHYLL FLUORESCENCE UPON THE ADDITION OF DCMU TO ALGAE

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Introduction

If polarized light is used to excite Chlorophyll (Chl) *a* molecules in the photosynthetic unit, only those Chl *a* molecules with absorption dipoles parallel to the polarization of the incident light are excited. As energy is transferred among the Chl *a* molecules, the "memory" of the initial polarization is lost if the Chl *a* molecules are arranged in a random fashion within the chloroplast. This loss of memory is reflected in the low degree of polarization (p = 0.01 to 0.06) of fluorescence of Chl *a* *in vivo* (ARNOLD & MEEK 1956, GOEDHEER 1957, WEBER 1958, TEALE 1960, GOEDHEER 1966, GOVINDJEE 1966, CEDERSTRAND & GOVINDJEE 1966, WEBER 1954).

Using a newly constructed instrument, we show here that the degree of polarization of Chl fluorescence decreases when DCMU* is added to algae. We assume that after DCMU is added to the cells in the dark, the centers remain open. But, upon absorbing photons (or exitons) the centers close. The decrease in the degree of polarization of Chl fluorescence - described in this paper - could be interpreted to mean that the excitation is transferred by a "hopping" process (FÖRSTER 1965, HOCH & KNOX 1968) and not by a "wave packet" mechanism (ROBINSON 1966) only if we can assume that there are no "unconnected" Chl that do not change under DCMU.

Methods of Measurement and Instrumentation

The polarization of fluorescence (p) is usually calculated as:

$$p = \frac{{}_{\shortparallel}F_{\shortparallel} - {}_{\shortparallel}F_{\perp}}{{}_{\shortparallel}F_{\shortparallel} + {}_{\shortparallel}F_{\perp}} \qquad (1)$$

where ${}_{\shortparallel}F_{\shortparallel}$ is the fluorescence polarized in the same direction as the incident light and given off perpendicular to incident light, and ${}_{\shortparallel}F_{\perp}$ is the fluorescence polarized perpendicular to the polarization of the incident light and given off perpendicular to incident light. Note that the polarization of the incident light is perpendicular both to the direction of observation and the direction in which the beam is travelling (Fig. 1). There are systematic errors in measuring p; they come mainly from instrumental factors (imperfect mounting of polarizers, polarization of cut off colored filters, and of photomultipliers (CLANCY 1952) which may selectively transmit one polarization more than

* DCMU, 1,1'dimethyl-3(3'4'-dichloro)-phenyl urea.

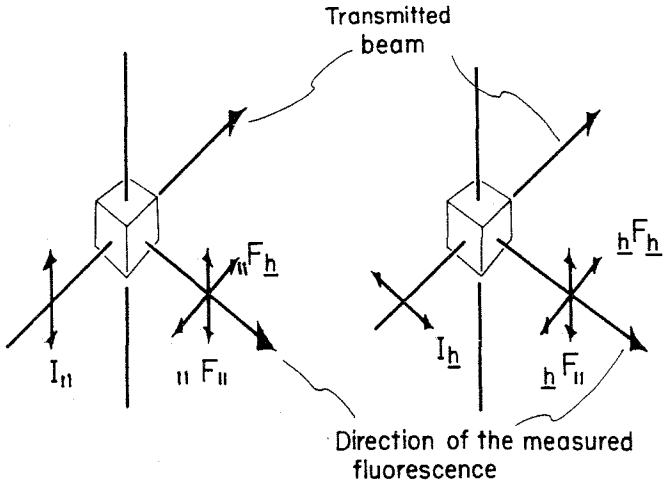

Fig. 1: Definition of "F" (see text), note that $\underline{h}$ is labelled as $\underline{\perp}$ in the text.

another. Other systematic errors in measuring p have been discussed in detail by WEBER (1956).

To overcome these systematic errors, we made two other measurements in addition to $_{\parallel}F_{\parallel}$ and $_{\parallel}F_{\underline{\perp}}$: $_{\underline{\perp}}F_{\parallel}$ and $_{\underline{\perp}}F_{\underline{\perp}}$ with the polarization of the incident light now rotated by 90° so that it is parallel to the direction of observation of the fluorescence but still perpendicular to its own path (Fig. 1). Geometrically, one can easily see that $_{\underline{\perp}}F_{\parallel}$ must be equal to $_{\parallel}F_{\underline{\perp}}$ because the polarization of the incident light is perpendicular to both $_{\underline{\perp}}F_{\parallel}$ and $_{\underline{\perp}}F_{\underline{\perp}}$, and there is no reason for fluorescence polarized in one direction to be different from fluorescence polarized in another direction since their fluorescing solution is isotropic. Any measured differences then must be due to instrumental factors. The ratio $_{\underline{\perp}}F_{\parallel}/_{\underline{\perp}}F_{\underline{\perp}}$ can be used to correct for the error in measuring $_{\underline{\perp}}F_{\underline{\perp}}$. Applying this correction factor to the definition of p, we have:

$$p = \frac{{}_{\parallel}F_{\parallel} - {}_{\parallel}F_{\underline{\perp}} \left(\frac{{}_{\underline{\perp}}F_{\parallel}}{{}_{\underline{\perp}}F_{\underline{\perp}}}\right)}{{}_{\parallel}F_{\parallel} + {}_{\parallel}F_{\underline{\perp}} \left(\frac{{}_{\underline{\perp}}F_{\parallel}}{{}_{\underline{\perp}}F_{\underline{\perp}}}\right)} \qquad (2)$$

Dividing both the numerator and the denominator by $_{\parallel}F_{\parallel}$ and rearranging the equation, we have

$$p = \frac{1 - \left(\frac{{}_{\underline{\perp}}F_{\parallel}}{{}_{\parallel}F_{\parallel}}\right)\left(\frac{{}_{\parallel}F_{\underline{\perp}}}{{}_{\underline{\perp}}F_{\underline{\perp}}}\right)}{1 + \left(\frac{{}_{\underline{\perp}}F_{\parallel}}{{}_{\parallel}F_{\parallel}}\right)\left(\frac{{}_{\parallel}F_{\underline{\perp}}}{{}_{\underline{\perp}}F_{\underline{\perp}}}\right)} \qquad (3)$$

We designed the instrument so that it could measure $_{\perp}F_{\parallel}/_{\parallel}F_{\parallel}$ and $_{\parallel}F_{\perp}/_{\perp}F_{\perp}$. To measure $_{\perp}F_{\parallel}/_{\parallel}F_{\parallel}$, the incident light alternated every few milliseconds fron one with one polarization ($I_{\parallel}$) to another with the perpendicular polarization ($I_{\perp}$). The resultant fluorescence signal $_{\parallel}F_{\parallel}$ and $_{\perp}F_{\parallel}$ was measured with its polarizer fixed at one polarization. Since both fluorescence signals are measured exactly the same way, systematic error in the measurement is exactly the same in both cases. By measuring $_{\parallel}F_{\parallel}$ and $_{\perp}F_{\parallel}$ within a short time, long time errors due to light intensity fluctuations and changes in fluorescence were eliminated. By turning the fluorescence polarizer 90° to that of the above measurements, $_{\parallel}F_{\perp}$ and $_{\perp}F_{\perp}$ were measured exactly as before. Again, since both fluorescence are measured exactly the same way, the systematic error is exactly the same on both measurements. By taking the ratio of $_{\parallel}F_{\perp}$ and $_{\perp}F_{\perp}$, the systematic error is cancelled. Hence, having the ratio $_{\perp}F_{\parallel}/_{\parallel}F_{\parallel}$ and $_{\parallel}F_{\perp}/_{\perp}F_{\perp}$, p is calculated from equation 3 (see above).

The instrument assembled to measure the polarization of fluorescence is shown in Fig. 2. Polarizer A is a nicol prism (5 mm in crossection, obtained from a polarizing microscope); the polarizers B, C and D are Glan Thompson prisms (12 mm in crossection, Karl Lambrecht Crystal Optics Co.). The excitation source is a He-Ne laser (Coleman Model 75; λ, 632.8 nm); this laser is placed between a 5000 gauss permanent magnet to stabilize its intensity and polarization direction (McMAHON 1969). The laser beam passes through a rotatable polarizer A to a beam splitter. One beam passes through polarizer B set at a fixed polarization; the other beam is deflected by two mirrors to polarizer C set at a polarization angle 90° to that of polarizer B. The two beams are recombined by another beam splitter and then are directed to the sample. A mechanical chopper is used to alternate the two beams 70 times per second.

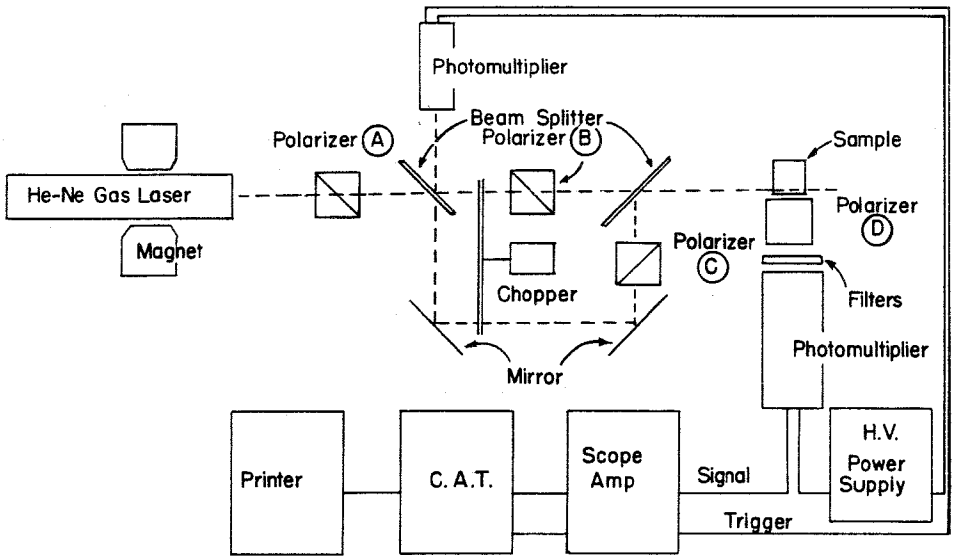

Fig. 2: Block diagram of the apparatus for the measurement of polarization of fluorescence (see text for details).

The sample sees first one beam, then a period of darkness, then the other beam, then another period of darkness, and then the first beam again and so on. The beam intensity was 550 ergs/cm^2 sec as measured with a radiometer (Yellowspring Model 65). Polarizer D is used as the observation polarizer. It is rotatable and it is in one of two positions. Its polarizing angle is either the same as that of polarizer B or it is the same as that of polarizer C. A cut-off colored filter (usually Corning CS 2-64, unless otherwise specified) is placed in front of the photomultiplier to separate the fluorescent light from the scattered incident light. The S-20 photomultiplier (EMI 9558 B) is operated at 900 volts for low noise. The signal from the photomultiplier is fed to channel A of a Tektronic 502 oscilloscope where it is amplified. To reduce the random noise of the photomultiplier, the amplified signal is stored into a computer of average transients (CAT, Model 400C, Mnemetron Division of Technical Measurements Corp.). As continually successive signals are added, the CAT averages out the random noise. After an averaging time of five minutes, the signal is recorded on a printer. The recorded signal (Fig. 3) is then analyzed.

Signal from another photomultiplier (RCA 7102) is used to trigger the CAT. This photomultiplier monitors the light that is reflected from the front face of polarizer B. This signal is passed through a high pass filter (a 25 mμf capacitor in series with the photomultiplier output and a 10^6 Ω resistor across the photomultiplier output to ground) into the Channel B of the oscilloscope. The amplified signal from the oscilloscope triggers the CAT.

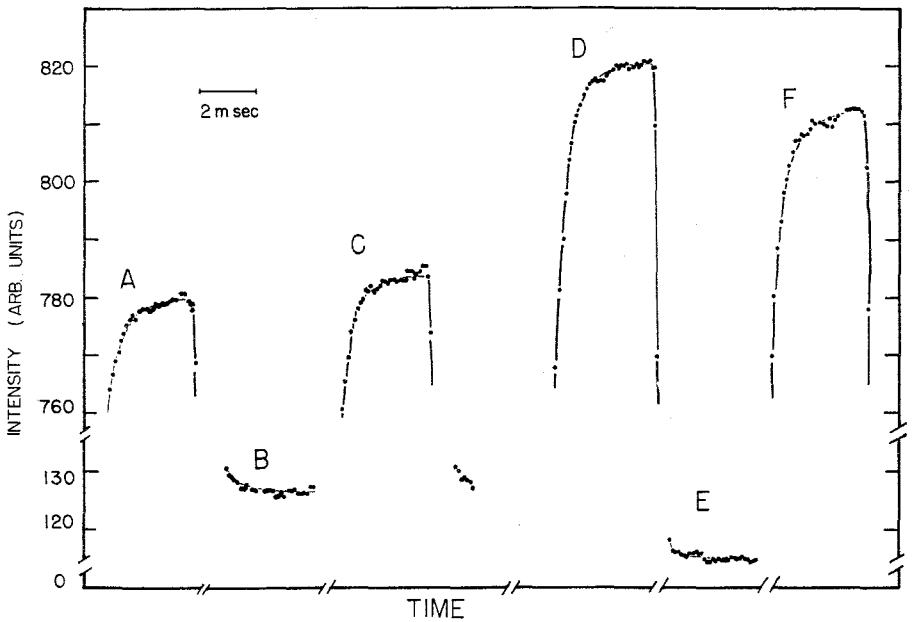

Fig. 3:Typical fluorescence signals from the output of the CAT used to calculate the polarization of fluorescence. A, is the fluorescence intensity of $_{\perp}F_{\parallel}$; B, dark base-line; C, $_{\perp}F_{\perp}$; D, $_{\parallel}F_{\parallel}$; E, dark base-line; F, $_{\parallel}F_{\perp}$; all signals are averages of five minutes (see text, and Fig. 1).

Results and Discussion

1. Effect of DCMU on polarization of Chl Fluorescence

Table I shows the polarization of steady state Chl fluorescence measured for *Chlorella* and *Porphyridium* (grown as previously described, GOVINDJEE & RABINOWITCH 1960) with and without the addition of 10^{-5} M (or 10^{-6} M) DCMU. The absorbance of the algae used was lower than 0.05 at 670 nm for all measurements. The polarization of Chl fluorescence of cells with DCMU added is smaller than the norml cells in both cases. The difference is clearly seen in the case of *Porphyridium* where "p" decreases from about 0.02 to 0.01. In this connection, we note that LAVOREL (1964) found that "p" for the variable fluorescence was smaller than "p" for the constant fluorescence. Our data are consistent with these findings if we assume that a large part of the steady state fluorescence in the presence of DCMU is equivalent to variable fluorescence.

Two explanations can be given for the decrease in p when DCMU is added to the cell. First, a "trivial" possibility. The decrease in p may be due to the presence of "unconnected" Chl-protein complexes with high p. We define "unconnected" as not being attached to any photosynthetic unit. Assuming that the p from the photosynthetic unit due to extensive energy migration is zero, then the small p measured could be due entirely to the unconnected Chl-protein complex. Since the fluorescence yield increases when DCMU is added to the cell, the percentage of the total fluorescence that is due to the loose Chl-protein complexes decreases. Hence p will also decrease as seen from the definition of p in equation 1. An increase in the fluorescence yield from the completely depolarized component will only add to the denominator $\perp F_{\parallel} + \perp F_{\perp}$. Hence the ratio $\frac{\perp F_{\parallel} - \perp F_{\perp}}{\perp F_{\parallel} + \perp F_{\perp}}$ or $\bar{p}$ will decrease.

Let us assume that under steady illumination, in the absence of DCMU, a fraction f_1 comes from Chl molecules connected with the reaction centers, and f_2 $(= 1-f_1)$ corresponds to unconnected Chl molecules that do not change under DCMU. Then:

$$\bar{p} = f_1 p_1 + f_2 p_2 \text{(no DCMU)}$$

and

$$\bar{p}_d = f_{1d} p_{1d} + f_{2d} p_2 \text{ (with DCMU,d).} \qquad (4)$$

The measured value of $\bar{p}$ is 0.01 in Chlorella (Table I), and if we assume that p_1 equals zero and the p_2 for the unconnected Chl complex is 0.20[3], then, using WEBER's summation law (see equation 4, WEBER 1958), the probability that the fluorescence comes from the unconnected Chl-protein complex can be calculated to be 5% for *Chlorella*. Assuming the fluorescence yield of the unconnected Chl-protein complex inside the cell is the same as the fluorescence yield of photosystem II and hence twice as large as the measured fluorescence yield (LATIMER et al. 1956), then the absorption crossection of the complex is estimated to be 2.5% that of the photosynthetic unit in *Chlorella*. In *Porphyridium* a similar calculation shows (as $\bar{p}$ = 0.02) that the absorption crossection of

Table I. Polarization of Fluorescence: Effects of DCMU and Hydroxylamine

Excitation wavelength, 632.8 nm; Corning filter CS-2-64 before the measuring photomultiplier; calculations using equation (3) (see text).

Sample	Normal	10^{-5} M DCMU	10^{-3} M Hydroxylamine
Chlorella	0.008	0.005	0.009
	0.009	0.006	-
	0.009	0.006	-
	0.008	0.006*	0.009
Porphyridium	0.021	0.010	0.020
	0.021	0.013	-
	0.021	0.011	0.020

* 10^{-6} M DCMU added

the unconnected Chl-protein complex is 5% that of the photosynthetic unit.

It is highly unlikely, however, that the cell, having its own machinery to control and to direct the synthesis of the photosynthetic unit, would waste energy to make imperfect units which in turn will compete with regular units for photons. Also, measurements by GOVINDJEE and MOHANTY (unpublished) indicate that $\bar{p}$ for dilute suspensions of *in vivo* Chl-protein complexes (prepared by P.THORNBER 1969) is close to 0.05*, and not 0.20. Assuming a p of 0.05 for the complex, we calculate the percentage of "unconnected"Chl-protein complex to be 20%, and we know this cannot be true because the high quantum yield of photosynthesis (GOVINDJEE et al. 1968) would not allow it! Thus, we feel that the polarization of fluorescence may not be caused by unconnected chlorophyll-protein complexes, as is also implied in all the past research. We cannot, however, unequivocally prove this.

The second more meaningful explanation, for the lowering of p upon the addition of DCMU, assumes that there are no unconnected Chl-protein complexes. That is, in equation (4) $f_2p_2 \rightarrow 0$ or $f_1p_1 >> f_2p_2$. The small value of p measured (in normal cells) is due to the partial retention of the initial polarization as energy migrates about a partially random system of Chl molecules (see Introduction). BAY & PELARSTEIN (1963), using as a model for the photosynthetic unit a sphere of radius 74Å with 400 Chl *a* molecules arranged randomly and a trap in the center of the sphere, calculated the mean number of jumps in a random walk, before it reaches the trap, to be 130. In this and other calculations

* WEBER (personal communication) has, however, pointed out that this value may be minimal especially because there could be energy transfer between a group of very complex molecules, or between the different chromophores in the same complex. Also the Chl-protein complexes isolated by THORNBER may be larger than the "unconnected" Chl-protein complex postulated here.

(TEALE 1960), the FÖRSTER mechanism (FÖRSTER 1948) of energy transfer was assumed. If a stronger interaction between the Chl molecules is assumed, then the number of jumps will be larger. Hence if Chl molecules are randomly oriented within the chloroplast, the measured polarization of fluorescence should be much lower than that observed. In this connection, we note that p values obtained in this report is one of the lowest observed so far. WEBER (1958) explains this discrepancy by pointing out that Chl in the chloroplast may be arranged in a partially random fashion and the calculated value for energy migration is the minimum value.

Using WEBER's Summation Law and assuming that Chl *a* molecules are oriented with respect to each other in a partially random way such that only the initial molecule that absorbed the polarized photon will emit light of high polarization, it can be shown (KNOX 1968) that

$$\frac{\bar{p}}{\bar{p}_d} = \frac{f_o}{f_{od}} \qquad (5)$$

where $\bar{p}$ is the polarization of Chl fluorescence measured in the normal cell, $\bar{p}_d$ be the polarization of fluorescence measured in cells with DCMU added, f_o is the fraction of total fluorescence contributed by Chl molecules that initially absorb the polarized photons in normal cells, and f_{od} is the fraction of the total fluorescence contributed by Chl molecules that initially absorb the polarized photons in cells with DCMU added.

The calculated ratio of $\bar{p}$ to $\bar{p}_d$ for *Chlorella* is 1.33 and for *Porphyridium* $\sim$ 2.0. This imples that the fraction of the total fluorescence that is emitted by the original absorber when the cells have most of their reaction centers open is greater than when the cells have all their reaction centers closed. If one assumes that the fluorescence yield of the initial absorber is the same in normal cells and in cells with DCMU added, than the ratio of the initial absorbing Chl molecule to the number of excited Chl molecules that can fluoresce is smaller in cells with DCMU added. This implies that the total number of excited Chl molecules that can fluoresce is greater in cells with DCMU added than in normal cells. Hence the number of molecules that are visited by the excitation energy when the reaction centers are closed is greater than when the reaction centers are open.

Polarization of fluorescence may be used to distinguish between two possible mechanisms (FÖRSTER 1965, HOCH & KNOX 1968, ROBINSON 1966) that have been proposed to explain excitation energy transfer among Chl molecules in the photosynthetic unit. One theory (see ROBINSON 1966) assumes that energy transfer is by a mechanism involving rapidly moving delocalized excitons ("wave packets"). By this mechanism, the excitation energy can spread over the entire photosynthetic unit - in a time that is about 1,000 times faster than the lifetime of the singlet state of Chl. At low intensities, when all the reaction centers are open, ROBINSON (1966) calculated that the trapping efficiency per encounter with the reaction center is only about 1%. In this case, the excitation energy will have an approximately equal probability of being

in each Chl molecule in the photosynthetic unit whether the reaction center is open or closed. Thus, the polarization of Chl fluorescence will be approximately the same with the reaction center open or closed. (However, the fluorescence yield will not be independent of the state of the reaction center.)

In the second theory (see FÖRSTER's "weak coupling" case) the interaction between two molecules is much less than the intramolecular interaction between electronic and nuclear motion. Under these conditions, thermal equilibrium is established in the excited vibrational level (*i.e.* the excitation is temporarily localized on a single molecule) before the excitation energy is transferred; this transfer is visualized as a sequence of uncorrelated individual transfer processes (the "hopping" process). The time needed for an excitation to reach the trap is much longer than that in the "intermediate (or strong) coupling" case, and the reaction center is assumed to be irreversible (or almost 100% efficient in trapping excitation). In this "weak coupling" case, the number of molecules that the localized exciton visits will depend upon its lifetime. When the reaction center is open, the number of molecules that the localized exciton visits is much smaller than when it is closed. If the molecules are arranged in a random fashion, the fluorescence will be more depolarized if more molecules are involved (closed reaction centers). Our results - and those of LAVOREL (1964) - may then be interpreted to mean that the energy migrates in a hopping motion and the pairwise transfer is due to the FÖRSTER's mechanism, and not be delocalized excitons ("wave packets"). However, because of the possibility of the existence of unconnected Chl molecules, we cannot come to any definite conclusion yet.

We may predict (as suggested by LAVOREL, personal communication) that in ultra-weak measuring light, addition of DCMU to photosynthesizing cells would not significantly decrease p because the reaction center would remain open in both the cases. Preliminary measurements confirm this prediction. Furthermore, in the absence of DCMU, a decrease of "p" would be observed if the intensity of our measuring light is increased - as it would tend to close the reaction centers. We could not test this prediction as we have no way of increasing the intensity of excitation of our instrument.

2+ Effect of Hydroxylamine on the Polarization of Chl Fluorescence

The addition of 10^{-3} M hydroxylamine to normal *Chlorella* and *Porphyridium* cells did not change the "p" values. This could be explained if we assume that hydroxylamine, at this concentration does not close the reaction center, and it simply acts as an electron donor replacing water as suggested earlier by other workers (MAR 1971, VAKLINOVA 1964, IZAWA et al. 1969, BENNOUN & JOLIOT 1969, STACY et al. 1971).

3. Wavelength Dependence of "p" in DCMU-Poisoned Cells

Table II shows the polarization of Chl fluorescence of *Chlorella* and *Porphyridium* measured with different cut-off filters transmitting different wavelengths to see if there was any wavelength dependence.

Table II. Polarization of Fluorescence: Wavelength Dependence.

Fluorescence is monitored with three Corning cut-off filters before the measuring photomultiplier; see Table I.

Sample	CS 2-64*	CS 7-59**	CS 7-69***
Chlorella + 10^{-5} M DCMU	0.005	0.004	0.004
Porphyridium + 10^{-5} M DCMU	0.011	0.012	0.010

* Zero transmittance up to 640 nm, 50% at 670 nm, and 85% at 720 nm and longer wavelengths.
** Zero transmittance up to 685 nm, 50% at 710 nm, and 85% at 750 nm and longer wavelengths.
*** Zero transmittance up to 710 nm, 50% at 740 nm, and a peak transmittance of 80% at 760 nm.

The polarization of fluorescence of both the algae with 10^{-5} M DCMU did not change with the wavelength of observation. We do not speculate on the significance of this result, and its apparent contradiction to those of other investigators (LAVOREL 1964, OLSON 1963, OLSON, et al. 1961, OLSON et al. 1962, OLSON et al. 1964, BUTLER et al. 1964). We, however, note that our experimental conditions are so different from those of the others that a valid comparison is not possible.

Summary

Using a newly constructed instrument (x 6328 AO) to measure precisely the degree of polarization (p) of chlorophyll (Chl) fluorescence, we found that "p" decreases from a value of 0.02 to 0.01 in the red alga *Porphyridium cruentum*, and from 0.009 to 0.006 in the green alga *Chlorella pyrenoidosa* when 10^{-5} to 10^{-6} DCMU - that closes the reaction center upon illumination - is added to the cells. However, the addition of 10^{-3} M hydroxylamine - that replaces H_2O as electron donor - does not change the "p" value. In the presence of DCMU, "p" of Chl fluorescence *in vivo* was found to be independent of the wavelength of the observation.

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