

interact to any appreciable extent, if indeed they interact at all. What this means in terms of chromosome structure is not yet clear. It is clear, however, that it cannot be assumed on the basis of the available evidence that interaction occurs through a common repair system that is unable to distinguish one broken bond from any other. It is possible that the repair system cannot join two unlike bonds or that there is more than one system operating in the process we call rejoining.

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### Fluorescence of Photosynthetic Organisms at Room and Liquid Nitrogen Temperatures

**Abstract.** Fluorescence spectra of algae and higher plants show two bands, ascribable to monomer and aggregate forms of chlorophyll. At low temperature, the long-wavelength emission is greatly enhanced and often appears as a new band. Photosynthetic bacteria, on the other hand, show no new bands at low temperature, within the spectral coverage and sensitivity of these measurements. A green fluorescence is also found in algae, which we attribute to carotenoids.

Fluorescence and absorption studies indicate that chlorophyll may exist in vivo in both monomeric and aggregated forms (1-4). Particularly strong evidence supporting this view has been given by S. Brody, who attributed a long-wave fluorescence appearing at low temperature to such an aggregate, on the basis of analogous behavior of concentrated chlorophyll solutions. It has been further suggested (3-5) that the decline of photosynthetic efficiency at long wavelengths, first observed by Emerson and Lewis (6), is due to pref-

erential light absorption by this aggregated species. Other explanations have also been discussed for this long-wavelength decline (7, 8). In this report, we present a summary of new experiments on the fluorescence of various photosynthetic organisms which further extend the considerations mentioned above.

Fluorescence spectra were determined at room and liquid nitrogen temperatures (9) for various algae (*Ochromonas danica*, *Chlorella pyrenoidosa*, *Euglena gracilis*, *Porphyridium cruentum*), photosynthetic bacteria (*Rhodospirillum rubrum*, *Rhodospseudomonas palustris*, *Chromatium d*), and leaves of higher plants (*Prunus virginiana*, *Betula papyrifera*). These forms were selected as representative of various plant pigment systems.

Figure 1 shows typical fluorescence spectra of *Ochromonas*. The room temperature chlorophyll spectrum consists of a single broad band, with maximum at 685 m $\mu$ . At low temperature, two bands are found, shifted from the room temperature peak toward longer wavelengths by about 3 m $\mu$  and 20 m $\mu$  respectively. The effects are reversible. The low-temperature, long-wave emission is again attributed to aggregated chlorophyll, while the band at shorter wavelength is assigned to the monomer. The slight shift in wavelength of this latter band with temperature is observed also in chlorophyll solutions in vitro (3), and is probably due to Franck-Condon effects.

In general, at low temperature (with, typically, 436 m $\mu$  excitation), the intensity of fluorescence from the chlorophyll aggregate relative to that from the monomer increases with increasing age of the algal culture or leaf, until a stable ratio is reached. In the case of *Ochromonas*, *Chlorella*, and the higher plants, the final relative (uncorrected) intensities of the two low-temperature bands are roughly equal (Fig. 1).

In another group of algae, the low-temperature aggregate emission in mature cultures far exceeds the monomer emission. This is the case, for example, in *Euglena* (Fig. 2) and *Porphyridium*. Direct measurements of absorption spectra of *Euglena* at room and liquid nitrogen temperatures show surprisingly little difference and rule out the possibility that the observed fluorescence changes are artifacts, due to selective reabsorption of fluorescent light. In these algae, we have confirmed the observations of French that, indeed, even the room-temperature fluorescence spectrum shows marked broadening, shifts in peak location, and appearance of shoulders, as the culture ages (10). Such effects, found to a lesser degree also in the other green

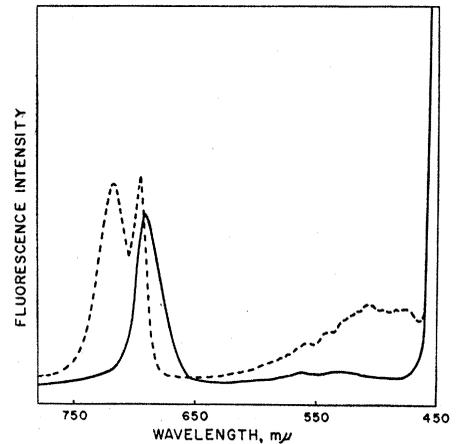


Fig. 1. Fluorescence spectra of 2-week culture of *Ochromonas danica*, at room temperature (solid line) and liquid nitrogen temperature (broken line). Excitation, 436 m $\mu$ . Spectra in Figs. 1, 2, and 3 are uncorrected for variation in photomultiplier sensitivity (Du Mont, 6911). Increased scattering, resulting from freezing of the algal suspension, makes the fluorescence yield at the lower temperature appear smaller than it actually is.

plants, may arise from a sufficiently strong aggregate emission in mature cultures to be observable even at room temperature. It is noteworthy that in *Porphyridium*, in which such large amounts of aggregated chlorophyll are found, the long-wavelength decrease in photosynthetic efficiency begins at about 650 m $\mu$  (7), whereas in algae of the first group, as typified by *Chlorella*, the decline sets in at about 685 m $\mu$  (6).

Several explanations are possible for the enhancement of long-wave fluorescence at low temperature. As pointed out earlier (3), cooling may cause an

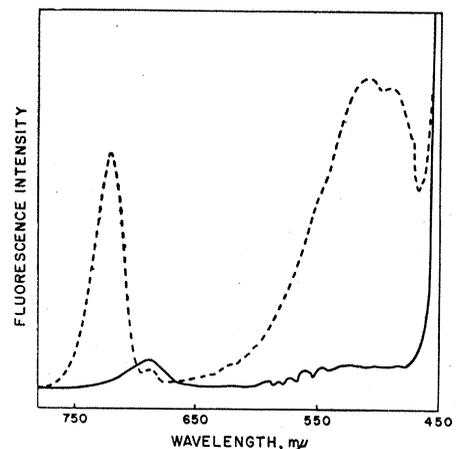


Fig. 2. Fluorescence spectra of 48-hour culture of *Euglena gracilis*, at room temperature (solid line) and liquid nitrogen temperature (broken line). Excitation, 436 m $\mu$ . In older cells the monomer band is difficult to detect because of the great height and breadth of the aggregate band.

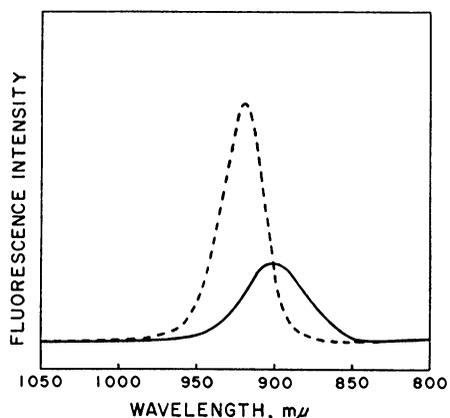


Fig. 3. Fluorescence spectra of 48-hour culture of *Rhodospirillum rubrum*, at room temperature (solid line) and liquid nitrogen temperature (broken line). Excitation, 365  $m\mu$ .

increase in aggregate concentration due to reversible association, or competing deactivation processes may be prevented. Another possibility is that low temperature may enhance energy-transfer processes into the aggregate from other pigments, by virtue of changes in relative molecular configuration, an increase in lifetime of the monomer excited state, or the shift to longer wavelength of the monomer luminescence. However, the most likely explanation seems to us to be a decrease in competing deactivation processes as the temperature is lowered.

In contrast to the situation in green plants, the various bacteria examined here show only one band in the low-temperature fluorescence spectrum, within the range of our fluorometer. This band is shifted about 20  $m\mu$  to longer wavelength, from the position of the room-temperature emission. The spectral sensitivity of the fluorometer was such that fluorescence bands as far out as 1020  $m\mu$  would have been detected, if their intensity were of the same order of magnitude as the single band observed at 910  $m\mu$ . We conclude, therefore, that only one type of fluorescent chlorophyll is present in the bacteria studied. This result is in agreement with the conclusions of Duysens, based on room temperature fluorescence data (11). Whether the single emitting state in bacteria corresponds to monomeric or aggregate bacteriochlorophyll is still uncertain. Experiments in vitro and lifetime measurements are in progress to establish this.

The differences noted here between the behavior of green plant and bacterial chlorophyll systems are especially intriguing, in view of the differences in the photosynthetic processes found in these two types of organism. Thus, one may suspect that the participation of two distinct fluorescent levels is

needed for evolution of molecular oxygen, whereas the availability of only one such state can carry photosynthesis only to the level of an oxidizing agent intermediate between water and oxygen.

We draw attention (Figs. 1 and 2) to the fluorescence band near 515  $m\mu$ , which we believe is due to carotenoid emission. Excitation and emission spectra of *Euglena* in this region are similar to those of EPA solutions of antheroxanthin (12).

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### Use of a Computer to Evaluate Alternative Insecticidal Programs

**Abstract.** A simple numerical routine which mimics the effects of density-dependent factors and weather has been used to simulate insect pest population trends without control, and with a variety of insecticidal procedures. Results of the analysis suggest that apparent benefits from spraying are illusory, since spraying elicits homeostatic response by the pest population.

In the last few years there has been great interest in novel techniques for insect pest control: species-specific sex attractants to lure adult male insects to a demise which precludes copulation (1), and manipulation of genetic composition of natural populations by releasing radiation-sterilized (2) or foreign (3) males. Two reasons for this concern with novel control methods are the failure of insecticides and the spectacular success of the program to control screwworms by mass release

of radiation-sterilized males (2). In view of the variety of insect pest control procedures available and the amount of money at stake in crops and forests, it would seem worthwhile to attempt construction of a mathematical theory of pest control. Such a theory should be designed to indicate the best type of control, or combination of types of control, for any situation, how to time control, and how intensive control should be for optimum effects.

There are a few well-documented cases showing what happens to a pest that has in fact been effectively controlled: it becomes extinct (2) or it persists at a very low level (4). With these cases as the standard of ideal control, it is clear that insecticides do not constitute ideal control. Failure of insecticide control has been attributed generally to selection of resistant strains (5), physiological stimulation by sublethal doses (6), and elimination of entomophagous species (7). However, perhaps there is a more basic explanation than any of these: use of insecticides reduces intraspecific competition pressure to such an extent that increased fecundity, fertility, and survival rates compensate, or more than compensate, for the drop in population (8).

As a first step in devising a mathematical model to compare the long-term effects of various control procedures, I have developed a simple numerical routine with which a computer can simulate pest population trends.  $N_i$  represents the number (per unit area) of adults in the  $i$ th generation;  $N_{i + \frac{1}{2}}$  represents the number of larvae present at the end of the third instar (that is, after half the larval growing stage has been completed);  $D_i$  represents the average number of third-instar larvae surviving per adult under average weather conditions;  $D_i^1$  represents the average number of adults surviving per third-instar larva under average weather conditions;  $S$  represents the proportion of third-instar larvae surviving spray treatment; and  $W_i$  is a factor by which the  $D_i$  and  $D_i^1$  values must be multiplied to express the effect of weather in the  $i$ th generation. Then

$$N_{i + \frac{1}{2}} = N_i D_i W_i \quad (1)$$

$$N_{i + 1} = N_{i + \frac{1}{2}} D_i^1 W_i S \quad (2)$$

$D_i$  is computed from the empirical formula

$$D_i = \frac{C_i}{N_i} \left[ 1.0 - \exp \left\{ -N_i \times \frac{(C_1 + \exp [C_2 - C_3 N_i])}{C_4 + \exp (C_5 - C_6 N)} \right\} \right] \quad (3)$$

where the  $C$ 's are constants. Arguments in support of this general form for  $D_i$  are given elsewhere (8).  $D_i^1$  has the same form, but a different set of