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FLUORESCENCE EMISSION SPECTRA OF CHLOROPLASTS AND SUBCHLOROPLAST PREPARATIONS AT LOW TEMPERATURE

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Summary

A study was made of the chlorophyll fluorescence spectra between 100 and 4.2 K of chloroplasts of various species of higher plants (wild strains and chlorophyll *b* mutants) and of subchloroplast particles enriched in Photosystem I or II. The chloroplast spectra showed the well known emission bands at about 685, 695 and 715—740 nm; the System I and II particles showed bands at about 675, 695 and 720 nm and near 685 nm, respectively. The effect of temperature lowering was similar for chloroplasts and subchloroplast particles; for the long wave bands an increase in intensity occurred mainly between 100 and 50 K, whereas the bands near 685 nm showed a considerable increase in the region of 50—4.2 K. In addition to this we observed an emission band near 680 nm in chloroplasts, the amplitude of which was less dependent on temperature. The band was missing in barley mutant no. 2, which lacks the light-harvesting chlorophyll *a/b*-protein complex. At 4.7 K the spectra of the variable fluorescence (F_v) consisted mainly of the emission bands near 685 and 695 nm, and showed only little far-red emission and no contribution of the band at 680 nm.

From these and other data it is concluded that the emission at 680 nm is due to the light-harvesting complex, and that the bands at 685 and 695 nm are emitted by the System II pigment-protein complex. At 4.2 K, energy transfer from System II to the light-harvesting complex is blocked, but not from the light-harvesting to the System I and System II complexes. The fluorescence yield of the chlorophyll species emittting at 685 nm appears to be directly modulated by the trapping state of the reaction center.

Abbreviations: *P*-700, *P*-680, reaction center chlorophylls, primary electron donors of System I and II, respectively; TSF-1, HP-700, System I pigment protein complexes containing about 90 and 40 chlorophyll molecules per reaction center, respectively; PS I, PS II, Photosystem I and II, respectively; Chl, chlorophyll.

Introduction

Experiments in various laboratories have shown that the intensity of chlorophyll fluorescence in intact cells and chloroplasts of algae and higher plants increases considerably upon cooling [1—3]. In addition, the shape of the fluorescence spectrum strongly changes, and long wave emission bands develop that are either absent or too weak to be observed at room temperature.

Three emission bands at about 685, 695 and 715—740 nm have been observed in a variety of photosynthetic organisms at liquid nitrogen temperature (refs. 4—6 and reviews in refs. 7—9). The band at 715—740 nm is commonly attributed to PS I [6,10]; the bands at 685 and 695 nm have been attributed to PS II [6,10—12]; The temperature dependence of the intensity of these bands suggested that drastic changes [12] occur in the efficiency of energy transfer between the various pigments and pigment-protein complexes upon cooling.

Most of the above mentioned experiments have been carried out at near liquid nitrogen temperature. Results obtained at still lower temperature showed that an additional strong increase in the yield of the various chlorophyll fluorescence emissions occurs upon further cooling [3]. Recent experiments from our laboratory [13,14] demonstrated that especially the so-called 'initial' fluorescence yield (F_0), i.e., the fluorescence yield when the reaction center traps of PS II are open, increases strongly below 77 K. Since the photochemistry of PS II was not basically altered [14,15], this effect is probably due to a decrease in the efficiency of energy transfer to the traps.

In order to gain information about the fluorescent components involved and about energy transfer within the system, an analysis was carried out of the emission spectra of chloroplasts and subchloroplast particles measured at temperatures between 100 and 4.2 K. Some of the results were reported earlier in a preliminary form [14].

Materials and Methods

Chloroplasts from spinach (*Spinacia oleracea*), barley (*Hordeum vulgare*), maize (*Zea mays*) and tobacco (*Nicotiana tabacum*) were prepared as described elsewhere [16] after grinding the leaves in a mortar or a blender. Spinach was obtained from the local market; barley, maize and tobacco were grown in the laboratory at about 22°C and a light intensity of about 8000 lux. The chloroplasts were resuspended in the isolation medium (50 mM Tricine (*N*-tris-(hydroxymethyl)methylglycine, pH 7.8), 0.4 M sucrose, 10 mM KCl and 5 mM $MgCl_2$) and stored in the dark on ice until use. For some experiments $MgCl_2$ was omitted from the medium.

Purified Photosystem I particles, TSF-1 and H*P*-700 [17] were isolated from spinach chloroplasts with the aid of 4% Triton X-100 (w/w) and sucrose gradient centrifugation. In the case of H*P*-700 the chloroplasts had been extracted with hexane to remove part of the carotenoids. The method used for purifying PS II particles from spinach was in principle the same as described for F_{II} by Wessels et al. [18]. In these preparations *P*-700 was determined from the light-induced bleaching at 698 or 700 nm in the presence of 1 mM ascor-

bate and 100 μM 2,6-dichlorophenol-indophenol using the differential extinction coefficients given by Hiyama and Ke [19]. *P*-680 was estimated from the bleaching in strong light at 677 nm, in the presence of 2.5 mM ferricyanide, assuming a differential extinction coefficient of 75 $mM^{-1} \cdot cm^{-1}$. The PS II preparation contained about 60 Chl per *P*-680 and a negligible amount of *P*-700 (1 per 2500 Chl). The TSF-1 and H*P*-700 preparations were free of PS II and contained 90 and 40 Chl per *P*-700, respectively.

Measurements of chlorophyll fluorescence at low temperatures were performed as described elsewhere [13] except that the apparatus was equipped with a monochromator and that it was on-line connected to a computer system. The monochromator was supplemented by Corning CS 2-62 and Schott RG 610 filters to absorb scattered excitation light; unless otherwise indicated it was set at a band width of 1.6 nm. A computer program was used to plot the emission spectra after correction for the wavelength dependent sensitivity of the apparatus. A standard ribbon filament lamp was used for the calibration. The spectra are plotted in arbitrary units proportional to W per wavelength interval. Except for the experiments of Fig. 4, the excitation light was filtered by a combination of two CS 4-96 and one long wave cut-off interference filter, transmitting between 390 and 580 nm.

The sample was contained in a perspex vessel of 1 mm thickness. Before the measurements the suspension of chloroplasts or subchloroplast particles was mixed with a solution of 0.4 M sucrose in glycerol in a ratio of 45 : 55 (v/v) in order to prevent crystallization upon cooling. The final chlorophyll concentration was 10 μg/ml, unless otherwise indicated. The samples were cooled in the dark. The fluorescence was detected at the illuminated surface of the vessel.

Results and Interpretation

Spinach chloroplasts

Emission spectra of spinach chloroplasts at various temperatures are shown in Fig. 1. The spectra show three major peaks near 685, 695 and 735 nm, corresponding to the three well known emission bands mentioned in the Introduction. In the following, we shall designate these bands F-685, F-695 and F-735, irrespective of their exact location. As was noted earlier for *Chlorella* [3] the intensities of these bands, especially of the first two show a considerable increase upon lowering the temperature to that of liquid helium. It can be seen that F-695 is small at 108 K; the band increases strongly upon further cooling, until below 75 K it becomes the predominant band in the emission spectrum. Initially, F-685 remains approximately constant or even decreases somewhat upon lowering the temperature and at 34 K it is only discernable as a shoulder on the now much stronger F-695 band. However, upon further cooling, F-685 starts to grow considerably, the growth of F-695 stops, and at liquid helium temperature the bands are of approximately equal amplitude. F-735 increases by about one-fourth between 100 and 70 K and becomes constant when the temperature is further lowered.

In addition to the above mentioned emission bands we observed a fourth band at even shorter wavelength. This band was not observed in our earlier work [14] because of the lower spectral resolution applied. It can be most

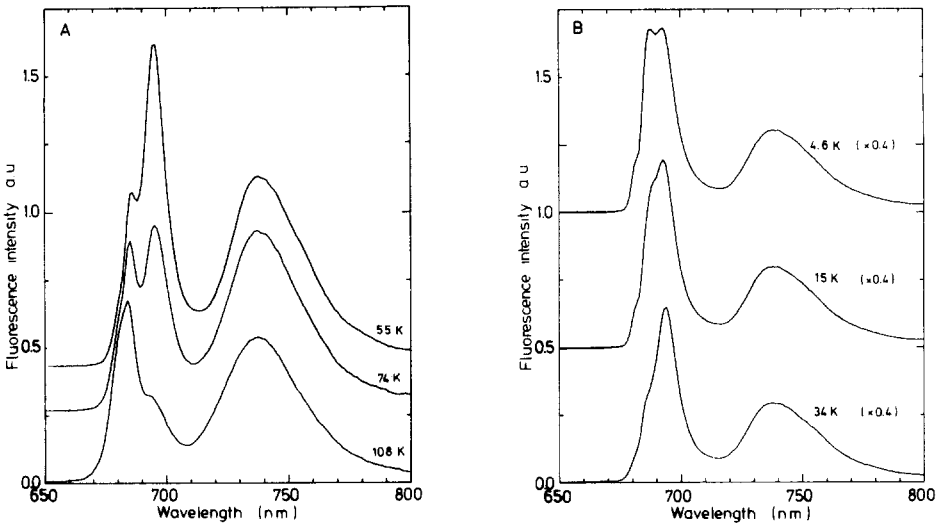

Fig. 1. Emission spectra of spinach chloroplasts at various temperatures. Note that the spectra measured at 34 K and below were recorded at lower amplification. In this and some of the other figures spectra were displaced vertically to enhance clarity.

clearly observed as a shoulder near 680 nm at 4.6 and 15 K, but closer inspection of the other spectra shows that it exists also at higher temperatures. Although the contribution of this band (F-680) to the various spectra is difficult to estimate, its height seemed to be little influenced by the temperature.

As Fig. 2 shows, basically the same results were obtained if Mg^{2+} was omitted from the suspension and isolation medium, except that F-685 and F-695 are relatively weaker. The latter effect was known already to occur at 77 K; it has been explained by a change in the efficiency of energy transfer but a more detailed explanation is still a matter of conjecture [8,11,20—22]. The ratio F-680/F-685 was higher in the absence than in the presence of Mg^{2+}, as can be most easily seen in the spectrum obtained at 4.6 K. Also, the intensity

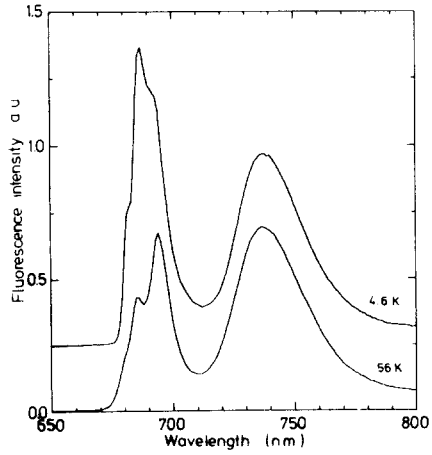

Fig. 2. Emission spectra of spinach chloroplasts obtained in the absence of $MgCl_2$.

of F-680 clearly increased with decreasing temperature in this case.

The spectra shown in the previous figures are those of the maximum fluorescence obtained during illumination (F_{max}). Fig. 3 compares these spectra with those of the so-called variable fluorescence (F_v), i.e. the increment of the fluorescence during illumination. Results obtained at 76 K are shown in Fig. 3A. In agreement with earlier measurements of Murata [23] and others, the F-735 was relatively low in the F_v spectrum. F-680, F-685 and F-695 appeared to be present in about the same ratio in the F_v and F_{max} spectra, with a slight preponderance of F-695. At 4.7 K, F-680 was absent in the F_v spectrum, as is clearly indicated by the low F_v/F_{max} ratio at 680 and 683 nm (Fig. 3B). Also, upon cooling, the ratio F_v/F_{max} decreased much stronger in the long wave region than around 685–695 nm. The F_v spectrum is low beyond 700 nm and may be attributed in this region to vibrational bands accompanying F-685 and F-695 only.

Emission spectra obtained with different excitation wavelengths are shown in Fig. 4. Excitation of chlorophyll *b* and carotenoid produced somewhat less emission at 735 relative to 695 and 685 nm than excitation of chlorophyll *a*. These differences, although small, are significant and cannot be explained by different extents of selfabsorption of fluorescence since light of 471 nm wavelength penetrates deeper in the sample than light of 430 nm. Nevertheless, it is clear that excitation of Chl *b* produces a considerable amount of F-735 emission, in agreement with action spectra of Murata obtained at 77 K [6] and with spectra obtained by Cho and Govindjee [12] with *Chlorella* at 4 K.

Wild strain and mutants of barley, maize and tobacco

Figs. 5 and 6 compare the emission spectra of wild strain and mutant barley chloroplasts. Emission spectra of the wild strain are shown in Fig. 5. The spectra are similar to those of spinach chloroplasts, but, as noted earlier by Boardman and Thorne [24], the band of F-695 is less pronounced, and F-735 is situated at a somewhat longer wavelength (745 nm at 55 K). This applies also at temperatures below 77 K. The spectrum of mutant no. 2 [25] is shown in

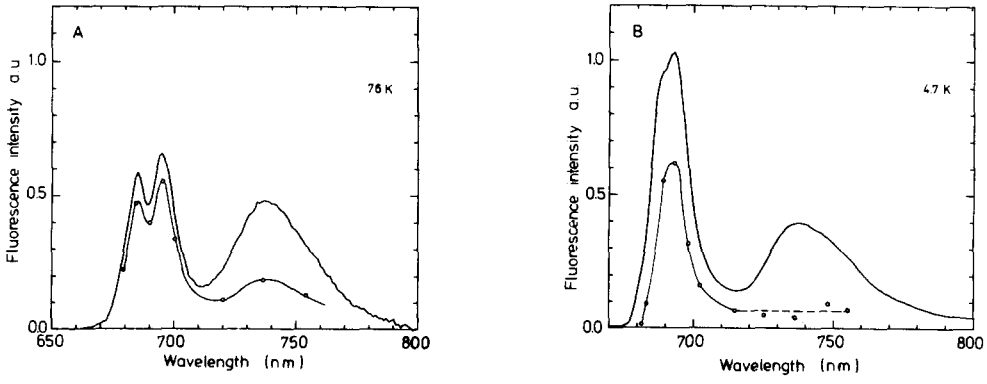

Fig. 3. Emission spectra (F_{max}) and points of the emission spectra of the variable fluorescence F_v (○) of spinach chloroplasts. A, 76 K; B, 4.7 K. The points were obtained by kinetic analysis of fluorescence recordings obtained upon illumination of dark-adapted samples. The monochromator was set at a half-width of 3.2 nm.

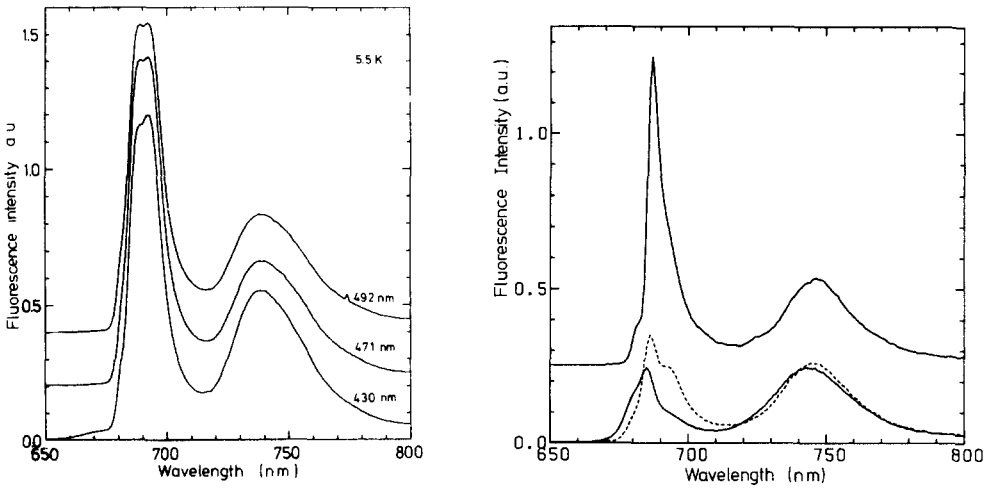

Fig. 4. Emission spectra of chloroplasts at 5.5 K obtained with three different excitation wavelengths. The intensities were adjusted such as to obtain about equal emission at 695 nm. Half-width of the excitation light was about 15 nm.

Fig. 5. Emission spectra of chloroplasts from barley (wild strain) at 94, 55 (- - - - -) and 4.2 K (top).

Fig. 6. This mutant lacks Chl *b* and the light-harvesting Chl *a*/*b*-protein complex [26]. The main difference with the spectra of chloroplasts from the wild strain is a shift of F-735 to 726 nm and the absence of F-680. F-685, F-695 and F-735 showed a similar temperature dependence in wild strain and mutant barley as in spinach chloroplasts. Emission spectra of maize were very similar to those of wild type barley: theys showed a clear-cut F-680 emission and only a weak F-695 component (relatively weaker than reported by Bazzaz and Govindjee [27,28]).

Spectra of the Su/su (var. *Aurea*) mutant of tobacco are shown in Fig. 7.

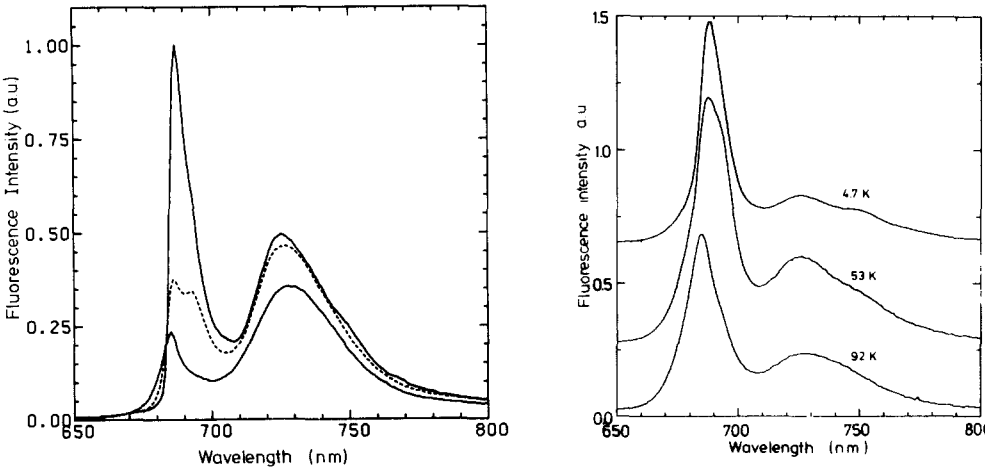

Fig. 6. Emission spectra of chloroplasts from barley mutant no. 2 at 89, 50 (- - - - -) and 4.6 K (top). Note the absence of F-680.

Fig. 7. Emission spectra of chloroplasts of the Su/su mutant (var. *Aurea*) of tobacco.

This mutant contains less Chl *b* than the normal strain [29]. At all temperatures, the predominant band was F-685, located at 685 nm at 92 K and at 689 nm at 4.7 K. F-695 was only visible as an inflection. It can be most clearly observed in the spectrum obtained at 53 K, but even here it is weaker than F-685. F-685 and F-695 showed the usual temperature dependence. Some spectra suggest a contribution of F-680, but the observation of this band is difficult because the short wavelength side of F-685 seemed to decline less sharply than in the other samples. Above 700 nm there were two major bands in this species, i.e. near 725 and 745 nm.

The Chl *a/b* ratio of the chloroplasts in Fig. 7 was 15. When tobacco plants were grown under less favorable conditions (lower light intensity, humidity and mineral content of the soil), the amount of Chl *b* increased. The spectra of chloroplasts obtained from these plants (Chl *a/b* ratio 3—3.5) were different from those in Fig. 7 and resembled more those of 'normal' spinach chloroplasts. In the lower wavelength region F-695 was relatively more intense and there was only one clear maximum beyond 700 nm, located at 730 nm at 50 K. Also, there was a clear F-680 emission in these chloroplasts.

Photosystem I and II protein-pigment complexes

Emission spectra of PS I particles prepared from spinach are shown in Fig. 8. As noted by other workers [30—33] the shape of the spectra, and especially the intensity in the long wave region were strongly dependent on the type of preparation. The upper spectrum is that of a TSF-1 preparation containing about 90 mol Chl per *P*-700. The predominant band, especially at low temperature, was located at about 722 nm; weaker bands are observed near 675 and

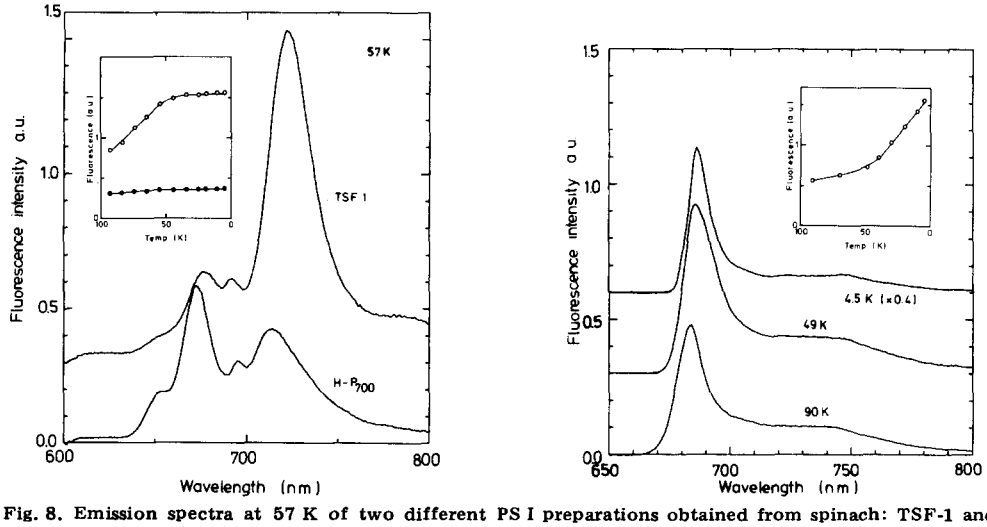

Fig. 8. Emission spectra at 57 K of two different PS I preparations obtained from spinach: TSF-1 and HP-700 (see Materials and Methods). Chl concentrations 8 and 16 μg/ml, respectively. The vertical scales are not comparable for the two spectra. Insert: temperature dependencies of the emission bands at 722 nm (○) and 676 nm (●) in TSF-1.

Fig. 9. Emission spectra of PS II particles (F_{II}, see Materials and Methods). Insert: amplitude of the band near 683 nm as a function of temperature.

692 nm. Similar spectra have been reported at 77 K by Vernon and coworkers [31,32,34]. The band at 678 nm is probably due to solubilized Chl [30,35]; its intensity was virtually independent of temperature (see Fig. 8, insert). The intensity of the 695 nm band was difficult to estimate but seemed to increase upon cooling. The amplitude of the 722 nm band increased strongly between 100 and 35 K and remained nearly constant upon further cooling. Its maximum shifted from 723.5 to 721 nm between 100 and 35 K and remained constant below that temperature.

HP-700 particles (with a higher P-700/Chl ratio) showed a much lower emission beyond 700 nm, and the long wave maximum was located at shorter wavelength (see also refs. 35 and 36). The intensity of this band was different for different preparations and decreased with increasing purity. Its intensity increased on storage at −20°C, and could be lowered again by repeated fractionation by sucrose gradient centrifugation. The spectra showed in addition bands near 673 and 696 nm. Again, the amplitude of the short wave band (673 nm) was little dependent on the temperature. The fluorescence yield of both types of preparations was at least an order of magnitude lower than of intact chloroplasts.

The emission spectra of the PS II chlorophyll-protein complex were relatively simple (Fig. 9). The main band was located at 682–684 nm [18], there was a week shoulder near 695 nm and only little emission beyond 700 nm. The temperature dependence of the main band is shown in the insert; its height increased with decreasing temperature, especially below 50 K.

Discussion

The data presented here show that at least four emission bands, near 680, 685, 695 and 715–740 nm can be observed in chloroplasts obtained from various sources. These bands are not only observed at 77 K, but with different relative intensities also at lower temperatures. The band near 680 nm occurs in the emission spectra of chloroplasts from wild type spinach, barley and maize, but not of the barley mutant. This band appears to be less sensitive to temperature than the other bands.

The origin and significance of the emission bands that occur at low temperature is not well established yet, and their complicated temperature dependence can only be explained in a tentative way on basis of the presently available evidence. The strong increase in Chl fluorescence that occurs in chloroplasts and chloroplast preparations upon cooling is not an intrinsic property of Chl *a* itself. Measurements of fluorescence life times indicate that the fluorescence yield of Chl dissolved at low concentration in organic solvents does not change significantly upon cooling [37]. The strong emission in the long wave region (F-735) at low temperature may be due to Chl species that normally transfer their energy directly or indirectly to a reaction center, but are unable to do so at low temperature and emit fluorescence instead. Recent experiments of Butler and coworkers [38] show a concomitant increase in the fluorescence life time, as would be expected in this case. Some of our emission spectra clearly show that there are at least two bands in the region 720–760 nm indicating that F-735 is due to more than one type of Chl. This was also observed with *Chlorella* by Cho and Govindjee [39].

On basis of the F_v/F_{max} ratios it has been proposed [10,23] that F-685 and F-695 belong to PS II and F-735 to PS I respectively. Our data (Fig. 4) and those of others [6,12] show that excitation of Chl *b* is only little less efficient in producing F-735 fluorescence than of F-695 and F-685 emission. This would then indicate a considerable rate of energy transfer from the light-harvesting complex to PS I, even at 55 K.

The early fractionation experiments (refs. 40, 41, see also ref. 30) supported the conclusion that F-685 and F-695 are emitted by PS II, but did not allow an unequivocal assignment of F-735, since the absolute yield of long wave emission was about the same in 'heavy' and 'light' chloroplast fractions. For both PS I and PS II particles the extent of the long wave emission appears to decrease with increasing degree of purification. In highly purified PS I particles the main bands are below 700 nm (Fig. 6 and refs. 35, 36). Purified PS II particles show only a band near 685 nm (Fig. 10 and ref. 18). Possibly a certain level of structural integrity is necessary for long wave emission to occur and the Chl species emitting at 695 and 735 nm may be lost of disaggregated by the detergent treatment [42]. Absence or reduced content of the light-harvesting complex in vivo also appears to affect the long wave emission (Figs. 6 and 7).

The presence of F-680 in the emission spectra of chloroplasts of spinach, maize and wild type barley, but not in the mutant barley lacking the light-harvesting Chl *a/b* pigment-protein complex, indicates that F-680 is emitted by the light-harvesting complex. The hypothesis of Butler and coworkers [11,43] that F-685 is due to the light-harvesting complex is at variance with the observation of a prominent emission band near 685 nm in the barley mutant. Thus it appears that both F-685 and F-695 belong to the PS II pigment protein complex. Reports in the literature on the emission spectra of the isolated light-harvesting complex are contradictory. Butler and coworkers [42,44] reported a maximum at 681 nm at 77 K, whereas Brown [33] obtained a maximum at 695 nm.

The insensitivity of F-680 to temperature indicates that energy transfer from the light-harvesting complex to the PS II complex (and presumably also to PS I) is not or little affected by cooling, as is also consistent with the emission spectra of Fig. 4. The absence of F-680 in the F_v spectrum at 4.7 K (Fig. 3) indicates that transfer from the PS II complex to F-680 is blocked at this temperature, and agrees with the very small contribution, if any, of F-735 to the F_v spectrum. The strong increase in amplitude of F-695 and at still lower temperatures of F-685 upon cooling may be explained in a similar way as for F-735. Although the intensities of F-685 and F-695 show a different temperature dependence, the F_v/F_{max} ratios of the two bands remain approximately equal to each other throughout the whole temperature range. This may be explained by the assumption that the Chl emitting at 695 nm is almost exclusively excited by energy transfer from the pigment emitting F-685 fluorescence and that the fluorescence yield of the latter pigment is directly modulated by the trapping state of the reaction center of PS II.

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