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Excitation energy transfer from the chlorophyll spectral forms to Photosystem II reaction centres: a fluorescence induction study

Robert C. Jennings, Giuseppe Zucchelli and Flavio M. Garlaschi

Centro CNR Biologia Cellulare e Molecolare delle Piante, Dipartimento di Biologia, Università di Milano, Milano (Italy)

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Excitation energy transfer from Photosystem II antenna to reaction centres as a function of excitation wavelength, between 646–701 nm, was studied by analysis of the fluorescence quenching efficiency of RCs in both a BBY-grana preparation and thylakoids of the chlorina barley mutant lacking LHCPII. For BBY-grana, maximum transfer was observed with an excitation wavelength slightly greater than 680 nm, with significant decreases occurring for both longer and shorter wavelengths. The data are analysed in terms of the chlorophyll spectral forms as determined by asymmetric gaussian deconvolution of room temperature absorption spectra. For the short-wavelength side of the transfer maximum (646–682 nm) the following relative transfer efficiencies have been determined: 684 > 670 > 650; 678 > 661; 684 > 678 nm. Energy transfer between Photosystem II units is shown to increase with decreasing absorption wavelength below 683 nm. Thus, the above relative transfer efficiencies are associated with transfer to reaction centres within Photosystem II units and not between PS II units. The data are discussed in terms of alternative antenna models. It is argued that they are best accommodated by a model in which the antenna spectral forms have no particular macroscopic distribution with respect to RCs and in which the lower-wavelength-absorbing spectral forms may function as 'antitraps' for the longer-wavelength forms as determined by the transfer microparameters. Analysis of the gaussian band associated with Chl *b* in BBY-grana and LHCII suggest that this antenna component has a low-transition dipole strength within Photosystem II antenna complexes. It is suggested that this will enhance the role of Chl *b* as an 'antitrap' for excited states associated with the longer-wavelength-absorbing chlorophyll species.

Introduction

The absorption of light energy by the photosystems of green plants is achieved by a large array of pigment molecules, mostly chlorophylls, which transfer the excitation energy to RCs where primary charge separation occurs. Though the number of antenna chlorophylls per reaction centre is variable, depending on the type of plant and the growth conditions [1], an average ratio of 200 ± 50 for normally grown sun plants is often encountered. All chlorophyll molecules seem to be bound to specific polypeptides, thus forming a number of Chl-protein complexes [2,3].

The antenna matrix system is formed by two distinct chlorophyll species, *a* and *b*, with Chl *a* being present in considerably greater amounts. Chlorophyll *a* is present in at least five different spectroscopic forms [4,5] which can be arranged, with respect to wavelength, in a series in which the absorption maxima differ by 7–11 nm. As these values are rather similar to the Stokes fluorescence shift for chlorophyll, a number of authors have suggested that energy may be transferred from the peripheral antenna towards the reaction centres along a 'downhill' energy gradient, i.e., from shorter- to longer-wavelength-absorbing forms [6–8] according to the dipole–dipole R^{-6} theory of Förster [9]. Experimental evidence in favour of such a model exists for antenna systems of red algae and photosynthetic bacteria [10].

In this communication we attempt to clarify the role of the different chlorophyll spectral forms in transferring excitation energy to PS II RCs. To this end we have measured the action spectrum of the chlorophyll fluorescence quenching efficiency of open reaction

Abbreviations: PS I, Photosystem I; PS II, Photosystem II; LHCPII, the light harvesting chlorophyll *a*/*b* protein complex; F_m, fluorescence yield with reaction centres closed; F_o, fluorescence yield with reaction centres open; F_v, variable fluorescence ($F_m - F_o$); RC, reaction centre, DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; Chl, chlorophyll; BBY, Berthold, Babcock, Yocum [11].

Correspondence: R.C. Jennings, Centro CNR Biologia Cellulare e Molecolare delle Piante, Dipartimento di Biologia, Università di Milano, Via Celoria 26, 20133 Milano, Italy.

centres in the wavelength range 645–701 nm by measuring the F_v/F_o ratio for both a BBY-grana preparation and thylakoids of the chlorina barley mutant lacking LHCPII, and determined the fractional contribution to absorbance of the chlorophyll spectral species.

Materials and Methods

BBY-grana were prepared from freshly harvested spinach leaves by the method of Berthold et al. [11] but omitting the last Triton-X treatment [12]. This preparation contains both LHCPII and the PS II core pigment-protein complexes and is free of PS I complexes as demonstrated by mild SDS-gel electrophoresis (unpublished observation). The chlorophyll recovery yield was typically around 30%. Final resuspension was in 30 mM Tricine (pH 8)/10 mM NaCl/5 mM $MgCl_2$/0.2 M sucrose and the chlorophyll concentration was adjusted to 4 μg/ml.

LHCPII, the principal PS II antenna complex, was prepared from spinach leaves according to Ryrie et al. [13]. Final resuspension was in a medium containing 0.05 M sucrose, and 5 mM Tricine (pH 8). The Chl *a*/Chl *b* ratio was 1.1.

Thylakoids were prepared from freshly harvested leaves of the chlorina barley mutant lacking LHCPII as previously described [14]. The final resuspension was as for the BBY-grana.

The F_o and F_m fluorescence levels were measured in the assembly described previously [15]. F_m was measured in the presence of DCMU (25 μM) and hydroxylamine (2 mM), while F_o was measured in the same sample in their absence as previously described [15]. To permit excitation in the wavelength range 645–701 nm, fluorescence was measured in the long-wavelength fluorescence vibrational band of Chl *a* (Baltzers B-40 745 nm and Corning 5-50 filters). Fluorescence was excited with different combinations of interference filters (Oriel sharp cut-off and Baltzers) with half-bandwidths between 2.5 nm and 7 nm. The stray light to signal ratio was considerably less than 0.05 in all cases, as shown by use of the fluorescence quencher, dibromothymoquinone. The absorption flux was approximately constant with all filter combinations as judged by the F_m fluorescence level [16] giving a half fluorescence rise time in the presence of DCMU in the range 0.35–0.7 s.

Energy transfer between PS II units was determined by analysing the variable fluorescence as a function of the area growth above fluorescence induction curves [17]. Fluorescence induction was measured as described above except that DCMU and hydroxylamine were added before illumination.

Deconvolution of the room-temperature absorption spectra of BBY-grana into asymmetric gaussian components was performed as described elsewhere [18]. The contribution of the single gaussian components to total absorptance (A_g) with the different filter combinations was evaluated by

$$A_g = \int d\lambda (1 - T(\lambda))_n T(\lambda)_f$$

where $(1 - T(\lambda))_n$ is the absorptance of the nth gaussian band and $T(\lambda)_f$ is the transmittance of the filter combination.

Results

The well known PS II chlorophyll fluorescence rise upon illumination of dark-adapted thylakoids from the F_o to the F_m level is usually interpreted as being due to the reduction of the primary stable quinone electron acceptor, Q_A [19–21]. The classical idea is that the oxidised reaction centre, functioning as an energy trap, quenches the fluorescence emission of the Chl-antenna matrix. Even though fluorescence lifetime studies in recent years have indicated that PS II emission does not follow a single exponential decay law [22–24], abundant evidence indicates that the simple rate constant expression $k_f/(\Sigma k + k_T)$ (where k_f is the fluorescence rate constant averaged over the antenna matrix, k_T is the overall trapping rate by oxidised reaction centres and Σk is the sum of all decay processes occurring in the antenna matrix) represents a good first approximation for describing fluorescence yield [17,20,21,25]. In the present paper we examine energy transfer to PS II reaction centres by determining fluorescence quenching by open RCs as a function of excitation wavelength. Data are presented as the F_v/F_o ratio, which is a measure of the RC trapping efficiency [17] and to a first approximation may be represented by the expression $k_T/\Sigma k$. It should be pointed out that this approach yields information on energy transfer to reaction centres only if this process is substantially diffusion-limited. A clear demonstration as to whether excitation transfer in higher plant photosystems is either diffusion- or trap-limited [26] is not yet forthcoming. In the case of trap-limited transfer we would not expect to see differences in the F_v/F_o ratio with different excitation wavelengths.

Fig. 1 shows F_v/F_o as a function of absorption wavelength in the range 646–701 nm for the BBY-grana preparation. This material was chosen as it is free of PS I and is also expected to be fairly homogeneous with respect to the PS II units. Only PS II units are thought to be present in grana membranes [27]. In addition, both the F_v/F_o ratios and the overall fluorescence lifetimes are similar to those of isolated thylakoids (unpublished observation), thus indicating that the energy transfer parameters should not be significantly altered by the preparation procedure. The data indicate that transfer to PS II reaction centres is a function of the

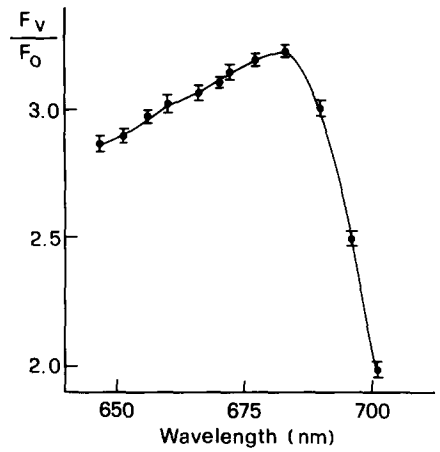

Fig. 1. F_v/F_o-trapping efficiency of Photosystem II RCs as a function of absorption wavelength in BBY-grana. Each data point represents the mean of at least 20 determinations performed with different BBY preparations. Owing to some variability of the F_v/F_o ratio between preparations (range limits less than 9%) the single values were appropriately normalised to the overall mean value for statistical analysis. The error bars indicate the interval estimate of the mean at the 99% confidence level. This signifies that all mean values falling outside a particular interval estimate are significantly different.

absorption wavelength, with maximal transfer occurring from antenna absorbing a little above 680 nm. At both longer and shorter wavelengths transfer decreases continuously. While a lower transfer efficiency to RCs on the long-wavelength side is expected for energetic reasons, this is not the case for wavelengths below 683 nm.

In Fig. 2 the asymmetric gaussian band deconvolution of both the BBY-grana and LHCPII room-temperature absorption spectra are presented. All the commonly observed spectral components are present in both preparations, with the major components peaking at 650, 660, 670, 677 and 684 nm.

We have analysed energy transfer to RCs in terms of the spectroscopic chlorophyll species for wavelengths below 683 nm (Fig. 3). To this end the F_v/F_o values have been plotted as a function of the fractional absorbance of each chlorophyll spectroscopic species (Fig. 3) determined as described in Materials and Methods. Within each of the three rectangular areas delimited by the broken lines, more than 95% of the total absorbance is by three spectral forms. By selecting F_v/F_o intervals in which one of these spectral forms has an unchanging absorbance contribution it is possible to establish the order of energy transfer efficiency to reaction centres of the other two chlorophyll species. Thus the following qualitative conclusion on excitation transfer to reaction centres are established:

$$684 > 670 > 650 \text{ nm} \quad (1)$$

$$677 > 660 \text{ nm} \quad (2)$$

Though it is not possible to compare neighbouring bands directly due to the large and regular spectral overlap between them, it can be seen that energy transfer seems to be a direct function of the peak wavelength of the different chlorophyll spectroscopic species up to 684 nm. The quantitatively minor bands absorbing at wavelengths above 684 nm (692 nm and 701 nm bands) are clearly less efficiently coupled to RCs (Fig. 1).

The sense of the 650 nm band in this scheme is not straightforward, as Chl *b* is not thought to give rise to fluorescence emission due to an energy transfer efficiency to Chl *a* within the LHCPII complex close to 100% [28–31]. While it is not known to which Chl *a* spectral forms energy is preferentially transferred from Chl *b*, it would seem from the energy-transfer sequences indicated above that significant energy acceptor contributions can be made only by either/or both the 660 nm and the 677 nm species. In this context it is interesting to note that, within the F_v/F_o intervals indicated by the selected areas in Fig. 3, the changes in absorption contribution of the spectral forms correlating with a given change in F_v/F_o are rather similar. This leads us to think that the differences in transfer efficiency be-

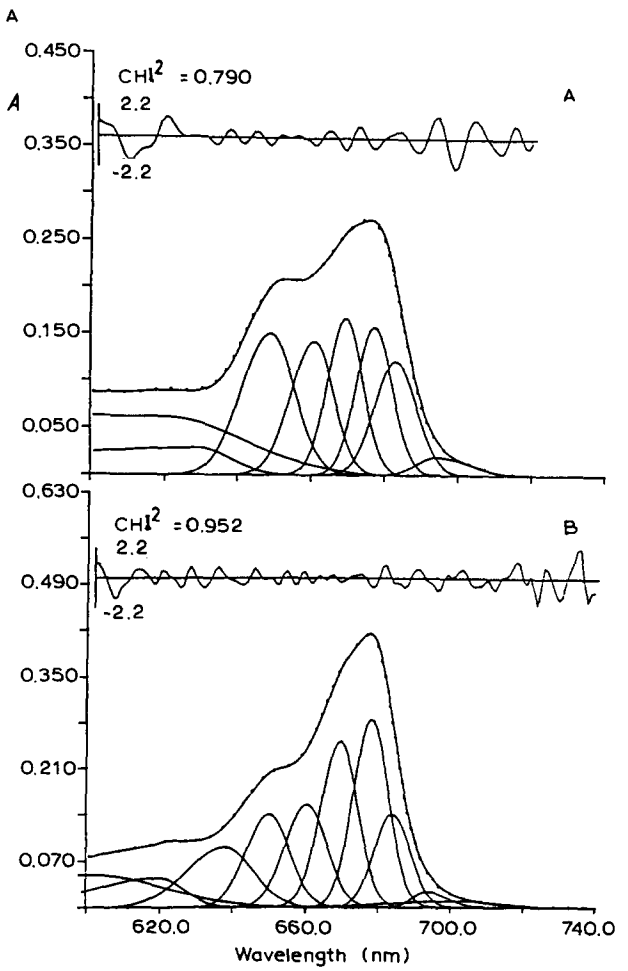

Fig. 2. Room-temperature absorption spectra of LHCPII (A) and BBY-grana (B). The experimental data are the dotted curves, while the full lines are the sum of the gaussian components. Plots of the residuals are also shown with the χ^2 values.

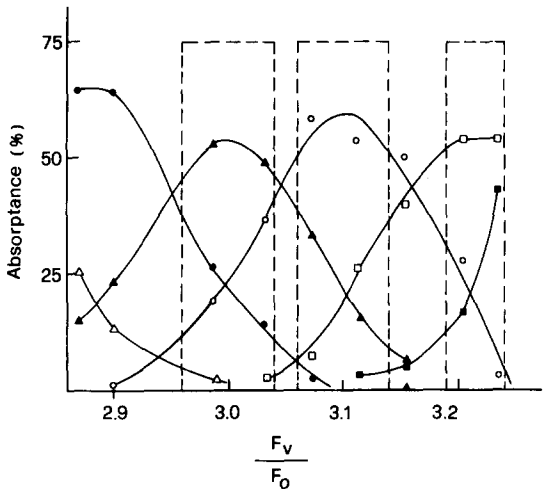

Fig. 3. F_v/F_0-trapping efficiency of Photosystem II RCs as a function of the fractional absorptance by the major spectroscopic chlorophyll forms from 650 to 684 nm. Fractional absorptance by the spectroscopic species was calculated as described in Materials and Methods. The symbols indicate the different spectral forms. △, 638; ●, 650; ▲, 661; ○, 670; □, 678; ■, 684 nm. The F_v/F_0 data have been taken from Fig. 1. The areas delimited by the broken lines represent parameter spacings within which the transfer efficiency sequences of the chlorophyll spectral forms (see text) were established.

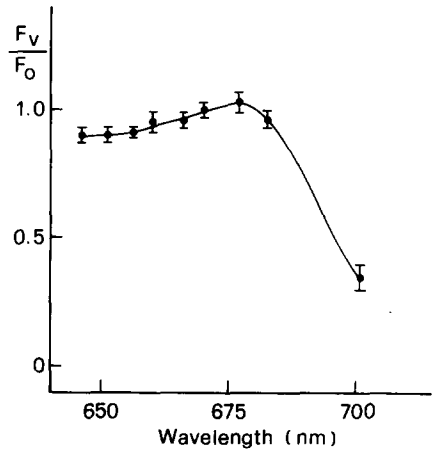

Fig. 4. F_v/F_0-trapping efficiency of Photosystem II reaction centres as a function of the absorption wavelength in thylakoids of the chlorina barley mutant. For experimental details see legend to Fig. 1.

tween the various spectral components in the above transfer sequences (1) and (2) are similar. It would therefore seem likely that sequence (2) lies somewhere to the right of the 684 nm species in sequence (1), therefore indicating the 684 nm species as the spectral component most efficient at transferring energy to PS II RCs.

It is generally accepted that PS II units are organised in a kind of limited matrix within the grana membranes, in which energy transfer between the different units is possible [32,33]. It is therefore necessary to establish whether the relative (F_v/F_0)-transfer efficiencies of the spectral forms represent transfer to RCs within or between photosystems. To this end we have measured excitation transfer between PS II units as a function of the absorption wavelength. This was achieved by determining the normalised variable fluorescence as a function of the area growth above the fluorescence induction curve in the usual way [17].

It has been pointed out [33] that the normalised variable fluorescence at a particular concentration of open RCs is a function not only of energy transfer between PS II units but also of the (F_v/F_0)-transfer efficiency to RCs. We have therefore calculated the Butler PS II connection parameter according to Eqn. 10 of Ref. 33 for the various excitation wavelengths (Table I). The data show that PS II-PS II energy transfer from the shorter wavelength spectral forms is greater than from the longer-wavelength-absorbing forms.

As the bulk of PS II antenna is made up of LHCPII (about 80% of the total chlorophyll) which contains all the spectral bands [2], it is reasonable to expect that these relative transfer efficiencies involve excitation transfer from LHCPII to RCs. We have therefore asked the question as to whether the different chlorophyll species which compose the core antenna of PS II might also transfer energy to reaction centres with different efficiencies. To this end we have measured the F_v/F_0 ratio as a function of wavelength in thylakoids of the chlorina barley mutant which lacks LHCPII, containing only the core antenna of PS II. The data (Fig. 4) are qualitatively rather similar to those for BBY-grana, with energy transfer to RCs decreasing significantly at absorption wavelengths lower than about 677 nm. The maximal F_v/F_0 ratio in this case was detected at shorter wavelengths than for BBY-grana. This difference could be due to an increasing contribution of PS I fluorescence to the F_0 value at excitation wavelengths above 680 nm in the barley mutant thylakoids.

TABLE I

Energy transfer between Photosystem II units as a function of absorption wavelength

Data are presented for the normalised variable fluorescence ($F_v(t)$) at 50% area growth with the interval estimates of the mean at 95% confidence level. The Butler PS II connection parameter [33] was calculated as described in the text.

Absorption (nm)	683	678	673	666	662	651
$F_v(t)$	0.357 ± 0.005	0.352 ± 0.007	0.347 ± 0.007	0.338 ± 0.007	0.337 ± 0.006	0.341 ± 0.01
ψ_{22}	0.32	0.33	0.36	0.39	0.40	0.40

It is interesting to note that, whereas energy transfer in BBY-grana decreased significantly at wavelengths below 656 nm, this was not the case with barley mutant thylakoids. This difference is thought to be attributable to the absence of Chl *b*, the principal band absorbing in this region in BBY-grana, in the chlorina mutant.

Discussion

In the present paper we have examined energy transfer from antenna to reaction centres in a PS II grana preparation by measuring the trapping efficiency by RCs for excitation light of different wavelengths. The data show that transfer to RCs is greatest at wavelengths slightly above 680 nm. Analysis of the fractional absorption by the various chlorophyll spectral forms, obtained by asymmetric gaussian band deconvolution on the short-wavelength side of the transfer maximum, suggests that transfer to RCs is a function of the wavelength position of the spectroscopic band, with the longer-wavelength-absorbing bands being more efficient than the shorter-wavelength-absorbing bands. We furthermore conclude that these relative (F_v/F_o)-transfer efficiencies are dominated by transfer to the RCs of the same PS II unit in which absorption occurs as transfer between PS II units is demonstrated to display an opposite absorption wavelength dependence, i.e., in this case the shorter-wavelength forms are more efficient than the longer-wavelength forms. These data are consistent with the idea that energy transfer to reaction centres in the BBY-grana preparation used here is diffusion limited.

We believe that our observations on the BBY grana preparation are not caused by Triton-X-induced uncoupling artefacts for the following reasons: (1) The (F_v/F_o)-transfer efficiencies seem to be directly related to the absorption wavelength of the spectral form. It is difficult to understand how Triton X might uncouple as a function of wavelength position. (2) Those spectral bands least efficient in transfering to RCs of the same PS II unit in which absorption occurs seem to be the most efficient in transferring energy to RCs of other PS II units. A detergent-induced energy uncoupling of a particular spectral form is not likely to display such specificity of effect, as energy transfer to all other antenna chlorophylls is expected to be reduced. (3) Qualitatively similar (F_v/F_o)-efficiency data were obtained for thylakoid membranes of the chlorina barley mutant. These membranes were not treated with Triton X-100.

The transfer rate from antenna to RCs is expected to be determined, in general terms, by the strength of energy coupling between transferring antenna chlorophyls and by the number of transfer steps (N) in the case of a localised transfer mechanism. Two antenna models may therefore be considered to explain the present observations. (1) A model in which the long-wavelength spectral forms, and in particular the 684 nm form, have a closer topological relationship with RCs than the short-wavelength bands. This is the kind of antenna model analysed theoretically by several authors [6–8] and forms the basis of the so-called 'funnel' concept of antenna organisation. Experimental evidence in favour of such a model exists for photosynthetic bacteria [10]. In this case, for the long-wavelength forms, N would be smallest for transfer to RCs within the PS II unit and greatest for transfer to other PS II units. (2) A model in which there is no particular macroscopic topological distribution of the spectral forms with respect to RCs. In this case transfer to RCs would be determined essentially by the transfer microparameters of the donor-acceptor antenna chlorophylls. The short-wavelength spectral forms are expected to be able to transfer energy to a greater variety of antenna chlorophylls than the longer-wavelength forms. In this context the shorter-wavelength forms will limit the number of transfer possibilities available to the longer-wavelength forms, thus bringing about a situation in which N is smaller for the longer-wavelengths forms. This suggestion is similar to the 'antitrap' model suggested by Knox [34]. The greater efficiency of energy transfer between PS II units for the shorter-wavelength forms can be explained by their greater transfer probability to other antenna chlorophyll forms than the long-wavelength forms.

On the basis of the above energy-transfer data alone it is not possible to distinguish beteen these two models. We have therefore analysed the relative amounts of the different spectral forms in both LHCII and BBY-grana (Fig. 5). These data show that the 684 nm form, associated with the highest F_v/F_o-transfer efficiency, is present at high levels in LHCII. This observation suggests that the 684 nm component is not enriched in the core antenna complexes and seems to be in agreement with

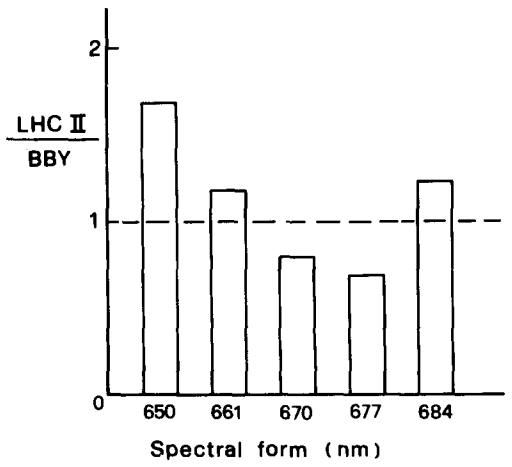

Fig. 5. The ratio of the fractional contribution of the spectral species of LHCPII with respect to BBY-grana.

the measurements of Van Dorssen et al. [35], who do not report the presence of the 684 nm component in the CP47 core complex. Thus it is difficult to explain the high F_v/F_o efficiency of this spectral form in terms of the 'funnel' model. We therefore suggest that 'antitrap' considerations best account for the high F_v/F_o-transfer efficiency of the 684 nm spectral form. As this component is present at relatively high levels in LHCPII (15–20% of Q_y absorption) we feel that 'antitrapping' may play an important role in energy transfer within the LHCPII outer antenna matrix of PS II.

From Fig. 5 it can also be seen that the shorter-wavelength bands (650 and 661 nm) are enriched in LHCPII with respect to BBY-grana and thus presumably also with respect to the core antenna complexes. While this is well known for the 650 nm component, Chl *b*, similar data do not seem to have been previously presented for the 661 nm form. On the other hand, both the 670 nm and 677 nm forms are present at high levels in BBY-grana, presumably indicating their enrichment in core complexes with respect to LHCPII. This interpretation is in agreement with Van Dorssen et al. [35], who found high levels of these two spectral forms in the CP47 complex. We therefore feel that, while the 'antitrap' concept best explains the 684 nm data, energy transfer from LHCPII to the core complexes may well have a 'funnel' component.

It is well known that the Q_y transition dipole strength of Chl *b* in organic solvents is weaker than that of Chl *a* [36]. Deconvolution of the room-temperature absorption spectra into the asymmetric gaussian bands for both BBY-grana and purified LHCII (Fig. 2) show that this is also the case within the PS II antenna. In the BBY grana Chl *b* constitutes about 35% of the total chlorophyll and in LHCII almost 50%, whereas its contribution to absorption, as judged by the integrated areas under the gaussian optical absorption bands, is much less (15 and 25%, respectively). Whilst the low Q_y absorption 'efficiency' of such an important antenna component as Chl *b* is difficult to understand in terms of the light-harvesting economy, it may be rationalised in terms of the above-described 'antitrap' energy-transfer hypothesis, as a weak Chl *b* transition dipole will further lower the energetically 'uphill' transfer rate from the Chl *a* spectral forms by decreasing the matrix interaction element, thus enhancing the 'antitrap' properties of Chl *b*. In this context it is interesting to note that linear dichroism measurements of both PS II and LHCII preparations show that the Q_y transitions of Chl *b* and the lower-wavelength-absorbing Chl *a* spectral forms have an average orientation which is rather different from that of the longer-wavelength Chl *a* spectral forms [37]. This may also be expected to enhance the 'antitrapping' role of these chlorophyll species.

In the context of 'uphill' transfer it is demonstrated here that energy can be transferred to PS II reaction centres from antenna chlorophylls absorbing at about 20 nm above the reaction centres themselves and its (F_v/F_o) efficiency, compared with the transfer maximum near 680 nm, is surprisingly high (over 60%). In Fig. 6 the gaussian component deconvolution of absorption with the 701 nm filter combination is shown. About 80% of the total absorption is by the long-wavelength bands peaking at 694 nm and 701 nm. This shows that even the long-wavelength forms have an effective antenna function.

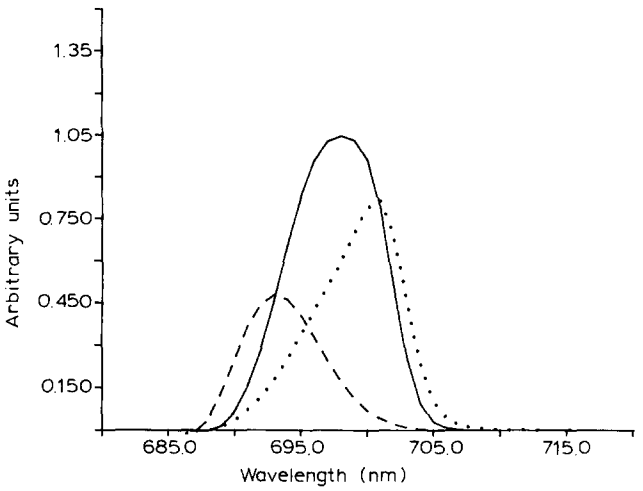

Fig. 6. Absorptance spectra of the single gaussian bands for the 701 nm filter combination. Spectra were calculated as described in Materials and Methods. The different spectral forms are: - - - - - -, 684; ———, 694; · · · · · ·, 701 nm.

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