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SPECTRAL AND FUNCTIONAL COMPARISONS BETWEEN THE CAROTENOIDS OF THE TWO ANTENNA COMPLEXES OF *RHODOPSEUDOMONAS CAPSULATA*

PABLO A. SCOLNIK, DAVIDE ZANNONI * and BARRY L. MARRS

E.A. Doisy Department of Biochemistry, Saint Louis University School of Medicine, Saint Louis, MO 63104 (U.S.A.)

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Summary

The spectral and functional properties of carotenoids associated with each of the two light-harvesting complexes of the *Rhodopseudomonas capsulata* photosynthetic antenna system have been distinguished by studying mutants lacking one or the other complex. In mutants containing only the light-harvesting I complex (LH-I), the absorption spectrum of the carotenoids is blue-shifted compared to wild type. Carotenoid absorption in mutants possessing only the light-harvesing II complex (LH-II) complex is red-shifted. The circular dichroism spectrum of carotenoids in each complex is also distinctive. Although carotenoids in each complex function with approximately the same efficiency in harvesting and transmitting light energy for photosynthesis, only the carotenoids associated with LH-II undergo an electrochromic bandshift upon generation of a transmembrane potential. These observations are interpreted to indicate that both the orientation of carotenoid molecules with respect to the plane of the membrane, and the immediate electrochemical environment of these molecules differ in the two light-harvesting complexes.

Introduction

Carotenoids play dual roles in the photosynthetic bacterium *Rhodopseudomonas capsulata* as in all other photosynthetic organisms, protecting the cells

* Present addess: Institute of Botany, University of Bologna, Bologna, Italy.

Abbreviations: BChl, bacteriochlorophyll; LH-I, light harvesting system I, which has a single absorbance maximum in the infrared region (about 880 nm); LH-II, light harvesting system II, which has two infrared absorbance peaks (about 800 and 850 nm); CD, circular dichroism; Mes, 2-(*N*-morpholino)ethanesulfonic acid; Mops, 3-(*N*-morpholino)propanesulfonic acid.

against photooxidative damage [1,2] and serving as receptors for light [3]. The light-harvesting function in *Rps. capsulata* is performed in conjunction with bacteriochlorophyll (BChl) in two different types of antenna complexes, LH-I and LH-II [4,5] which transmit the energy to a third complex, the reaction center, responsible for productive photochemistry [6].

Carotenoids in *Rps. capsulata* were found to be associated with LH-II and reaction centers isolated after disruption of the chromatophore membrane with detergents [7,8]. LH-I has not yet been isolated from carotenoid-containing strains of *Rps. capsulata*, but in the closely related bacterium, *Rhodopseudomonas sphaeroides*, the two antenna complexes and the reaction center have been isolated [9—11] and carotenoids were found to be associated with each. These in vitro associations might reflect the composition of the complexes in situ, or they might be artifactual associations between carotenoids and the lipophilic membrane complexes. Since a particular chemical species of carotenoid is associated with at least one of the complexes (reaction center), rather than a sample of the various carotenoids present in the membrane, the carotenoid-complex association is not random [12]. Furthermore, spectral studies have suggested that the carotenoids in membranes of *Rps. sphaeroides* exist in two pools [13], and only a fraction of the carotenoids undergo an electrochromic bandshift [14]. We have constructed, via mutations and genetic manipulations, a set of strains of *Rps. capsulata* in which to study carotenoid-antenna associations in situ. This became possible with the isolation of a mutant that lacks LH-II but carries out normal carotenoid biosynthesis. This mutant is a source of membranes that possess only LH-I and reaction center associated carotenoids. Since the reaction centers are a quantitatively minor component of these membranes, the properties of LH-I predominate spectral data obtained from these membranes. A reaction centerless mutant (Y142) provides a source of membranes containing only LH-II complexes, since both LH-I and reaction center complexes are absent in this mutant [15].

We have used two alternative strategies to circumvent certain difficulties that arise as a result of the inability of reaction centerless mutants to grow photosynthetically. These organisms can grow and produce pigmented membranes when incubated at low oxygen tensions, but growth of *Rps. capsulata* in the presence of O_2 results in mixture of spheroidene, spheroidenone and the hydroxylated derivative of each, a pigment composition unfavorable to spectral analysis. We have been able to introduce into each strain of interest, a mutation blocking the oxidation of the 3,4-bond of the carotenoids, thus creating 'green' mutants that accumulate neurosporene, hydroxyneurosporene and methoxyneurosporene, whether the cells are grown aerobically or photosynthetically. Alternatively, cells may be grown anaerobically in the dark by including an accessory oxidant and a fermentable sugar in the growth medium [16]. Membranes isolated from fermentatively grown cells appear to contain normal pigment-protein complexes, although the electron transport properties of these membranes are unlike those of membranes produced in other growth modes (Zannoni, D. and Marrs, B.L., unpublished results). We present here studies on the properties of the carotenoids in membrane-bound light-harvesting complexes in these mutant strains. We found striking differences in their absorption and circular dichroism spectra and their response to transmembrane electrical

potential, all of which indicate that the carotenoids interact with the two antenna complexes in distinctly different ways.

Materials and Methods

Bacterial strains. The strains employed are listed in Table I. All strains used are descended from *Rps. capsulata* strain B10. MW442 lacks the absorption peaks characteristic of LH-II antenna complexes, but it contains normal amounts of carotenoids. Strain Y142 (a reaction centerless mutant) has been described previously [13]. 'Green' derivatives of these strains were prepared by crossing the mutants containing wild type carotenoids with gene transfer agent obtained from the 'green' strain R121 [18]. In this way, we isolated the strains MT1131, a 'green' derivative of a wild type strain, MW4422, derived from MW442, and BY1424, from Y142. SB1003 is a wild type strain. Strains BPY31 and BJS11 are spontaneous carotenoidless mutants. BW604 is a carotenoidless mutant described in Ref. 18.

Cell growth. The media and growth conditions were as previously described [20]. When indicated, the cells were grown in the presence of dimethylsulfoxide as previously described [16]. Oxygen tension was maintained at con-

TABLE I

BACTERIAL STRAINS

Strains	Genotype *	Phenotype *	References and comments
SB1003	wild	wild	[17]
W4	*crtB4*	carotenoidless, no LH-II	[17], accumulates no carotenoid
BW604	*crtE6*	carotenoidless, no LH-II	[18], accumulates no carotenoid
BPY31	*crtF129, crt-31*	carotenoidless, no LH-II	accumulates no carotenoid
BJS11	*crt-711*	no colored carotenoid, no LH-II	accumulates phytoene
MW442	*crtB4, crt-742*	wild type carotenoids, no LH-II	survivor of POK ** selection on W4
Y142	*rxc-142*	wild type carotenoids, reaction center deficient, no LH-I	[15]
MT1131	*crtG121*	green carotenoids, wild type LH-I and LH-II	[19], accumulates nonaene carotenoids
MW4422	*crtB4, crtG121, crt-742*	green carotenoids, no LH-II	accumulates nonaene carotenoids; constructed from MW442 with GTA from strain R121 [18]
BY1424	*crtG121, rxc-142*	green carotenoids, reaction center deficient, no LH-I	accumulates nonaene carotenoids; constructed from Y142 with GTA from strain R121 [18]

* Genotypic and phenotypic descriptions are provided with regard to the photosynthetic apparatus only.
** POK is photooxidative killing (see Ref. 17).

stant values in growing cultures, where indicated by a Virtis Dissolved Oxygen Controller.

Vesicles preparation. French press chromatophores were prepared according to Ref. 20.

Spectrometric analysis. Absorbance spectra were recorded in a Heath model EU700 spectrophotometer. CO spectra were obtained in a Jasco-Durum model 20 CD spectrometer, with 1-cm pathlength cuvettes.

Carotenoid bandshift. The chromatophores were suspended in buffer, 100 mM choline chloride, 20 mM Mes (pH 6.4) in a 1 × 1 cm clearside cuvette. The concentration was adjusted to give an absorbance of 0.4 at the wavelength of maximum carotenoid absorption. Absorbance was recorded on an Aminco DW2 dual beam spectrophotometer, using the dual beam mode. The reference wavelength was shown to be isobestic in parallel split-beam experiments. Actinic light was obtained through a side illumination accessory with a Corning CS 7-69 colored glass filter (infrared transmitting) and the photomultiplier was protected from scattered light with a Corning CS 4-76 colored glass filter. Salt-induced carotenoid shifts were obtained according to the method of Jackson and Crofts [21]. Reaction center carotenoid bandshifts were measured on the computer-linked spectrophotometer built by Dr. A.R. Crofts.

Proton pumping measurements. Chromatophores containing approx. 1.4 mg of BChl were resuspended in 2 ml of buffer (2 mM glycine-glycine (pH 7.8), 100 mM KCl, 2 mM MgCl and 0.02 mM valinomycin) and kept at 28°C in a water-jacketed titration chamber. The pH changes generated upon illumination of the sample using an 870 nm interference filter were detected with a pH electrode place inside the chamber.

Energy transference. The photobleaching of the reaction centers at 605 nm (*P*-605) [22] was used to measure the ability of the carotenoids to transfer energy to the antenna BChl. The transmittance curve of the corresponding interference filter was integrated to determine the actinic light intensity. The signal obtained illuminating the chromatophores at 590 nm was used to standardize the results. The chromatophores were suspended in 10 mM Mops (pH 7.0), 100 mM KCl, 1 mM potassium cyanide, 0.002 mM valinomycin, 1 mM ascorbate and 0.01 mM DAD (2,3,5,6-tetramethyl-*p*-phenylenediamine).

Results

Absorption spectra of the different mutants

The absorption spectrum of strain MW4422 (Fig. 1A) indicates the presence of an antenna formed only by LH-I complexes, with an absorbance maximum located at 880 nm. Strain MW442, grown under photosynthetic conditions, also has an infrared maximum at that wavelength. When the green strain MT1131 (which contains both antenna systems) is grown under moderate oxygen tensions, the synthesis of LH-II complexes is repressed. Therefore, the resulting cells have LH-I as the main antenna complex. In this case, the absorption spectrum overlaps with the one of the strain MW4422 grown under the same conditions (Fig. 1A). In contrast are the BChl absorption spectra of four strains that lack colored carotenoids. Determination of the carotenoid content of these strains showed no polyenes in strains W4, BW604 and BPY31, while

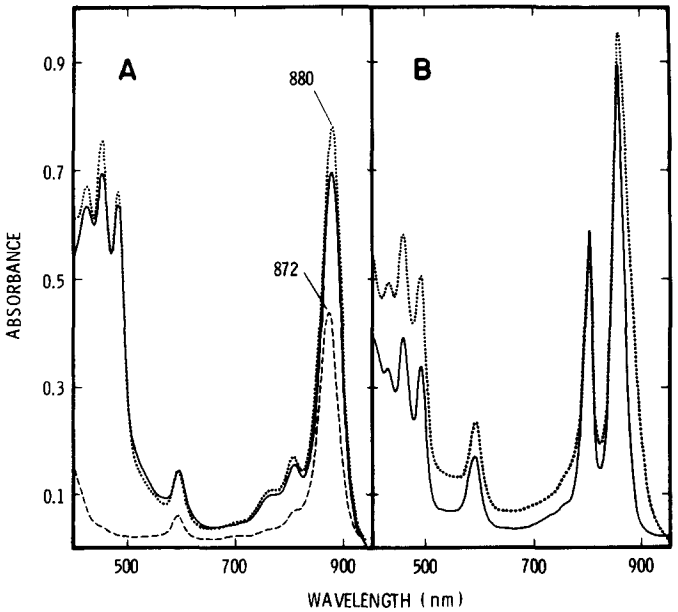


Fig. 1. Absorption spectra of chromatophores of the different mutants. A: strain MW4422 cultured under photosynthetic conditions (———); strain MT1131 grown under 20% oxygen concentration (· · · · · ·); strain W4 photosynthetically grown (- - - - - -). B; strain MT1131, grown under photosyntehtic conditions (· · · · · ·); strain BY1424 grown under 0.5% oxygen tension (———).

phytoene (15-*cis*-7,8,11,12,7′,8′,11′,12′-octahydro-ψ-ψ-carotene) is accumulated in strain BJS11. Each of them has an absorbance maximum at 872 nm, thus bacteriochlorophyll absorbance in the LH-I complex is affected either directly or indirectly by the absence of colored carotenoids.

The absorption spectrum of another mutant strain, BY1424 ('green' derivative of Y142) showed an antenna formed only by LH-II complexes (Fig. 1B). This strain is unable to grow photosynthetically because of the lack of reaction centers, which are normally coordinately synthetized with the LH-I antenna [4]. The absence of LH-I and reaction center in BY1424 results in both an absence of the shoulder of absorbance at 880 nm seen in MT1131 grown photosynthetically (Fig. 1B) and less absorbance in the Soret region.

A detailed analysis of the spectra of the mutants containing wild type carotenoids indicated (Fig. 2A, C and E) that the absorption maxima of the carotenoids in membranes containing only LH-I BChl are shifted 10 nm towards shorter wavelengths with respect to the strain containing only LH-II. Reflecting the simultaneous occurrence of both antenna systems, the carotenoid absorbance maxima obtained in the wild type strain SB1003 were intermediate between the values found in mutant strains (Fig. 2E). Membranes for the spectra in Fig. 2 were prepared from anaerobic/dark-grown cells in order to avoid spheroidenone formation. Membranes from either SB1003 or MW442 grown photosynthetically have the same carotenoid absorption spectrum as from the corresponding strain grown anaerobically in the dark (compare Fig. 2 and Fig. 6).

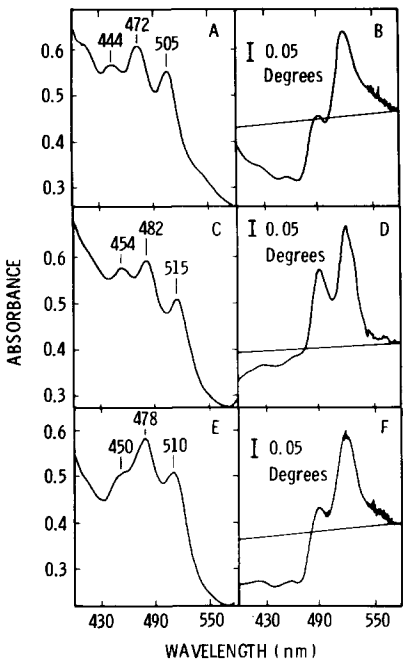


Fig. 2. Absorption and CD spectra of chromatophores in the carotenoid region of the spectrum. All the strains were grown anaerobically in the dark in the presence of dimethylsulfoxide. A: strain MW442; C: strain Y142; E: strain SB1003; B, D, and F: CD spectra of the same samples of A, C and E, respectively.

CD spectra

To further characterize the carotenoids of both types of mutants, we determined CD spectra of the strains MW442, Y142 and SB1003 (Fig. 2B, D and F). We found that the carotenoids of the strains Y142 and MW442 differ in the intensity of the signal at 490 nm (which is more intense when LH-II is present) and in the shape of the peak located at 520 nm, which is more symmetrical for the strains Y142 and SB1003 and asymmetrical for the strain MW442. No CD signals were detected in the region of the spectrum between 400 and 550 nm with chromatophores from the blue-green strain W4 or with carotenoids in a hexane solution (data not shown).

The carotenoid bandshift

The generation of an 'inside positive' transmembrane potential can be achieved by either the excitation of the reaction center or the use of potassium and the ionophore valinomycin [23]. In either case, a shift of the carotenoid absorption bands towards longer wavelengths can be observed in MT1131 (Fig. 3C). We did not observe significant bandshifts with strain MW4422 upon either illumination or valinomycin potassium treatment (Fig. 3A). In the strain BY1424, defective in reaction centers, it is obviously not possible to effect a charge separation by illumination, but a clear response can be chemically induced (Fig. 3B).

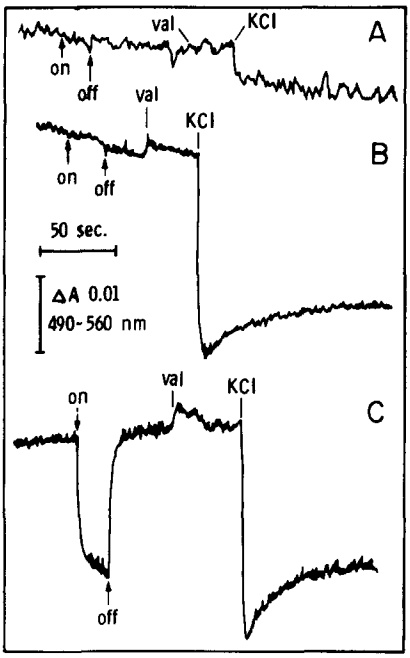


Fig. 3. Carotenoid bandshifts induced by light or valinomycin-KCl. Each strain was grown under 0.5% oxygen tension. A: strain MW4422; B: strain BY1424; C: strain MT1131. On and off refer to the illumination period. Addition of valinomycin (val) or KCl is indicated by lines.

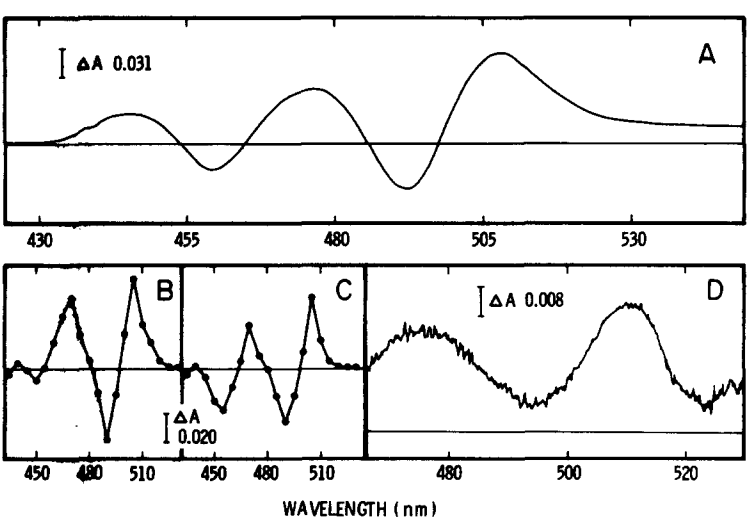


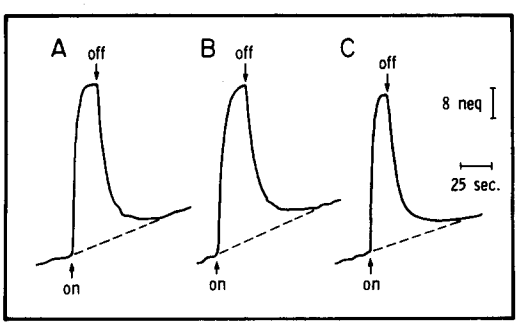
Fig. 4. Spectra of carotenoid bandshifts. Each strain was grown under 0.5% oxygen except for D, in which the strain MW442 was photosynthetically grown. The carotenoid concentration of each sample was adjusted to an absorbance of 0.40 at the wavelength of maximum absorbance, except in sample D, which was adjusted to 0.75. A: strain MT1131, light minus dark; B: strain MT1131, valinomycin-KCl minus KCl alone; C: strain BY1424, valinomycin-KCl minus KCl alone; D: strain MW442, light minus dark.

The spectra of these bandshifts are shown in Fig. 4. Similar results were obtained with the strains containing wild type carotenoids cultured in dimethylsulfoxide (data not shown). Using a computer-linked spectrophotometer [24] it was possible to detect small absorbance changes upon illumination of MW442 chromatophores (Fig. 4D). Unlike the antenna carotenoid bandshifts, the small changes in MW442 were insensitive to antimycin. Based on this fact and on the light minus dark difference spectrum (Fig. 4D), these changes probably correspond to reaction center carotenoid bandshifts [25]. It is interesting to note that we detected a much smaller reaction center carotenoid bandshift in membranes of MW4422, which contain the neurosporene group of carotenoids.

The proton pump present in chromatophore membranes [26] can be driven by infrared light in strain MW442 as well as in strains SB1003 (wild type) and W4 (carotenoidless), showing that the ability of the vesicles that contain only LH-I complexes to create and sustain a transmembrane potential is not impaired (Fig. 5).

Energy transference from carotenoids to chlorophyll

In order to test the ability of the carotenoids associated with either LH-I or



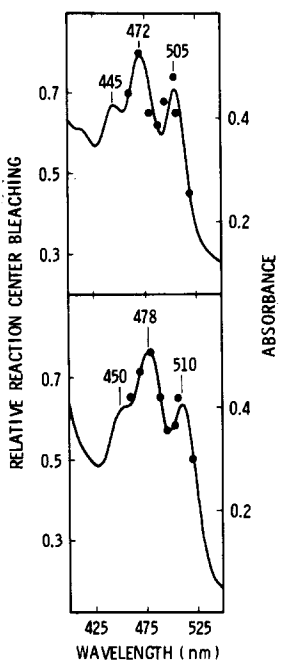


Fig. 5. Light-driven proton pumping in membrane vesicles. Membrane vesicles prepared from photosynthetically grown cells of each strain were illuminated with 870 nm light, and proton uptake and release were measured with a pH electrode. A, strain W4; B: strain SB1003; C, strain MW442.

Fig. 6. Energy transference from carotenoids to BChl, measured by the photobleaching of *P*-605. Both strains were photosynthetically grown. A: MW442; B: SB1003. The continuous traces are absorbance spectra. The data points are relative reaction center bleaching responses, calculated as the change in A_{605} (reaction center bleaching) induced by illumination of the sample at right angles with an actinic beam of wavelength indicated, relative to the change induced by 590 nm actinic light, correcting for the incident light intensity.

TABLE II

CAROTENOID CONTENT OF THE STRAINS SB1003 AND MW442

The quantitative determination of carotenoids was performed on photosynthetically grown cells as previously described [18].

Strain	μg carotenoids per mg of dry weight	Carotenoid content (% of total)		
		Spheroidene	Hydroxy-spheroidene	Spheroidenone
SB1003	2.6	83.6	4.9	11.5
MW442	2.7	85.3	5.8	8.9

LH-II to transfer the absorbed energy to antenna BChl, we tested the efficiency of the carotenoids of strains MW442 and SB1003 to induce photobleaching of the reaction center absorption band at 605 nm (*P*-605). The results (Fig. 6) indicate that in both cases the carotenoids can serve as antenna pigments with 60 to 70% of the efficiency of light absorbed by bacteriochlorophyll in the antenna. Under the same conditions, the blue-green strain W4 gave a totally flat response in the carotenoid region of the spectrum (data not shown). Note that the action spectrum for MW442 is clearly blue-shifted compared to that for SB1003.

The carotenoid content

The observed spectral and physiological differences between carotenoids in each antenna system could be accounted for by a difference in either the total amount or the relative composition of these compounds in the different strains. However, a quantitative determination of these parameters (Table II) showed no significant differences between the wild type and the MW442 strains.

Discussion

Carotenoids located in membranes containing only the LH-I antenna system show an absorbance spectrum that is shifted towards the blue with respect to that of wild type *Rps. capsulata*, and no changes in this spectrum are detected when a transmembrane potential is created by either light or valinomycin plus potassium. In contrast, carotenoids located within the LH-II microenvironment are red-shifted compared to the wild type, and a transmembrane potential causes a typical carotenoid band shift.

These data strongly suggest that at least two identifiable pools of carotenoids exist in wild type membranes of *Rps. capsulata*. The differences in spectral properties between these pools are attributed to different electronic environments in each antenna complex. The following reasoning further suggests that one pool is comprised of carotenoids within the domain of the LH-I antenna system, the other the LH-II, rather than one of the pools being carotenoids unassociated with either antenna system. The efficiency of energy transference from carotenoid to bacteriochlorophyll is fairly high and approximately con-

stant in membranes rich in LH-II (wild type, grown photosynthetically in dim light) and in membranes containing only LH-I (MW442). This suggests that in each type of complex the carotenoids are an integral part of the antenna, since carotenoids dissolved outside the antennae domains would not be expected to transfer energy to the productive light harvesting system as efficiently as carotenoids within an antenna domain. An independent line of evidence also suggests that carotenoids are an integral part of the H-I complex. A blue shift in LH-I BChl absorbance seen in carotenoidless membranes compared to caro-, tenoid-containing membranes. This shift implies an electronic response of BChl to the presence of carotenoids or some other membrane component intimately associated with carotenoids.

It should be noted that our observation of a KCl/valinomycin induced carotenoid bandshift in a reaction centerless mutant of *Rps. capsulata* stands in contrast to the results of Sherman and Clayton [27], who were unable to demonstrate any bandshift in the *Rps. spheroides* reaction centerless mutant PM-8. This difference may be due to differences in the exact nature of the mutations affecting reaction centers in each case, but the fact that the *Rps. capsulata* strain has no reaction center activity, and yet shows the carotenoid bandshift, demonstrates clearly that localized charge separation at the reaction center is not essential for the bandshift.

That the carotenoid bandshift is observed only in carotenoids associated with the LH-II system can be understood in terms of the orientation of the carotenoid molecules with respect to the plane of the membrane [28]. The carotenoids within the LH-II domain may adopt an orientation that may occur spontaneously in synthetic membranes, since carotenoid shifts are observed in them [29]. Hence it is possible that the presence of LH-I structures in the membrane restricts the orientation of the carotenoid molecules so that they cannot become properly aligned to undergo an electrochromic shift in response to the transmembrane field.

In interpreting our results we have assumed that the mutations that resulted in the loss of the LH-II complex in MW442 have not affected the properties of the residual LH-I, and similarly, we assume that the LH-II complex in Y142 has not been altered by the absence of LH-I and reaction center. The validity of these assumptions is supported by the complementarity of the spectra (both absorption and CD) from the mutants, which may be summed to give the wild type spectrum. Studies on independently isolated mutants with similar phenotypes should indicate to what degree the properties which we have ascribed to LH-I and LH-II are dependent upon the specific mutational alterations in MW442 and Y142. Nevertheless, our results are consistent with others authors' previous reports. Broglie et al. [11] have reported similar differences in the absorption spectra of carotenoids associated with LH-I or LH-II after isolation of these complexes. Symons et al. [13] and Holmes and Crofts [14] using curve-fitting techniques found that the carotenoids undergoing bandshifts are red-shifted with respect to the bulk carotenoids and are only a small fraction (10—20%) of the overall population in *Rps. sphaeroides*. A quantitation of the amount of carotenoids shifting in the strain Y142 obtained by using analogous techniques might indicate what fraction of the LH-II associated carotenoids are responsible for the bandshift.

Acknowledgements

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