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A COMPARISON OF THE LH2 ANTENNA COMPLEX OF THREE PURPLE BACTERIA BY HOLE BURNING AND ABSORPTION SPECTROSCOPIES

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Abstract The light harvesting 2 or B800-B850 complexes of *Rhodospirullum molishianum, Rhodopseudomonas acidophila* (strain 10050) and *Rhodobacter sphaeroides* are compared on the basis of thermal broadening and shifting of the B800 and B850 absorption bands, the B800→B850 energy transfer time and B870 which is the lowest exciton level of the B850 ring of BChl *a* dimers. The existence of B870 for *Rs. molischianum* is established and its B800→B850 energy transfer time, 1.9 ± 0.2 ps at 4.2 K, reported for the first time. The properties of the complexes of *Rs. molischianum* and *Rps. acidophila* bear a close resemblance. LH2 of *Rb. sphaeroides* is distinct, e.g. the thermal shifting of its B850 band is significantly weaker, consistent with weaker excitonic couplings in the B850 ring. For all species, these couplings strengthen upon glass formation near 150 K. Thermal broadening of B850 is interpreted in terms of inter-exciton level relaxation.

INTRODUCTION

In purple photosynthetic bacteria the light harvesting 2 (LH2) antenna complex functions to transfer excitation energy to the LH1 complex which is proximal to the reaction center and transfers energy to it. The structures, Q_y (S_1)-excited states and excitation energy transfer dynamics of these two complexes have long attracted much attention.[1,2] Recently, an X-ray structure of the LH2 (B800-850) complex from *Rps. acidophila* was reported[3,4] which reveals that it is a cyclic 9-mer of α,β polypeptide pairs. The arrangement of the bacteriochlorophyll *a* (BChl *a*) molecules is shown in Fig. 1[5] along with several relevant Mg...Mg distances. The large separation distance of 21 Å between neighboring B800 molecules results in weak excitonic coupling (V ~ 20 cm^{-1} [5,6]),

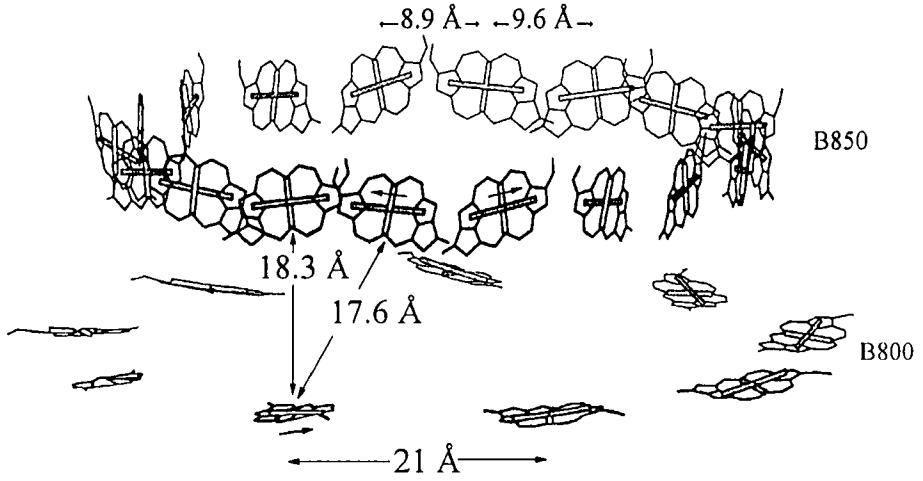

FIGURE 1 Schematic (based on Fig. 1 of ref. 5) showing the C_9-arrangement of the 18 B850 and 9 B800 molecules in the LH2 complex from *Rps. acidophila*. Nearest neighbor Mg...Mg distances between BChl *a* molecules of B850 are 8.9 and 9.6 Å with the latter that of the two BChl *a* molecules associated with the α,β polypeptide pair. The two B850 molecules closest to a B800 molecule are separated from it by 17.6 and 18.3 Å. Note the large distance (21 Å) between adjacent B800 molecules.

consistent with earlier biochemical and spectroscopic data[1,2] including those from hole burning studies.[7-9] However, the B850 nearest neighbor distances of 8.9 and 9.6 Å lead to large couplings of about 300 cm^{-1}.[5] Symmetry dictates that the B850 ring be viewed as a 9-mer of BChl *a* dimers, the choice of dimer (8.9 or 9.6 Å) being quite arbitrary. Earlier hole burning studies had indicated that exciton level structure and ultra-fast (~ 100 fs) interexciton level relaxation were important for understanding the nature of the B850 absorption band of LH2 in both *Rhodobacter sphaeroides*[10] and *Rps. acidophila*.[9] Electronic structure calculations[5] which utilized the X-ray structure coordinates and femtosecond pump-probe data[11,12] provided considerable support for their importance.

The 9-fold cyclic symmetry of LH2 exhibited in crystals from *Rps. acidophila* was unanticipated. Other cyclic symmetries and structural arrangements of the BChl *a* molecules had been considered.[2,13] Very recently, the X-ray structure of the isolated LH2 or B800-850 complex of *Rhodospirillum molischianum* was reported.[14] Interestingly, LH2 was shown to be an 8-mer of α,β polypeptide pairs. A detailed discussion of the differences in the two structures is given by Koepke et al.[14] Suffice it to say now that the

picture which has the B800 molecules weakly coupled and the B850 molecules strongly coupled remains intact for LH2 of *Rs. molischianum*. This is also true for the model that has the coupling between B800 and B850 molecules sufficiently weak for a Förster mechanism to be applicable to B800→B850 excitation energy transfer. (The most detailed experimental and theoretical study of this energy transfer process is given in ref. 15.)

The purpose of this paper is to present temperature dependent absorption and 4.2 K hole burning data for isolated LH2 complexes of *Rs. molischianum*, *Rb. sphaeroides* (for which an X-ray structure does not exist) and *Rps. acidophila*. Comparison between the three species is made on the basis of the temperature dependence of LH2's Q_y $(S_1)\leftarrow S_0$ absorption spectrum (4.2- ~300 K), the zero-phonon hole action spectrum of B870 which has been assigned as the lowest exciton level of the B850 ring in *Rps. acidophila*[9,16] and *Rb. sphaeroides*,[10] and the B800→B850 energy transfer rate at 4.2 K. A determination of this rate or the existence of B870 for *Rs. molischianum* have not previously been reported. Interestingly, the results show that LH2 of *Rs. molischianum* exhibits properties which are considerably more similar to those of LH2 of *Rps. acidophila* than *Rb. sphaeroides*.

RESULTS

The hole burning apparatus, which is based on a Bruker HR 120 Fourier transform spectrometer and Coherent CR 899-21 Ti:sapphire laser (linewidth of 0.07 cm^{-1}), is described elsewhere.[17] Hole spectra were read with a resolution of 0.5 cm^{-1}. Burn intensities and times are given in the figure captions. Temperature dependent absorption spectra were recorded with a resolution of 2 cm^{-1}. Isolation and purification of the LH2 complexes from *Rs. molischianum* and *Rps. acidophila* (*Rb. sphaeroides*) was performed as in refs. 14 and 18.

Figure 2 compares the 4.2 K Q_y-absorption spectra of LH2 (B800-850) for the three bacterial species. The values of the B800-B850 energy gap are given in cm^{-1}. Given in parentheses are the values at room temperature. (The B850 exciton level energy level diagram at the bottom of the figure is discussed in the following section.) The energy gap results from *Rps. acidophila* and *Rs. molischianum* are similar with the gap increasing significantly from 830 to 955 cm^{-1} and 825 to 990 cm^{-1}, respectively, in the low temperature limit. The gap for *Rb. sphaeroides* increases by only 55 cm^{-1}. The temperature dependencies of the gap and width of the B850 absorption band are shown in Fig. 3 for *Rps. acidophila* and *Rb. sphaeroides*. Focusing first on the gap, one observes

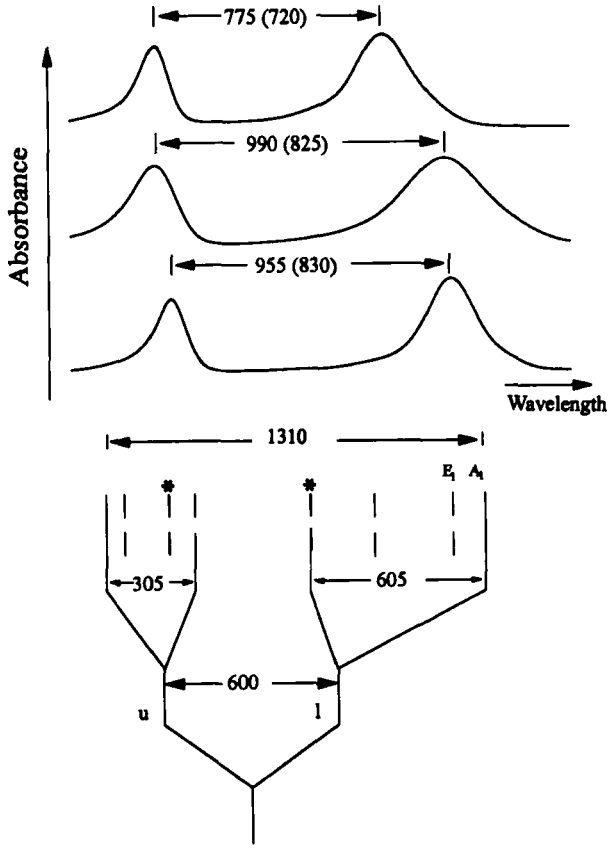

FIGURE 2 4.2 K Q_y-absorption spectra of the LH2 (B800-850) complex of *Rb. sphaeroides* (top), *Rs. molischianum* (middle) and *Rps. acidophila* (bottom). Unit for the B800-B850 energy gap is cm^{-1}. Room temperature values are given in parenthesis. The exciton level energy diagram for the B850 ring of BChl *a* is from ref. 16 which assumes perfect C_9-symmetry, i.e. no diagonal or off-diagonal energy disorder. With this assumption and the X-ray structure, it is the second level (E_1) from the bottom of the l-manifold that carries almost all the absorption intensity. The asterisks indicate closely-spaced doubly degenerate levels.

that for both species it is constant from 4.2 to ~ 150 K and then decreases in a near linear fashion. The decrease is due solely to blue-shifting of the B850 band for $T \gtrsim 150$ K since the frequency of the B800 band is independent of temperature to within ± 5 cm^{-1} (results not shown). Thus, the temperature dependence of the energy gap is also that of the B850

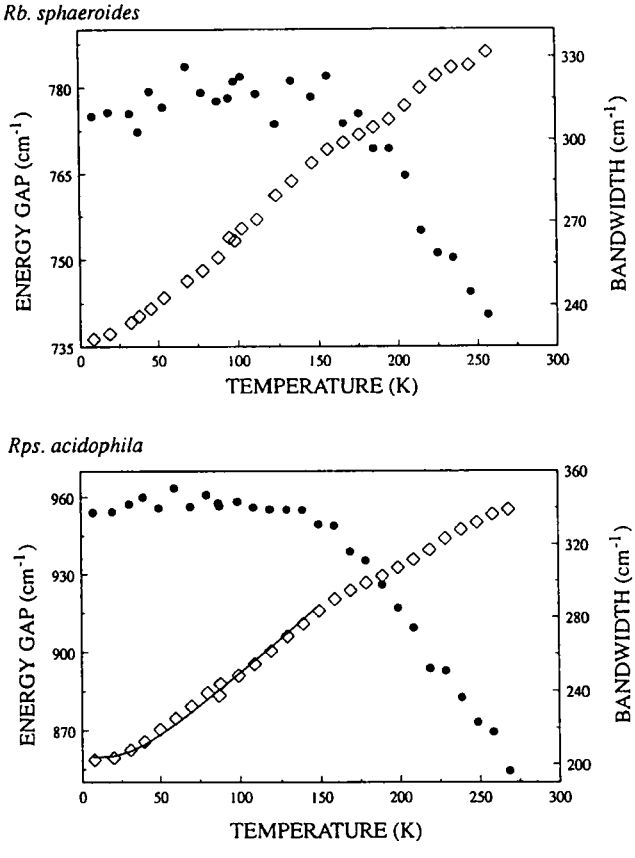

FIGURE 3 Temperature dependencies of the B800-B850 energy gap (circles) and B850 bandwidth (diamonds) for *Rb. sphaeroides* (upper frame) and *Rps. acidophila* (lower frame). Since the B800 band maximum frequency is independent of temperature, the temperature dependence of the gap is that of the position of the B850 band maximum. Note that the T-dependence of the gap for *Rb. sphaeroides* is significantly weaker and, for both species, that there are "breaks" in the data near 150 K, ~ the glass transition temperature of the glycerol:water based glass. The solid curve through the thermal broadening data for *Rps. acidophila* is a theoretical fit, cf. text.

band position. Note that the blue-shifting of B850 of *Rps. acidophila* is significantly larger than that of *Rb. sphaeroides* (–0.87 cm^{-1} K^{-1} vs. –0.44 cm^{-1} K^{-1}). Preliminary data obtained for *Rs. molischianum* indicate that the temperature dependence of its B800-B850 gap mimics that of *Rps. acidophila*, consistent with the results of Fig. 2.

Turning next to the B850 bandwidth data in Fig. 3, one observes a distinct break near 150 K for both species. The rate of thermal broadening is slower at temperatures higher than ~ 150 K. The solid line through the data points below ~ 150 K for *Rps. acidophila* is a theoretical fit based on dephasing from inter-exciton level relaxation, cf. following section. The significance of the temperature 150 K becomes apparent when it is noted that it is close to the glass transition temperature (T_g) of the glycerol:water based solvent used. The results presented thus far show that B850 of *Rs. molischianum* behaves very similarly to B850 of *Rps. acidophila* with both exhibiting a temperature dependence for the B800-B850 gap which is much stronger than that of *Rb. sphaeroides*. This finding is interesting given that the X-ray structures revealed that the LH2 complexes of *Rps. acidophila* and *Rs. molischianum* are, respectively, 9-mers and 8-mers of α,β-polypeptide pairs. Again, the structure of LH2 for *Rb. sphaeroides* has not been determined.

A closer resemblance of LH2 of *Rs. molischianum* to LH2 of *Rps. acidophila* rather than *Rb. sphaeroides* is also suggested by the B800→B850 energy transfer rate at 4.2 K (but see following section). Zero-phonon holes were burned in B800 of *Rs. molischianum* at the positions indicated by the arrows in Fig. 4. Averaging of the holewidths yielded a value of 5.7 ± 0.4 cm^{-1} which corresponds to a B800→B850 energy transfer time of 1.9 ± 0.2 ps. A typical zero-phonon hole profile is shown in the inset of Fig. 4. Recently, 2-color femtosecond pump-probe and hole burning spectroscopies yielded a time of 1.8 ± 0.2 ps for the isolated LH2 complex from *Rps. acidophila* in the low temperature limit.[15] Earlier low temperature hole burning studies by two groups led to a rate of $(2.4 \pm 0.2 \text{ ps})^{-1}$ for LH2 from *Rb. sphaeroides*,[7,8] which is about 30% slower than the rates for *Rps. acidophila* and *Rs. molischianum*.

To conclude this section we consider the zero-phonon hole (ZPH) action spectrum associated with the B850 band of *Rs. molischianum*, Fig. 4. Indicated in the region of the low energy tail of B850 are a series of zero-phonon holes burned at different frequencies with a constant laser fluence. An expanded view of the action spectrum is shown in the upper right hand corner. The contour of the ZPHs is centered at 11230 ± 10 cm^{-1} (890.5 ± 0.8 nm) which is 290 cm^{-1} lower in energy than the B850 absorption maximum. The width (inhomogeneous) of the contour is 160 ± 10 cm^{-1}. The ZPH action spectrum represents the absorption profile of B870, the lowest exciton level of the B850 ring of BChl *a* molecules, cf. Introduction. (It is referred to as B870 because in *Rb. sphaeroides* it is located near 870 nm.) For comparison of these results for B870 of *Rs. molischianum*, we note that for *Rb. sphaeroides*[10] and *Rps. acidophila*[16] B870 lies, respectively, 250 and 200 cm^{-1} below the B850 absorption maximum. Since the results presented here

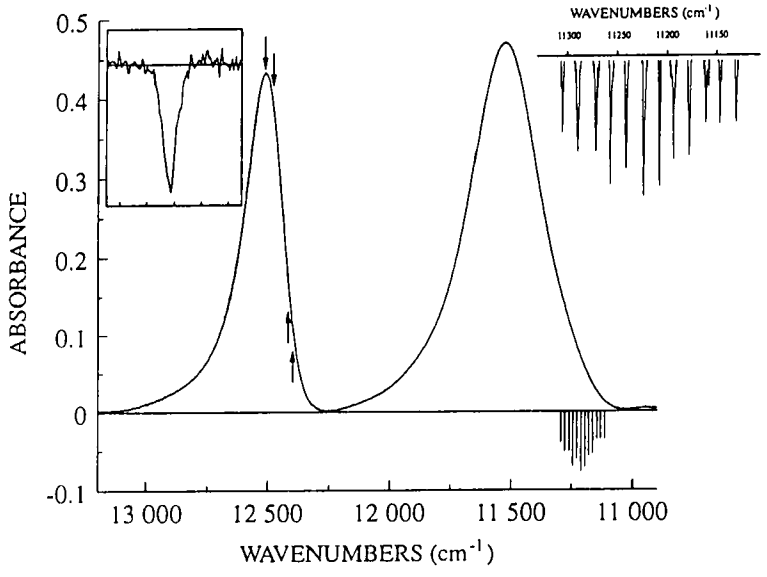

FIGURE 4 Absorption and B870's zero-phonon-hole action spectrum (arbitrary units) for LH2 of *Rs. molischianum* at 4.2 K. An expanded view of the action spectrum is shown in the upper right hand corner. The maximum of B870 lies 290 cm^{-1} below the maximum of the B850 absorption band. The burn fluence used to generate the action spectrum was 20 J cm^{-2}. The vertical arrows located in B800 indicate the wavelengths used to burn zero-phonon holes whose widths led to a B800→B850 energy transfer time of 1.9 ± 0.2 ps at 4.2 K. Burn intensity and burn time were 2 W/cm^2 and 10 sec. A typical ZPH is shown in the inset for a burn wavelength of 802.5 nm; division on horizontal axis = 10 cm^{-1}.

establish, for the first time, that B870 also exists for *Rs. molischianum*, it is reasonable to assert that B870 is a common feature of the B850 BChl *a* ring of purple bacteria. As reported for *Rb. sphaeroides*[10] and *Rps. acidophila*,[6,16] burning near and to the blue of the B850 absorption maximum of *Rps. molischianum* produced only a very broad hole (bleach) in B850 which we interpret, again, as being a consequence of ultra-fast (~ 100 fs) downward inter-exciton level relaxation of the levels in the B850 band which lie above B870.

DISCUSSION

We begin by considering the question of whether the temperature dependences of the B850 band and B800-B850 energy gap reported here are only to be associated with the isolated LH2 complex. The answer is no since the peak frequencies of the B800 and B850 bands in chromatophores of *Rps. acidophila* and *Rb. sphaeroides* at room temperature and 4.2 K were observed to be nearly the same as in the isolated complexes (ref. 15, unpublished results). Furthermore, B850 of chromatophores also begins to blue-shift near 150 K. One may conclude that the isolation and purification procedures used in our work had little effect on the structural arrangements of the BChl *a* molecules in LH2.

The breaks seen near 150 K in the thermal broadening of the B850 band and temperature dependence of the B800-B850 energy gap, Fig. 3, are most likely triggered by formation of the glycerol:water based glass (this solvent was also used for chromatophores, *vide supra*). As discussed in ref. 16, data of the type shown in Fig. 3 strongly indicate that nearest neighbor couplings between B850 molecules strengthen upon formation of the glass. (This is an important finding for theoretical modeling of the Q_y-electronic structure of LH2 based on the room temperature X-ray structures and low temperature spectroscopic data.) The question of the nature of the structural change near 150 K is very difficult. At this point we can only mention relevant results for B800. For all three species, the thermal broadening and peak frequency showed no break near 150 K (results not shown). Thus, the structural change of LH2 is not dramatic although it suffices to affect excitonic interactions within the B850 ring.

Next, we briefly consider the thermal broadening data of B850 shown in Fig. 3, specifically those for *Rps. acidophila* for which theoretical analysis has been completed. In particular, the solid line theoretical fit to the data for $T < \sim 150$ K will be discussed. But first we note that, with the observation that the B850 band (also B800 band) does not shift with temperature below ~ 150 K, one can safely conclude that anharmonicity is not responsible for the thermal broadening, i.e. structural changes below about 150 K are negligible. Second, the thermal broadening data for B850 is very different from the thermal broadening curve of B800 (not shown) which shows considerable curvature consistent with dephasing due to the Raman phonon-scattering mechanism which was developed for isolated impurities in solids (details to be published elsewhere). The solid line fit to the data for *Rps. acidophila* in Fig. 3 was obtained with the model that has the temperature dependent dephasing due to downward relaxation from one B850 exciton level to another by one-phonon emission. Thus, the contribution to the homogeneous width of the main part of the B850 band is given by[19]

$$\Gamma(T) = \Gamma(0\,K)\,(\bar{n}_{\omega} + 1),$$

where $\bar{n}_{\omega} = [\exp(\hbar\omega / kT) - 1]^{-1}$ is the thermal occupation number of a phonon with frequency ω equal to the effective gap between exciton levels. Note that $\Gamma(T) \propto T$ in the high temperature limit. The fit to the data yielded $\omega = 70\ cm^{-1}$ and $\Gamma(0\ K) = 80\ cm^{-1}$. The latter value corresponds to an inter-exciton level relaxation rate of 130 fs for the low temperature limit. As mentioned in the Introduction, intra-B850 relaxation processes which occur on this time scale have been measured. Importantly, a recent analysis of the 4.2 K B850 absorption profile of *Rps. acidophila* based, in part, on the ZPH action spectrum of B870 yielded a homogeneous width $\Gamma(0\ K) = 75\ cm^{-1}$,[16] which is in good agreement with the above value.

Although informative, the above equation is a simplification since it provides only an effective energy gap. The B850 exciton level energy diagram from ref. 16 given in Fig. 2 was calculated under the assumption of perfect C_9-symmetry using the nearest neighbor dimer-dimer coupling approximation. The lower (l) and upper (u) levels of the basic dimer spawn two exciton manifolds. Of the ten levels, eight of which are doubly degenerate, only the E_1 level of the l-manifold carries significant absorption intensity.[5] The inter-exciton level relaxation considered above could correspond to relaxation from the E_1 to A_1 level which lies lowest in energy. However, Wu et al.[16] concluded that the association of the A_1 level with B870 is problematic under the assumption of perfect cyclic symmetry and that diagonal and/or off-diagonal energy disorder of the B850 ring needs to be taken into account. Such energy disorder mixes the zero-order levels, making previously forbidden levels allowed and splitting degeneracies. Thus, the thermal broadening of the B850 band becomes a multi-level relaxation problem. Nevertheless, the finding that a two-level model with an effective gap of $70\ cm^{-1}$ accounts for the thermal broadening provides guidance for more detailed theoretical studies.

We conclude by considering the similarities and differences in the results obtained for LH2 of the three bacterial species. In doing so we include some data for B800 which were not presented because of space limitation. For all three species, the frequency of the B800 maximum is independent of temperature. Furthermore, their B800 thermal broadening curves are very similar. Differences in the position of the B800 maximum at 4.2 K are only ~ 4 nm. Earlier hole burning studies for *Rb. sphaeroides*[7,8] and *Rps. acidophila*[6,16] had proven that the B800 band is largely inhomogeneously broadened and characterized by weak electron-phonon coupling. This is also the case for *Rs. molischianum*. Thus, data of the above types do not allow for distinction between the three complexes. (Note that differences in the low temperature width of the B800 band

are not relevant since they reflect, to a considerable extent, sample quality/heterogeneity.) This finding is not so surprising given that neighboring B800 molecules are separated by a large distance of ~ 21 Å and, as a consequence, are weakly coupled.

The most significant different is seen in the temperature dependence of the B800-B850 energy gap or, equivalently, the frequency of the B850 band maximum. The finding that this dependence is very similar for *Rps. acidophila* and *Rs. molischianum* is interesting given that the X-ray structures of their LH2 complexes revealed they are, respectively, 9- and 8-mers of α,β polypeptide pairs. However, the nearest neighbor B850-B850 distances of 8.9 and 9.6 Å for *Rps. acidophila*,[4] Fig. 1, are not so different from the 8.9 and 9.2 Å values for *Rs. molischianum*[14] and the orientations of neighboring Q_y-transition dipoles appear to be nearly identical.[14] We hasten to add, however, that our studies pertain to isolated LH2 complexes in a glass. Thus, it is possible that the samples studied were say a mixture of 8-mers and 9-mers, i.e. the finding that LH2 of *Rps. acidophila* and *Rs. molischianum* are 9- and 8-mers, respectively, might be a consequence of the initial nucleation processes which yielded the crystals studied. Be that as it may, the data establish that the temperature dependence of the B850 band position for *Rb. sphaeroides* is significantly weaker than those of *Rps. acidophila* and *Rs. molischianum*. Our results strongly indicate that nearest neighbor B850-B850 couplings for *Rb. sphaeroides* of LH2 (including chromatophores) are weaker than those of the other two species at all temperatures. Hopefully, an X-ray structure for LH2 of *Rb. sphaeroides* will soon be available so that this assertion can be tested.

Although there are differences in the thermal broadening curves of B850 for the three species (Fig. 3, preliminary results for *Rs. molischianum* not shown), they are too small to be considered significant at this time. Similarly, not too much significance should be attached at this time to the finding that the B800→B850 energy transfer rates for *Rps. acidophila* are identical within experimental uncertainty, $(1.8\ ps)^{-1}$, about 30% faster than for *Rb. sphaeroides* since the rate depends on several parameters,[15] including energy disorder. Furthermore, the X-ray structures of LH2 for *Rps. acidophila* and *Rs. molischianum* reveal that there are significant differences in the relative orientations of the B800 and B850 Q_y-transition dipoles.[14]

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