Biochimica et Biophysica Acta, 503 (1978) 26—36

BBA 47523

FLASH-INDUCED CHANGES IN THE IN VIVO BACTERIOCHLOROPHYLL FLUORESCENCE YIELD AT LOW TEMPERATURES AND LOW REDOX POTENTIALS IN CAROTENOID-CONTAINING STRAINS OF PHOTOSYNTHETIC BACTERIA

NIGEL G. HOLMES *, RIENK VAN GRONDELLE and LOUIS N.M. DUYSENS

Department of Biophysics, Huygens Laboratory of the State University, Wassenaarseweg 78, 2300 RA Leiden (The Netherlands)

(Received October 24th, 1977)

Summary

The changes in the in vivo bacteriochlorophyll fluorescence induced by a Xenon flash at low temperatures (77—200 K) with the "primary" acceptor X chemically prereduced have been examined in whole cells of several species of photosynthetic bacteria which contain carotenoids absorbing in the visible part of the absorption spectrum. Two groups of species with different behaviour could be distinguished. In both cases a flash-induced rise of the fluorescence yield was observed with X prereduced at 77 K; as the temperature was increased the ratio of the maximum fluorescence (F_M) and the basal fluorescence (F_0) decreased and the kinetics of the decay of the high fluorescent state, as observed during the tail of the flash, apparently accelerated. Of the species examined the flash-induced changes in fluorescence-yield kinetics appeared to occur at higher temperatures in the members of one group (*Chromatium vinosum*, *Rhodopseudomonas gelatinosa* and *Rhodopseudomonas palustris*) than in the members of the other (*Rhodopseudomonas sphaeroides* and *Rhodospirillum rubrum*). These effects are interpreted in terms of the light-induced generation of triplet states within the reaction centre. It is suggested that the species-dependent differences may reflect differences in the molecular organisation of the reaction centre. It was found that in all species the reaction centre carotenoid triplet does not act as a fluorescence quencher under these conditions.

Abbreviations: for a definition of the symbols used in this paper, see the preceding paper.

* Present address: Department of Biochemistry, University of Bristol, Medical School, University Walk, Bristol BS8 1TD, U.K.

Introduction

Results reported recently concerning the events occurring in the reaction centres of photosynthetic bacteria immediately after excitation have led to a much greater understanding of the reactions involved [1—12]: the scheme shown in Fig. 1 of the preceding paper [27] summarises the reactions currently thought to take place in reaction centres of *Rhodopseudomonas sphaeroides*. In so far as they have been examined other species seem to resemble *Rps. sphaeroides* [6,8—12].

After the generation of the first excited singlet state of the bacteriochlorophyll dimer (*P*-870) by a quantum of light, an electron is transferred from *P*-870 to the long-wavelength bacteriopheophytin (I) to form the radical pair P^+I^-. Under normal conditions the electron is rapidly transferred to the "primary" electron acceptor, an iron · quinone complex, X, this reaction having a half time of about 200 ps, to give $[PIX^-]$. If, however, the "primary" acceptor X has already been chemically reduced, or removed by extraction, this electron transfer cannot take place. Three possible fates have to be considered for the state $[P^+I^-X^-]$: the formation of the reaction centre triplet $[P^{TR}IX^-]$, charge recombination to the first excited singlet state $[P^*IX^-]$ or the direct decay to the ground state $[PIX^-]$. In the accompanying paper [27] we present evidence to suggest that of these possibilities the direct recombination to the ground state is not very probable and that the relative importance of the other two decay rates depends on the temperature. In the presence of coloured carotenoids (i.e. carotenoids having absorbance bands in the visible part of the spectrum) the triplet state of the bacteriochlorophyll dimer apparently generates a carotenoid triplet state within 50—60 ns at 77 K [6]. It has been suggested that the reaction centre bacteriochlorophyll triplet (P^{TR}) and the carotenoid triplet (car^{TR}) may be in some sort of (temperature dependent) equilibrium. In carotenoid-containing reaction centres of *Rps. sphaeroides* the generation of the carotenoid triplet from P^{TR} seems to become increasingly less probable as the temperature decreases to very low values [7].

Previous work has shown that the generation of P^{TR} in a mutant of *Rps. sphaeroides* lacking coloured carotenoid (R26) leads to a high fluorescent state at 77 K similar to that resulting from the generation of $[P^+IX^-]$ [13]; at room temperature the generation of P^{TR} probably also leads to an increase in fluorescence yield [14].

The results discussed below extend our previous observations on the fluorescence yield changes induced in a short flash at low temperature to strains containing coloured carotenoids.

Materials and Methods

Cultures of *Rps. sphaeroides* wild type were grown in a modification of the medium of Cohen-Bazire et al. [15] and of *Chromatium vinosum* in Hendly medium [16] as previously described. The cells were harvested resuspended in 250 mM morpholinopropane sulphate (MOPS)/50 mM KCl/1 mM ascorbate at pH 7.0 and adjusted to an absorbance of 0.3 mm^{-1} at 850 nm—960 nm for *Rps. sphaeroides* wild type and 0.3 mm^{-1} at 880 nm—960 nm for *C. vinosum*.

This preparation was then made 1 M in sucrose and mixed 45 : 55 (v/v) with glycerol.

Fluorescence yield changes during a 15 μs flash were measured as previously described [13]. The flash was passed through a filter combination consisting of a Calflex C, a Balzers K1 and a Schott BG18/2 filters to select blue exciting light with a peak wavelength of 414 nm; the fluorescence was observed using a photomultiplier with an S1 response protected from the actinic light by a Schott RG780/2 filter together with an appropriate interference filter: a Schott AL928 (maximum transmission at 928 nm, half width 20 nm) for measurements with *C. vinosum* and a Schott AL911 (maximum transmission 911 nm, half width 20 nm) for *Rps. sphaeroides.*

Samples for measurement, in a 1 mm path length perspex cuvette, were frozen by slowly immersing in a dewar vessel containing liquid nitrogen; care was taken to ensure that no cracking of the sample occurred. The temperature was monitored by a copper-constantan thermocouple placed in the sample and measured against a similar thermocouple immersed in an ice/water mixture.

For samples in which the primary acceptor was to be reduced, sodium dithionite was added to the sample before freezing, at the concentration indicated, in a sealed vessel.

Fluorescence yield changes were related to changes in the fraction of photochemically active traps, T, assuming a "lake" model as suggested by the work of Vredenberg and Duysens [17] and Clayton [18], the fraction of open traps for a fluorescence yield F being given by the formula

$$T = \frac{\frac{F_M}{F} - 1}{\frac{F_M}{F_0} - 1} \tag{1}$$

where F_M is the fluorescence level obtained with all traps closed and F_0 is the basal or "dark" fluorescence level obtained with all traps open.

Results

The fluorescence yield changes seen during a flash at low temperatures in samples of cells of various photosynthetic bacteria in which X had been chemically prereduced were found to be dependent on the species used. Broadly speaking, two types of behaviour could be identified, one exemplified by *C. vinosum* and the other by *Rps. sphaeroides* wild type. Of other species investigated, *Rhodopseudomonas palustris* and *Rhodopseudomonas gelatinosa* behaved similar to *C. vinosum; Rhodospirillum rubrum* wild type similarly to *Rps. sphaeroides.*

In Fig. 1 the flash-induced changes in the fluorescence yield of *C. vinosum*, with X chemically prereduced, are displayed. As an indication of the temperature dependency the results at four different temperatures were selected. At each temperature a flash of low intensity was given to measure the F_0 or "dark" fluorescence level and a flash of a higher intensity to obtain the fluorescence induction. The intensity of the first flash was chosen low enough to cause only

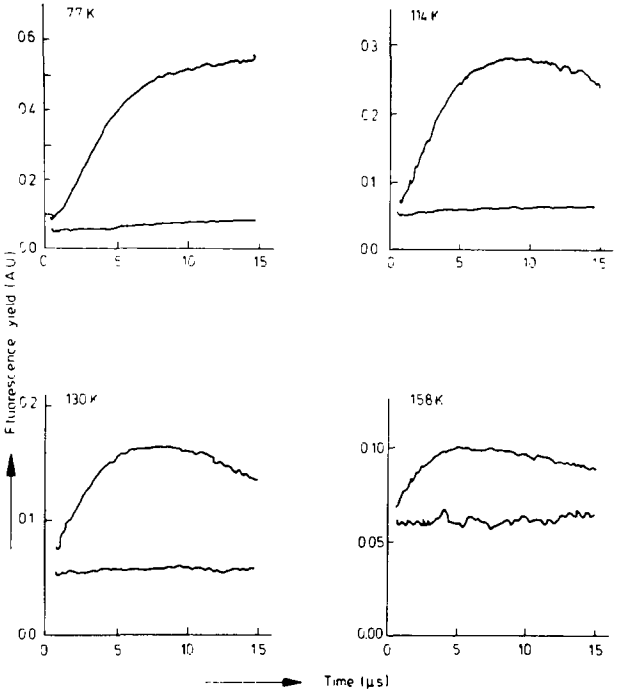

Fig. 1. Fluorescence yield changes in *C. vinosum* at different temperatures with X prereduced. The sample (see Materials and Methods) was reduced by the addition of 100 mM dithionite to give a sample of cells in which the reaction centres are in [*P*IX$^-$]. The lower curve at each temperature shows the fluorescence yield as caused by a low intensity flash which caused only little change in the fluorescence yield (at 77 K) in a sample with reaction centres in [*P*IX]; the upper curves at each temperature show the changes in fluorescence yield as caused by a flash which was intense enough to induce a maximal fluorescence rise (at 77 K) in a sample with reaction centres in [*P*IX] before the flash (see Fig. 2).

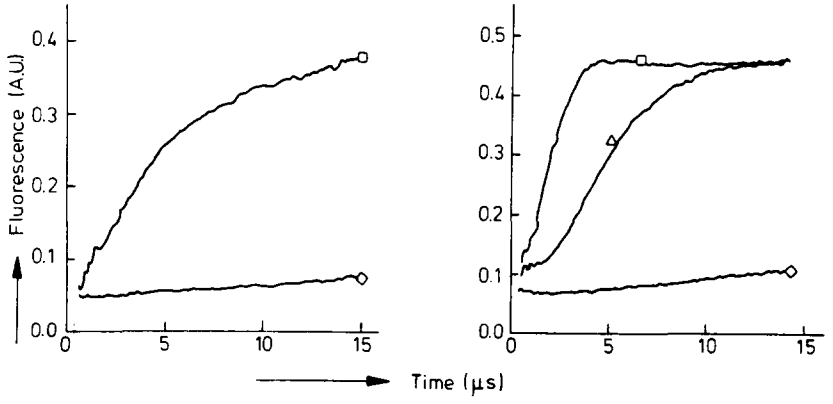

Fig. 2. Fluorescence rises in *C. vinosum* and *Rps. sphaeroides* with X in the oxidised state before the flash ([*P*IX]). Left, *C. vinosum:* ◇, low intensity flash, low enough to cause only a small rise in the fluorescence yield; □, high intensity, just intense enough to induce a maximum fluorescence rise. Right, *Rps. sphaeroides:* ◇, low intensity flash, again low enough to cause only minor changes in the fluorescence; △, just saturating flash; □, flash four times more intense than the "just saturating" flash.

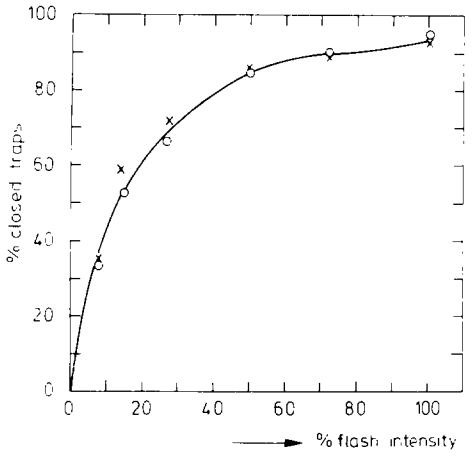

Fig. 3. Saturation curve for the observed rise in fluorescence yield in whole cells of *C. vinosum* at 77 K, calculated as described in the text. The change is that 4 μs after the start of the flash for various flash intensities. X, sample of cells with reaction centres in [*P*IX]; ○, sample with reaction centres in [*P*IX$^-$]. X was reduced with 100 mM sodium dithionite. Apart from the presence of the sodium dithionite the samples in the two types of experiments were identical.

little change of the observed fluorescence level (Fig. 1, the lower curve at each temperature), the intensity of the second flash was chosen high enough to induce a maximal fluorescence rise at 77 K ("saturating") in a sample where X was oxidized before the flash. For comparison, the behaviour of a sample without X prereduced, i.e., the fluorescence yield change due to the reaction [*P*IX] → [*P*$^+$IX$^-$], at 77 K, is also shown using flashes of the same intensities as in Fig. 1 (Fig. 2, left). At 77 K the flash-induced increase in fluorescence yield in the two samples can be seen to be similar in shape and amplitude although a slightly greater maximal fluorescence rise (10—20%) was routinely seen in samples with X chemically prereduced; the significance of this difference is still unclear. Fig. 3 compares the fraction of traps closed, as calculated from the fluorescence yield (see Material and Methods) 4 μs after the start of the flash, for various intensities of the flash, in samples with and without X prereduced. For the values of F_M and F_0 in Eqn. 1 we used the maximal value reached in a saturating flash and the fluorescence yield at the beginning of a low intensity flash, respectively, for both preparations. The quantum efficiencies for the generation of the high fluorescent states in the two differently treated samples are essentially identical. Assuming the charge separation in unreduced samples is a one quantum process and is of high efficiency [19,20], the high fluorescent state produced in samples with X prereduced must then also be generated by a single quantum process. Increasing the temperature (Fig. 1) results in a decrease of the maximal fluorescence yield reached with a given intensity of the flash and alters the kinetics during the flash. With increasing temperature the decay of the fluorescence yield during the tail of the flash (the peak of the flash occurs after 7 μs) becomes visible.

Fig. 4 shows the behaviour with increasing temperature of the ratio F_M/F_0. F_0 was again determined using a low intensity flash, in this case low enough to cause no essential change in the observed fluorescence level at all tempera-

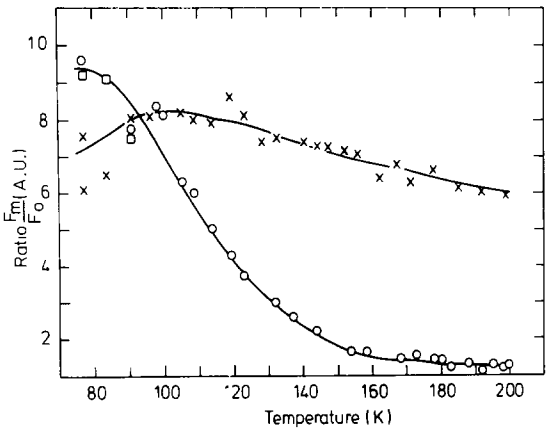

Fig. 4. Temperature dependence of the rise of the fluorescence yield (plotted as the ratio F_M/F_0) in whole cells of *C. vinosum*. F_M is the maximum yield of fluorescence during the time of observation (15 μs from the start of the flash), F_0 is again the dark fluorescence level. The flash intensities used to determine F_0 and F_M are defined in exactly the same way as described in the legend of Fig. 1. X, sample with reaction centres in [*P*IX] before the flash; ○, sample with reaction centres in [*P*IX$^-$], where X was reduced with 100 mM sodium dithionite; □, sample with reaction centres in [*P*IX$^-$], but refrozen at the end of the experiment.

tures examined; F_M was the maximum fluorescence obtained during the time of the observation (15 μs after the start of the flash) induced by a flash which was just intense enough to induce a maximal fluorescence rise at 77 K in a sample with X oxidised (see Fig. 2, left). The ratio F_M/F_0 can be seen to decrease steeply between 90 K and 150 K. Also shown is the same ratio for cells without X prereduced for comparison, in this case only a slight variation with temperature is seen.

The changes with increasing temperature in the kinetics of the fluorescence yield during a flash suggest that the decay of the light-generated high fluorescent state accelerates as the temperature increases, becoming above 100 K, sufficiently rapid that the decay of the fluorescence yield can be seen within the tail of the flash.

In contrast to *C. vinosum*, results obtained with *Rps. sphaeroides* wild type show a much smaller increase of fluorescence yield in cells with X prereduced than in cells with X oxidised even at 77 K (Fig. 2, right, and Fig. 5). With a flash just saturating for the fluorescence rise in an unreduced sample at 77 K (where a 5—7-fold increase in fluorescence is seen) a rise of just under 1.5 occurs at 77 K in samples with X chemically prereduced. Even a flash that is four times more intense than a just saturating flash gives only a 2-fold rise in the fluorescence. From these results using Eqn. 1 with F_M taken from the unreduced sample it can be calculated that a flash just saturating for [*P*IX] → [P^+IX$^-$] leads to a closing of only a part, 33%, of the traps in samples with X chemically reduced, and a four times saturating flash a closing of 62% of the traps. Again using the ratio F_M/F_0 as an indication of the decline of the flash-induced increase in fluorescence yield it is apparent from Fig. 6 that the rise of fluorescence yield seen during the flash declines sharply from 77 K to 140 K at which temperature it is almost insignificant.

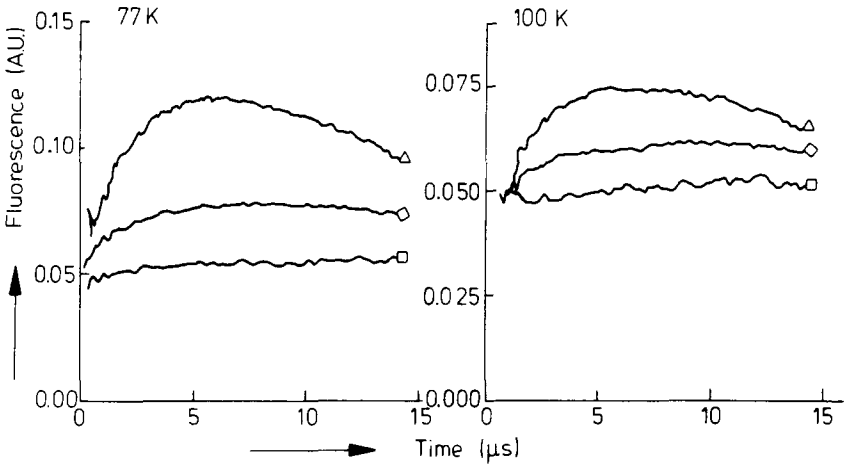

Fig. 5. Fluorescence yield changes in *Rps. sphaeroides* wild type with X prereduced at 77 K and at 100 K. Sample was reduced by addition of 100 mM sodium dithionite. Flashes shown are: □, low intensity to give F_0, ◇, a flash just saturating for the formation of $[P^+IX^-]$ in an unreduced sample; △, a four times saturating flash.

The kinetics of the fluorescence yield changes seen during the course of the flash again suggests the generation of a high fluorescent state which decays rapidly.

Measurements made at higher temperatures with *Rps. sphaeroides* wild type indicate the appearance of a fluorescence quencher during the course of a four times saturating flash in samples with X prereduced.

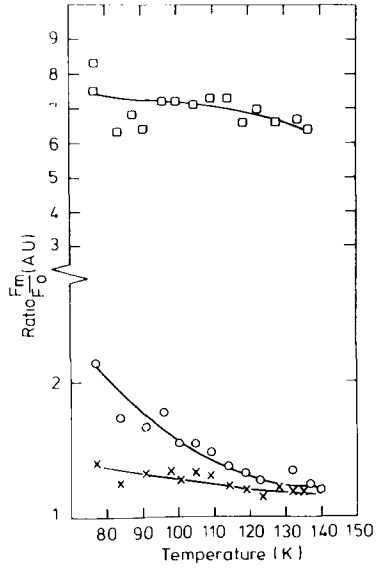

Fig. 6. Temperature dependence of the fluorescence yield rise (plotted as F_M/F_0) in *Rps. sphaeroides* wild type. □, unreduced samples; X, sample reduced with 100 mM sodium dithionite in flash saturating for unreduced sample; ○, sample reduced with 100 mM sodium dithionite in a four times saturating flash.

Discussion

The difference in behaviour between the flash-induced fluorescence yield changes seen in *Rps. sphaeroides* and in *C. vinosum* at low temperatures can be reconciled within a single scheme if it is assumed that the high fluorescence state generated shows a temperature dependence that is shifted to lower temperatures in the case of *Rps. sphaeroides.*

As judged from the high quantum efficiency with which the high fluorescent state is formed at 77 K after illumination of a sample with reaction centers in [PIX^-] before the flash, it seems logical to assume that the high fluorescent state is caused by a light-induced state of the reaction centre in which no primary photochemistry can take place (a so called "closed" state of the reaction centre).

We have tried to simulate the observed flash-induced fluorescence kinetics on the simple assumption of a temperature-dependent decrease of the decay rate of the closed state of the reaction centre, presumably the triplet state of the reaction centre which is made with high efficiency at low temperature [5]. Such a phenomenon has been observed by Parson and Monger [7] in isolated reaction centres of *Rps. sphaeroides* 2.4.1, although at lower temperatures than those examined here; they observed a concomitant reduction in the amplitude of the absorbance signal due to car^{TR} and interpreted their results as a shifting of the $P^{TR} \leftrightharpoons car^{TR}$ equilibrium to the left with decreasing temperature. The results of such a simulation, although capable of explaining the fluorescence changes observed in *C. vinosum* at very low temperatures, did not give a good fit to the changes seen at higher temperatures with *C. vinosum* or to the changes seen with *Rps. sphaeroides* wild type, that is to say, the changes occurring with more rapid decay rates. In particular, it was found impossible to obtain a sufficiently small fluorescence increase in the simulation maintaining a reasonable (greater than 2 μs) half time for the triplet decay rate.

It is possible that the anomalously small fluorescence increase we observe then at high temperatures is a result of not only an increase in the decay rate of the closed state of the traps but also a decrease in the flash-induced yield of closed traps. There is evidence for a decrease in yield of the reaction centre triplet state in *Rps. sphaeroides* R26 reaction centres [5] and in cells of *Rps. sphaeroides* wild type and *R. rubrum* wild type [27] with increasing temperature, but this would be small over the temperature range investigated here. It may, however, be that only P^{TR}, and not car^{TR}, acts as a closed trap and that at higher temperatures the yield of P^{TR} declines sharply due to the temperature-dependent equilibrium between P^{TR} and car^{TR} discussed above. Our results then suggest that the temperature dependence of this equilibrium is shifted to higher temperatures in *C. vinosum* compared with *Rps. sphaeroides* wild type. Support for such a hypothesis is provided by the fact that P^{TR}, like P^+ [17], does not significantly quench the fluorescence of antenna bacteriochlorophyll [13]. This interpretation suggests however that, for example, in *C. vinosum* at 77 K in almost all the reaction centres P^{TR} is formed, whereas at 140 K almost only car^{TR} is formed. Thus, a steep decline in the amount of flash-induced car^{TR} would be expected decreasing the temperature from

140 K to 77 K. Preliminary absorbance measurements (van Grondelle, R., Rademaker, H. and Holmes, N.G., unpublished observations) indicate that the amount of car^{TR} formed after a short laser flash in this temperature range is almost independent of the temperature.

Therefore, we suggest another possibility; that there is a change in the nature of the triplet state as the temperature decreases and that it may be more appropriate to think of the triplet at lower temperatures as being delocalised over both the bacteriochlorophyll and the carotenoid molecules; such a concept would agree better with absorbance measurements mentioned above which indicate that there is no decrease in the amount of car^{TR} between 140 K and 80 K, and can also explain the fluorescence yield data discussed above by postulating that such a delocalised triplet state of the reaction centre bacteriochlorophyll would not quench the fluorescence.

From our data we cannot rule out the possibility that the presence of a triplet state within the reaction centre is altering the processes occurring in and around the reaction centre in other ways; for example, a conformational change caused by the presence of the triplet state might, at low temperatures, interrupt energy transfer from antenna pigments to the reaction centre or electron transfer from *P* to I.

It is possible to make triplet states of antenna pigments (both carotenoid and bacteriochlorophyll) and these have been shown to quench the fluorescence yield [14,21,22]. The effect described above indicating that a triplet state in the reaction centre leads to an increase in fluorescence yield is then, at first sight, anomalous. However, the pigments of the reaction centre may differ from those in the antenna in such a way that they have either no, or a greatly diminished, ability to quench the fluorescence. There is evidence from circular dichroism studies [23] that the carotenoid molecule linked to the reaction centre is indeed different from the bulk carotenoid molecules. As the temperature was increased, in the case of a four times saturating flash, a quenching could be seen in samples of *Rps. sphaeroides* wild type (in state $[PIX^-]$). At about 170 K the fluorescence was quenched by about 5% and at 190 K by about 10%. In samples without X prereduced, quenching during the peak of the flash, which can be ascribed to the generation of bulk car^{TR}, could also be observed at temperatures as low as 77 K and may very well have occurred even in samples in state $[PIX^-]$ but was masked there due to the complex fluorescence yield kinetics exhibited.

As mentioned above, the carotenoid-containing bacterial species examined can be divided, broadly speaking, into two types on the basis of the behaviour of the fluorescence yield at low temperatures. This can be seen more clearly in Table I where the ratio of maximum fluorescence reached in a saturating flash to the basal fluorescence level (F_M/F_0) is shown for various bacterial species.

The similar behaviour of *C. vinosum* and *Rps. palustris* on the one hand, and of *Rps. sphaeroides* and *R. rubrum* on the other, are clear. The fluorescence yield of *Rps. gelatinosa* in state $[PIX^-]$ is less at 77 K than that in state [*P*IX] in contrast to *C. vinosum;* this may indicate that there is a real difference in the maximal fluorescence levels reached or that *Rps. gelatinosa* shows a temperature dependency shifted to slightly lower temperatures than *C.*

TABLE I

COMPARISON OF FLUORESCENCE YIELD RISE OBSERVED AT 77 K IN STATE [P I X^-] WITH THAT OBSERVED IN STATE [P I X] INDUCED BY A SATURATING FLASH IN SEVERAL SPECIES OF PHOTOSYNTHETIC BACTERIA

Filter combinations used to protect photomultiplier: 1, as Material and Methods; 2, Schott RGM 9/2 with Schott AL 907 interference filter; 3, Schott UG 8/4.

Species	$\frac{F_m}{F_0}$ for saturating flash at 77 K	
	Unreduced [P I X]	Reduced [P I X^-]
C. vinosum [1]	7.5	9.2
Rps. palustris [2]	4.7	5.5
Rps. gelatinosa [2]	5.0	4.2
Rps. sphaeroides wild type [1]	6.9	1.4
R. rubrum wild type [3]	3.9	1.3

vinosum. If the latter case is true and the real maximum increase in fluorescence yield F_M/F_0 of *Rps. gelatinosa* generated from state [PIX^-] in a flash bears a similar relationship to that generated from [PIX], as do the respective fluorescence yields of *C. vinosum* (i.e. 9.2 : 7.5) the maximal level seen in the flash for *Rps. gelatinosa* (4.2) still represents a closing of more than 90% of the traps. Thus, the behaviour of the fluorescence yield of this species is much nearer to that of *C. vinosum* than to that of *Rps. sphaeroides*.

What distinguishes these two classes is not obvious and may well depend on the detailed molecular organisation of their reaction centres; there is no clear distinction between the two classes on the basis of the carotenoid compositions reported in the literature [24]. There is some support in the literature for differences in the organisation of the reaction centres between the two classes: *Rps. palustris*, *Rps. gelatinosa* and *Chromatium* all contain a *c*-type cytochrome which is photooxidisable at los temperatures, whereas the other two species do not [25] and this may indicate a differing relationship between the *c*-type cytochrome and the reaction centre in these species. Work on isolated reaction centres has indicated that the back reaction [P^+IX^-] → [PIX] is temperature dependent in *Rps. sphaeroides* but shows no temperature dependence in *C. vinosum* [26].

The decrease in F_M/F_0 seen in *Rps. sphaeroides* wild type with increasing temperature has also been seen by us in experiments on a slower time scale and is discussed in the accompanying paper [27].

Acknowledgements

N.G.H. gratefully acknowledges a European Science Exchange Programme fellowship from the Royal Society. N.G.H. and R.v.G. are indebted to Dr. Arnold Hoff for the many stimulating discussions on the subject. Financial support for this investigation was given by the Dutch Organisation for the Advancement of Pure Research in part via the Foundation for Biophysics (S.v.B.) and for Chemistry (SON).

References

1 Rockley, M.G., Windsor, M.W., Cogdell, R.J. and Parson, W.W. (1975) Proc. Natl. Acad. Sci. U.S. 72, 2251—2255
2 Kaufmann, K.J., Dutton, P.L., Netzel, T.L., Leigh, J.S. and Rentzepis, (1975) Science 188, 1301—1304
3 Kaufmann, K.J., Petty, K.M., Dutton, P.L. and Rentzepis, P.M. (1976) Biochem. Biophys. Res. Commun. 70, 839—845
4 Dutton, P.L., Kaufmann, K.J., Chance, B. and Rentzepis, P.M. (1975) FEBS Lett. 60, 275—280
5 Parson, W.W., Clayton, R.K. and Cogdell, R.J. (1975) Biochim. Biophys. Acta 387, 265—278
6 Cogdell, R.J., Monger, T.G. and Parson, W.W. (1975) Biochim. Biophys. Acta 408, 189—199
7 Parson, W.W. and Monger, T.G. (1977) Brookhaven Symp. 28, 195—212
8 Van Grondelle, R., Romijn, J.C. and Holmes, N.G. (1976) FEBS Lett. 72, 187—192
9 Shuvalov, V.A. and Klimov, V.V. (1976) Biochim. Biophys. Acta 440, 587—599
10 Tiede, D.M., Prince, R.C. and Dutton, P.L. (1976) Biochim. Biophys. Acta 449, 447—467
11 Prince, R.C., Leigh, J.S. and Dutton, P.L. (1976) Biochim. Biophys. Acta 440, 622—636
12 Netzel, T.L., Rentzepis, P.M., Tiede, D.M., Prince, R.C. and Dutton, P.L. (1977) Biochim. Biophys. Acta 460, 467—479
13 Holmes, N.G., van Grondelle, R., Hoff, A.J. and Duysens, L.N.M. (1976) FEBS Lett. 70, 185—190
14 Monger, T.G. and Parson, W.W. (1977) Biochim. Biophys. Acta 460, 393—407
15 Cohen-Bazire, G., Sistrom, W.R. and Stanier, R.Y. (1957) J. Cell. Comp. Physiol. 49, 25—68
16 Hendley, D.D. (1955) J. Bacteriol 70, 625—634
17 Vredenberg, W.J. and Duysens, L.N.M. (1963) Nature 197, 355—357
18 Clayton, R.K. (1966) Photochem. Photobiol. 5, 807—821
19 Wraight, C.A. and Clayton, R.K. (1972) Biochim. Biophys. Acta 12, 46—63
20 Clayton, R.K. and Yamamoto, T. (1976) Photochem. Photobiol. 24, 67—70
21 Duysens, L.N.M., den Haan, G.A. and van Best, J.A. (1974) Proc. 3rd Int. Congr. Photosynth. Rehovot, Israel (Avron, M., ed.), pp. 1—13, Elsevier, Amsterdam
22 Zankel, K.L. (1973) Biochim. Biophys. Acta 325, 138—148
23 Cogdell, R.J., Parson, W.W. and Kerr, M.A. (1976) Biochim. Biophys. Acta 430, 83—93
24 Jensen, S.L. (1963) Bacterial Photosynthesis (Gest, H., San Pietro, A. and Vernon, L.P., eds.), pp. 19—34
25 Kihara, T. and Chance, B. (1969) Biochim. Biophys. Acta 189, 116—124
26 Romijn, J.C. (1977) Thesis, University of Leiden
27 Van Grondelle, R., Holmes, N.G., Rademaker, H. and Duysens, L.N.M. (1978) Biochim. Biophys. Acta 503, 10—25