Biochimica et Biophysica Acta, 547 (1979) 417—428

BBA 47715

EFFECTS OF LIGHT INTENSITY ON MEMBRANE DIFFERENTIATION IN *RHODOPSEUDOMONAS CAPSULATA*

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(Received January 23rd, 1979)

Key words: Membrane differentiation; Photosynthetic apparatus; Bacteriochlorophyll; Reaction center; Light-harvesting complex; Light effect (Rhodopseudomonas capsulata)

Summary

Cells of *Rhodopseudomonas capsulata*, strain 37b4, *leu*$^-$, precultivated anaerobically under low light intensity, were exposed to high light intensity (2000 W · m^{-2}). The cells grew with a mass doubling time of 3 h. The synthesis of bacteriochlorophyll (BChl) began after two doublings of cell mass. Reaction center and light-harvesting BChl I (B-875) were the main constituents of the photosynthetic apparatus incorporated into the membrane. The size of the photosynthetic unit (total BChl/reaction center) decreased and light-harvesting BChl I became the dominating BChl species. Concomitant with the appearance of the different spectral forms of BChl the respective proteins were incorporated into the membrane, i.e. the three reaction center polypeptides, the polypeptide associated with light-harvesting BChl I, the two polypeptides associated with BChl II. A polypeptide of an apparent molecular weight of 45 000 was also incorporated. A lowering of the light intensity to 7 W · m^{-2} resulted in a lag phase of growth for 6 h. Afterwards, the time for doubling of cell mass was 11 h. The concentration of all three BChl complexes (reaction center, light-harvesting BChl I and II complexes)/cell and per membrane protein increased immediately. Also the size of the photosynthetic unit and the amount of intracytoplasmic membranes/cell increased.

The activities of photophosphorylation, succinate dehydrogenase, NADH dehydrogenase and NADH oxidation (respiratory chain)/membrane protein are higher in membrane preparations isolated from cells grown at high light intensities than in such preparations from cells grown at low light intensities.

Abbreviations: BChl, bacteriochlorophyll; SDS, sodium dodecyl sulfate.

Introduction

Rhodopseudomonas capsulata, *R. sphaeroides*, *R. palustris* and other Rhodospirillaceae are photosynthetic bacteria which can produce ATP either by a cyclic electron transport photophosphorylation under anaerobic conditions or by an oxidative respiratory chain phosphorylation under aerobic conditions [1]. The photosynthetic apparatus of these species, which are principally localized on intracytoplasmic membranes, consist of three bacteriochlorophyll (BChl)-carotenoid-protein complexes, i.e. photochemical reaction center, light-harvesting BChl I (*B*-875), light-harvesting BChl II (*B*-800—850) and electron carriers. The isolation and characteristics of these complexes in *R. capsulata* have been described elsewhere [2,3]. Although varying growth conditions did not affect the molar ratio of reaction center and light-harvesting BChl I synthesized, the ratio light-harvesting BChl II/reaction center was found to vary [4]. Formation of the photosynthetic apparatus has been induced in numerous photosynthetic bacteria by lowering of the oxygen partial pressure in the culture medium [5—8]. When the oxygen tension in cultures of *R. capsulata* was lowered from 400 to 1—2 mmHg the growth rate was greatly reduced but the components of the photosynthetic apparatus were still incorporated into the membrane system [9]. Initially there was a high rate of synthesis of photochemical reaction center and light-harvesting BChl complex I, while antenna BChl II was synthesized at a lower rate. When the oxygen tension was lowered to 0.5 mmHg, the same kinetics were observed for 150 min of incubation. This contrasted with the kinetics at 1—2 mmHg where the rate of synthesis of light-harvesting BChl II increased with time of incubation and became the dominating subunit after 130 min incubation. Thus, a lowering of oxygen tension caused a differentiation of the membrane system, i.e. a modification of structure, function and composition of the membrane system by changing of the biosynthetic patterns [10].

Since the early investigations on the photosynthetic bacteria it is known that light intensity under anaerobic conditions influences the rate of BChl synthesis [11,12]. It was shown that the contents of cellular BChl and of intracytoplasmic membranes were inversely related to the incident light intensity [11—13]. The size of the photosynthetic unit, i.e. the molar ratio of total BChl/reaction center, increased when the light intensity decreased. This was observed in *R. sphaeroides* [14,15], *R. palustris* [16], but not in *Rhodospirillum rubrum* [14].

In the present study the influence of a change in light intensity on the synthesis of the photosynthetic apparatus in anaerobically grown cells of *R. capsulata* was investigated. It will be shown that the rates of synthesis of the pigment complexes and of respiratory enzymes were influenced in quantitatively different ways.

The results are discussed in the light of the regulation of membrane differentiation and adaptation to growth-limiting conditions.

Materials and Methods

Organisms. *R. capsulata*, strain 37b4, *leu*$^-$, was used during the investigations. The strain was derived from the wild-type strain 37b4 (German collec-

tion of microorganisms, Göttingen, strain 938) by mutation with 1-methyl-3-nitro-1-nitrosoguanidine (80 μg/ml, 90 min, pH 6.5, aerobic, dark) and selection with penicillin G or ampicillin (5—10 μg/ml). The mutant strain showed wild-type characteristics with respect to composition and formation of the photosynthetic apparatus and growth rate. The reversion rate was approx. $5 \cdot 10^{-6}$.

Culture conditions. The bacteria were cultivated anaerobically in the light at 2000 lux in screwcap bottles filled with a malate medium [17] supplemented with 0.5 mM leucine. Growth experiments at high light intensities were performed in a hollow cylindrical glass vessel (inner diameter 12 cm, outer diameter 18 cm, height 27 cm; content 3 l, thickness of culture layer 3 cm). The vessel was inoculated with 10—30 ml of a fresh culture and illuminated with 24 X 60 W Osram-Opalin candle-shaped bulbs arranged around the vessel and a 200 W bulb in the central hole. The average light intensity behind the culture layer was 2000 $W \cdot m^{-2}$. During some experiments at high light intensities the cell density was held between 0.07 and 0.15 absorbance (1.0 cm light path; 660 nm) to avoid self-shadowing of cells. The temperature of the culture was hald at 30°C during all experiments. The culture was continuously stirred and freed from oxygen by bubbling with purified nitrogen (99.999%) for 30 min. For experiments at low light intensities (7 $W \cdot m^{-2}$) a 15 W bulb was placed in the center at the vessel. [U-^{14}C]Leucine (0.1 μCi/ml) was added to low light cultures containing 0.25 mM leucine. After 30 min incubation the concentration of unlabeled leucine was increased to 0.5 mM.

Analytical procedures. The cell mass of the culture was estimated by measuring absorbance at 660 nm (optical path length 1 cm). Bacteriochlorophyll (BChl) was extracted from cells and membrane suspensions with an acetone/methanol mixture (7 : 2, v/v). The extinction coefficient was $\epsilon = 76\ mM^{-1} \cdot cm^{-1}$ at 770 nm for BChl [18]. The amount of reaction centers was determined from light-induced absorption changes at 880 nm and calculated using an extinction coefficient of $\epsilon = 113\ mM^{-1} \cdot cm^{-1}$ [18] *.

The sample cuvette was cross-illuminated with actinic light filtered through a K-60 filter (Balzers, Liechtenstein). A RG 695 filter (Schott and Co., Mainz) was arranged between the sample cuvette and the photomultiplier to absorb scattered actinic light below 695 nm. Light intensity of the actinic light was 500 $W \cdot m^{-2}$ at the surface of the cuvette. It was taken care that the specifications for reversible absorbance change given by Aagaard and Sistrom [14] were observed. Absorbance spectra at liquid nitrogen temperature (77 K) were measured with a Cary 14 R spectrophotometer, using an Oxford cryostate DN 704 LN_2. The method is described elsewhere [16]. The preparation of the membranes was done as described previously [20]. Protein measurements were performed according to Lowry et al. [21]. Membrane proteins were separated on 1 mm slab gels by the method of Laemmli [22] using a continuous 11.5—16.5% acrylamide gradient. Gels with radioactively labeled proteins were soaked with the scintillant PPO according to Bonner and Laskey [23]. The dried gels were exposed to Kodak-X-omat film X R5 for up to one week at —80°C.

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* One reaction center contains 4 mol BChl [19].

Photophosphorylation was measured by the method of Cusanovich and Kamen [24] using freshly prepared membranes. The sample cuvette was cross-illuminated with red light (filter RG 780, Schott and Co., Mainz) under saturating light intensity (100 W · m^{-2}).

The respiratory chain-dependent oxidation of NADH of the membranes were estimated by the absorbance change at 340 nm [25]. NADH dehydrogenase (EC 1.6.99.3) and succinate dehydrogenase (EC 1.3.99.1) activities were assayed spectrophotometrically as described previously [26].

All data presented in this paper are results of single experiments. However, all experiments were repeated and the results confirmed.

Results

Growth of R. capsulata leu⁻ at high light intensity

The culture vessel was inoculated with exponentially, at low light intensity growing bacteria to give a final absorption of 0.025—0.05. Growth began immediately (Fig. 1) and reached the exponential phase after 7 h of incubation with a mass doubling time of 3 h. During the first 5 h of incubation at high light intensity the BChl content/ml culture remained constant (0.07—0.08 nmol/ml). The cellular BChl concentration was consequently reduced as a function of growth (from 19 to 11.9 nmol BChl/mg cell protein). After the second doubling of cell mass, biosynthesis of BChl started and the cellular BChl concentration decreased at a lower rate to a final level of 3.6 nmol/mg cell protein. After the third doubling of cell mass the total BChl content of the membrane fraction decreased with every doubling of cell mass by a factor of 0.5, i.e. from 36.5 to 4.5 nmol/mg membrane protein. The concentration of reaction centers decreased during the first generation from 0.5 to 0.24 nmol/mg membrane protein. Thus, almost no BChl was synthesized and the size of the photosynthetic unit (mol total BChl/mol reaction center) did not change significantly. During the second and third mass doubling the content of reac-

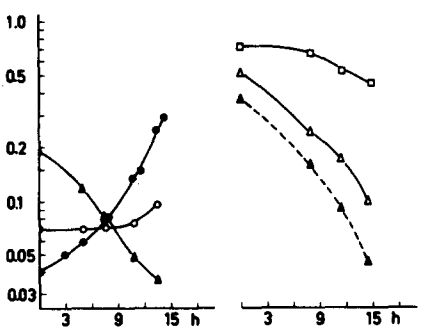

Fig. 1. Growth, bacteriochlorophyll concentration and size of the photosynthetic unit under high light intensity incubation (2000 W · m^{-2}) of *R. capsulata*. The experimental conditions are described in Materials and Methods. ●———●, absorbance of the culture at 660 nm and 1 cm light path; ○———○, nmol BChl/volume of suspension; ▲———▲, nmol BChl/mg cellular protein (X100); ▲- - - - -▲, nmol total BChl/mg membrane protein (X100); △———△, nmol reaction center/mg membrane protein; □———□, size of the photosynthetic unit (X100) (mol total BChl/reaction center).

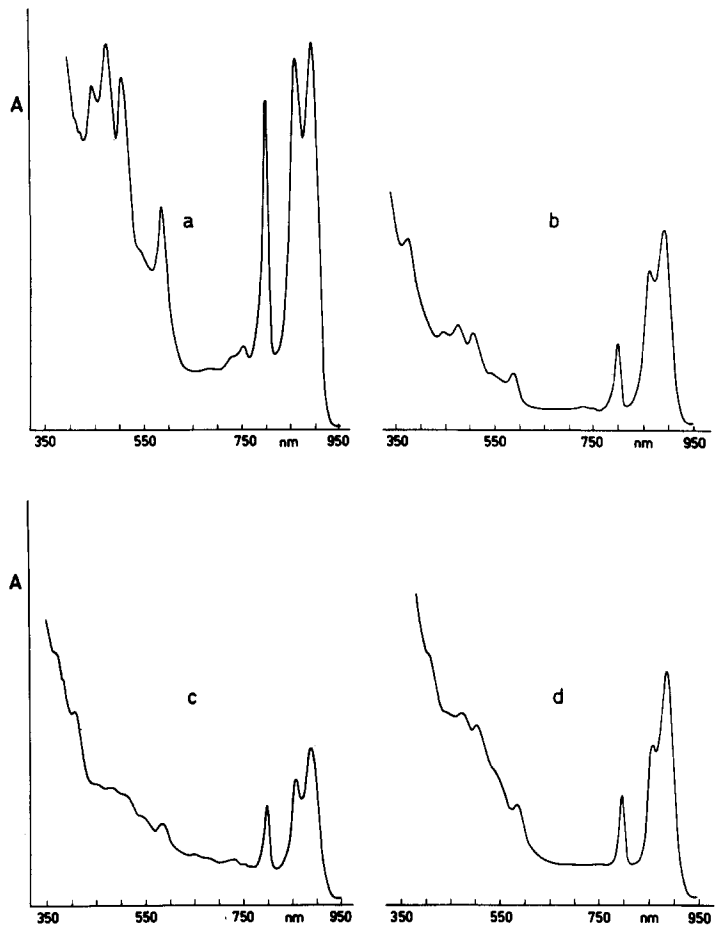

Fig. 2. Low temperature absorbance spectra (77 K) of membranes of *R. capsulata* during incubation at high light intensity (2000 $W \cdot m^{-2}$). (a) Spectrum of membranes of the inoculum. (b) Spectrum after the first mass doubling of the culture. (c) Spectrum after the second mass doubling of the culture. (d) Spectrum after the third mass doubling of the culture. The membranes were resuspended in phosphate buffer (0.05 M; pH 7.6) containing 60% glycerol. The spectra are not corrected for scattering. The samples contained different amounts of protein and BChl. The spectra show a clear increase of the peak at 890 nm (B-870) relative to the peaks at 800 and 860 nm (B-800—850) during incubation at high light intensity.

tion centers membrane protein decreased with a lower rate than the total BChl. Therefore the size of the photosynthetic unit was reduced from 72 to 45.

Low temperature absorption spectra (Fig. 2) reflected the observed variations in the levels of BChl species. Whereas light-harvesting BChl I (B-875) and light-harvesting BChl II(B-800 + B-850) were present in approximately equal amounts at the beginning of incubation at high light intensity, (Fig. 2a) the peak at 890 nm dominated the near infrared spectrum after the second and third mass doubling due to an increase of reaction center and light-harvesting BChl I content (Fig. 2c and d).

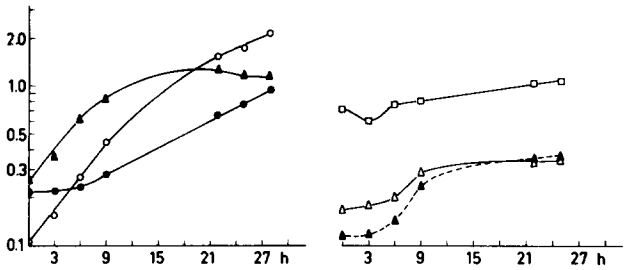

Fig. 3. Effects of a shift from high to low light irradiation of anaerobic cultures of *R. capsulata*. The incident light intensities were lowered from 2000 W · m^{-2} to 7 W · m^{-2}. Other experimental details are described in Materials and Methods. ●———●, absorbance at 660 nm and 1 cm path; ○———○, nmol BChl/volume of culture suspension; ▲———▲, nmol BChl/mg cellular protein (X10); ▲- - - - -▲, nmol BChl/mg membrane protein (X100);△———△, nmol reaction center/mg membrane protein; □———□, size of the photosynthetic unit (mol total BChl/mol reaction center) (X100).

Adaptation of high light intensity-grown cells to low light intensities

Cells grown for 2—3 mass doublings at light intensities of 2000 W · m^{-2} were irradiated with a light intensity of 7 W · m^{-2}. This decrease of light intensity resulted in an immediate stop of growth (Fig. 3). After a lag-phase of approximately 6 h the bacteria grew exponentially with a mass doubling time of about 11 h. In contrast to the strong reduction of growth rate, the rate of BChl synthesis was increased considerably during the lag-phase of growth. This, consequently, led to a five-fold increase of BChl concentration/cellular protein. In the last period (22—28 h), growth paralleled BChl synthesis. Cellular BChl content had reached steady-state level. Though there was a significant increase of the BChl content in the cells, the total membrane content of BChl did not change much during the first 3 h of induction. Consequently the amount of intracytoplasmic membranes/cell mass increased. This was confirmed by electron microscopical studies on ultrathin sections of cells.

The reaction center BChl was synthesized faster than light-harvesting BChl at the beginning. Thus, the size of the photosynthetic unit was reduced from 71 to 60. In contrast, from 3 to 9 h of incubation at low light intensity the size of the photosynthetic unit increased. Between 22 and 25 h low light intensity incubation, the amount of total as well as reaction center BChl/membrane protein remained nearly constant. Consequently no significant change in the size of the photosynthetic unit was observed.

Low temperature absorption spectra (Fig. 4) showed clearly that during incubation at low light intensity the relative proportion of light-harvesting BChl II (B-800 + B-850) was increased relative to light harvesting BChl I (B-875).

Activities of photophosphorylation and respiratory chain at high and low light intensities

During incubation at high light intensity the cells were grown in a semicontinuous manner. At every mass doubling one-half of the culture was withdrawn and used for membrane isolation. The remaining suspension was diluted with fresh medium to give the initial density. However, this method did not lead to a significant decrease in the size of the photosynthetic unit during the first two

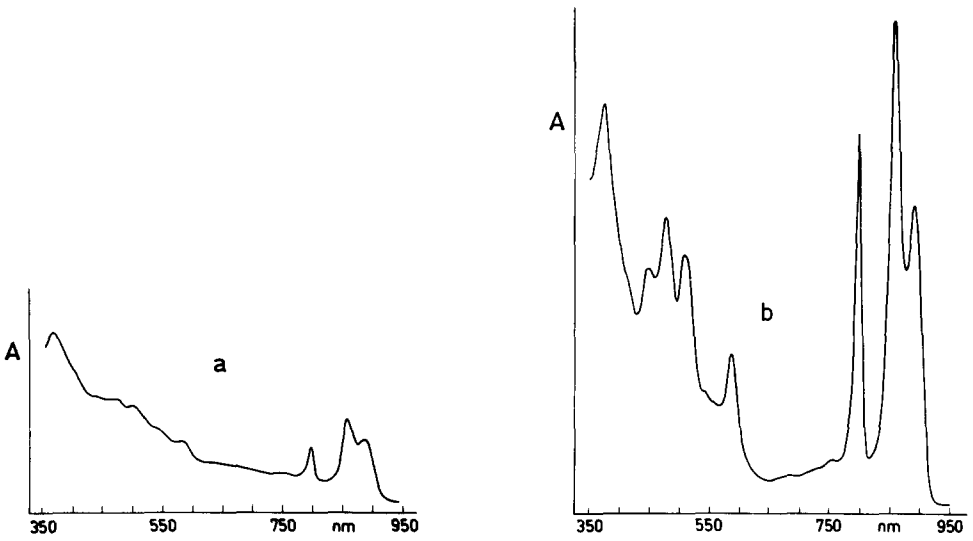

Fig. 4. Low temperature absorbance spectra (77 K) of membranes of *R. capsulata* after shifting from high to low light intensities. (a) Spectrum after 6 h of low light intensity. Due to scattering of the sample the peak at 860 nm appears greater relative to the peak at 890 nm. (b) Spectrum after 24 h of low light intensity incubation. The membranes were frozen in phosphate buffer containing 60% glycerol. The spectra show a relative decrease of the height of the peak at 890 nm relative to the peaks at 800 and 860 nm, after incubation of 18 h at low light intensity.

generations but rather to a decrease of the membrane BChl content.

The rate of photophosphorylation was increased by a factor of three on a BChl basis during the first 5 h of incubation at high light intensity (Table I) and again from 5 to 8 h. However, the activity on a protein basis was only increased by a factor of 1.6 during 11 h of incubation. Low light intensities led to a significant decrease in photophosphorylating activity on a BChl and on protein basis. The activity was lowered four-fold during the first 6 h of low light intensity incubation and again a four-fold decrease in activity from 6 to 24 h was measured on BChl basis.

The activities of all assayed respiratory enzymes increased during the first period of high light intensity growth by a factor of 1.5/protein (Table III), but

TABLE I

ACTIVITY OF PHOTOPHOSPHORYLATION AND BACTERIOCHLOROPHYLL CONTENT OF THE MEMBRANE FRACTIONS

Time/incubation (h)	μmol ATP/min per μmol BChl	nmol ATP/min per mg protein	nmol BChl/mg protein
High light intensity			
0	0.375	25	66.0
5	1.100	25	22.7
8	3.030	40	13.7
11	3.270	40	12.0
Low light intensity			
6	0.873	23	24.6
24	0.217	15	60.9

TABLE II

ACTIVITIES OF THE RESPIRATORY CHAIN UNDER STRONG AND LOW LIGHT INCUBATION

Time of incubation (h)	Dehydrogenases				Respiratory oxidation of NADH	
	nmol substrate/min per mg protein		nmol substrate/min per nmol BChl		nmol NADH/ min per mg protein	nmol NADH/ min per mol BChl
	Succinate	NADH	Succinate	NADH		
High light intensity						
0	226	36	3.4	0.6	48	0.7
5	303	56	13	2.5	72	3.2
8	295	51	22	3.7	61	4.5
11	308	57	26	4.8	82	6.8
Low light intensity						
6	190	43	8	1.8	16	0.7
24	177	41	3	0.7	13	0.2

four-fold on a BChl basis. Slight fluctuations could be measured between 8 and 11 h of incubation, but a significant change on a protein basis was not obvious. However, concomitant to decreasing BChl in the membranes, the activities/ BChl increased.

Under conditions of low light intensity the activities of the succinate dehydrogenase and NADH dehydrogenase decreased almost to the initial values of the inoculum. The respiratory oxidation of NADH, however, showed about 4-fold lower activity.

Radioactive labeling to the membrane proteins during low light intensity incubation

The labeling pattern of the membrane polypeptides showed during the first 12 h exclusively the synthesis of the photosynthetic apparatus (Fig. 5). At 3 h only very weak radioactive incorporation (39 400 cpm/mg protein) could be detected which mainly contributed to the light-harvesting BChl I-associated polypeptide (band 2) [3,27,28], though light-harvesting BChl II-associated bands (1, 3 and 4) [3,28], reaction center proteins (L, M, H) [2,29] as well as a band of apparent M_r 45 000 showed very faint blackening of the film. Band 2 remained the preferentially labeled protein till 9 h. Reaction center bands (L, M and H) were labeled simultaneously as shown in densitometer scans of SDS-polyacrylamide gel autoradiograms and by measurements of the radioactive label in each polypeptide band. Strongest incorporation proceeded from 3 to 9 h to reaction center and light-harvesting BChl I-associated bands (Fig. 5). Finally light-harvesting BChl II protein bands 3 and 4, which were shown to be associated with BChl [3], show almost the same density as band 2 in the scans of autoradiograms. The 14 kilodalton polypeptide was only weakly labeled, though it stained by Coomassie blue as strongly as the other light-harvesting associated polypeptides (Fig. 5, right). Towards the end (23 and 25 h) other proteins were labeled, due to growth of the culture.

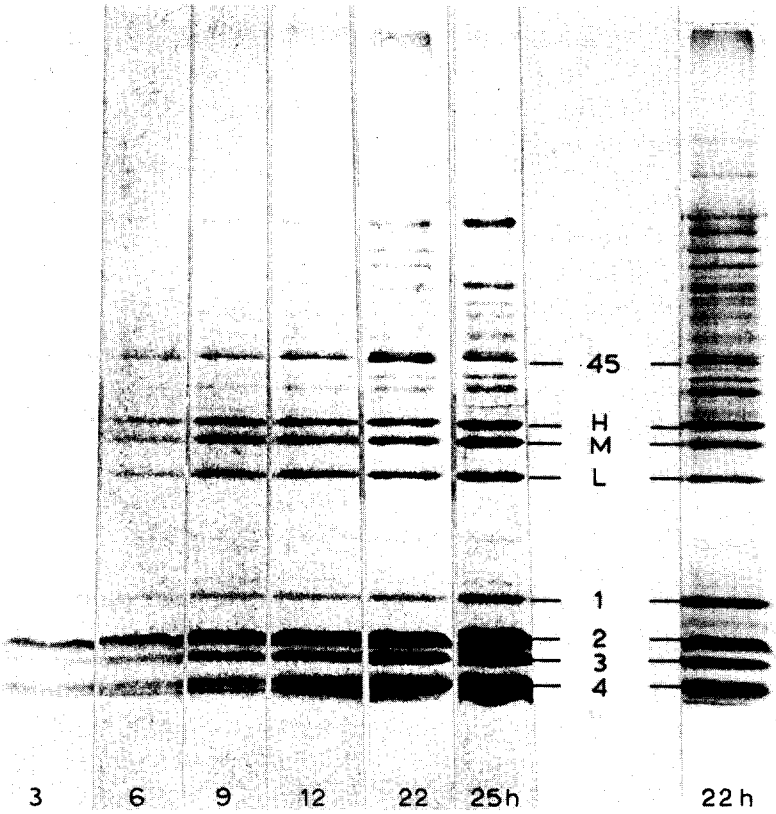

Fig. 5. Incorporation of [^{14}C]leucine in the membrane fraction of cells after lowering of light intensity (see Fig. 3). Left. Scintillation autoradiogram of a polyacrylamide slab gel. The membrane fractions were isolated from a low light intensity (7 W · m^{-2})-grown culture of *R. capsulata* at the times indicated below each slot. The gel slot at the right side, designated 22 h represents the Coomassie brillant blue R 250-stained polypeptide pattern at 22 h of low light intensity incubation for comparison. H, M and L, proteins of the reaction center BChl complex; 45, a polypeptide of a mol. wt. of 45 000. Bands 1—4 were found to be associated with the light-harvesting BChl's. Polypeptide 2, was shown to form the light-harvesting BChl I (B-875) complex; bands 1, 3 and 4, the light-harvesting BChl II (B-800 + B-850)-associated proteins [3].

Discussion

Transfer of *R. capsulata* from low light to high light intensities reduced the BChl content/cell and per membrane protein. During one or two doublings of cell mass no BChl synthesis was detectable and the proportion of light-harvesting BChl II to reaction center and light-harvesting BChl I was unchanged. After the second mass doubling of cells the size of the photosynthetic unit was reduced due to a relative higher rate of synthesis of reaction center and light-harvesting BChl I relative to light-harvesting BChl II (Fig. 2c). The cellular content of intracytoplasmic membranes was lowered, and tubular structures were formed (Golecki, J.R., personal communication).

A shift to growth-limiting low light intensities resulted in an increase in the size of the photosynthetic unit due to different rates of synthesis of all

three BChl-protein complexes. The amount of intracytoplasmic membranes/cell was increased as measured on micrographs of ultrathin sections of *R. capsulata* cells. It was reported that in a chemostat, which was growth limited by ammonium, the size of the photosynthetic unit was dependent on the growth rate, but concentrations of reaction center and light-harvesting BChl I/membrane protein were constant [20]. Thus limitation of growth by energy or nitrogen supply also influences the formation of the photosynthetic apparatus in addition to the major external factors, such as oxygen partial pressure and light intensity. *R. capsulatq* has three mechanisms to adapt the photosynthetic apparatus to changing culture conditions: first, variation of the size of the photosynthetic unit; second, variation of the amount of intracytoplasmic membrane/cell, and third, variation of the number of photosynthetic units/area intracytoplasmic membrane [10]. This study has shown that a change of the light intensities influenced all three mechanisms, but that different rates in the formation of the components were observed. Takemoto and Huang Kao [15] studied the influence of light intensity (4300—48 000 lux) on the development of the photosynthetic apparatus in *R. sphaeroides.* A lowering of light intensity caused a five times higher rate of incorporation of light-harvesting polypeptides in comparison with reaction center polypeptides into the membrane fraction. The relative amounts of reaction center polypeptides relative to total membrane protein were approximately the same with varying incident light levels. Thus, the size of the photosynthetic unit and presumably the amount of intracytoplasmic membrane were increased after lowering the light intensity.

The potential rate of photophosphorylation in *R. capsulata* measured under saturating light conditions and calculated on the basis of membrane protein, increased by a factor of 1.6 when membranes from high light cultures were compared with membrane preparations isolated from cells grown at low light intensity. A similar results was obtained with *Rhs. rubrum* [30]. The potential higher rate of photophosphorylation is correlated with a higher respiratory activity (Table II). Thus, the electron transport capacity/reaction center seems to be increased.

The in vitro measured activity of photophosphorylation varied ten-fold between membrane preparations from cells grown at low and high light intensity, respectively, when calculated on BChl basis (Table I). This conspicuous difference is mainly due to the variation of the size of the photosynthetic unit and was not observed in *Rhs. rubrum* [30]. Cells growing under low light intensities have large photosynthetic units to increase the efficiency of excitation energy turnover in the reaction centers [31]. The number of reaction centers/cell is also increased. The quantum uptake rate, the efficiency of photophosphorylation, and the quantum yield of growth are relatively high under middle to low effective irradiance [31], but the cells of *R. capsulata* were not able to adapt to very low light intensities, i.e. less than 3 nEinstein/s per cm^2 at 860 nm [31] or 20 lux of white light [32]. Under these conditions the relative proportion of maintenance energy becomes high, the quantum yield decreased and the doubling time exceeded 20 h.

The increase of membrane activities (Tables I and II) after a shift to a higher irradiance level is interpreted as a function of a decrease in BChl concentration, an increase in proportion of electron transport constituents to pigment com-

plexes and an increase in growth rate. It has been shown that, under different culture conditions, the variation in cytochrome *c* oxidase activity in *R. palustris* is greater than that of other respiratory enzymes [33]. It has to be studied whether the synthesis of this enzyme increased relative to membrane protein under strong irradiance or the cytochrome *b-c* part of electron transport chain, common for both energy-producing systems, is increased specifically. After switching from high to low light intensities the membranes incorporate radioactive leucine predominantly into proteins of the photosynthetic apparatus (Fig. 5). The labeling patterns of the membrane proteins are in accordance with other kinetic studies and show a stepwise assembly of the photosynthetic apparatus beginning with an increase of the intracytoplasmic membrane system, followed by a preferred incorporation of reaction center and light-harvesting BChl complex I and finally by an increased incorporation of light-harvesting II complex into the membrane leading to an increase of the size of the photosynthetic unit (Fig. 4 and Refs. 29 and 34).

A labeled band with an apparent mol. wt. of 45 000 was observed during experiments at low oxygen partial pressure in the dark [9] and at low light intensity (Fig. 5). It has to be studied whether this protein is a precursor of light-harvesting polypeptides. The weak radioactive labeling of the 14 000 band of light-harvesting complex II was observed under both test conditions. This protein is part of the isolated light-harvesting complex II but not associated with BChl [3].

Thus, the formation of the photosynthetic apparatus in *R. capsulata* follows similar kinetics whether the synthesis is induced by lowering the oxygen tension in dark cultures or by lowering of the light intensity under anaerobic conditions. However, the relative rates in formation of reaction center plus light-harvesting BChl I and light-harvesting BChl II complex and of membranes/cell varied depending on growth-regulating factors as concentrations of energy, carbon or nitrogen sources [7,10,20,31].

Acknowledgement

This work was supported by the Deutsche Forschungsgemeinschaft, S.F.B. 46.

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