THE RATE OF CO₂ ASSIMILATION BY PURPLE BACTERIA AT VARIOUS WAVE LENGTHS OF LIGHT

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INTRODUCTION

The group known as "purple bacteria" which use light for the synthesis of organic matter, as do green plants, are generally purple, brown, or red in color. There are also green photosynthetic sulfur bacteria. Oxygen is not produced by photosynthesis in bacteria, but instead a hydrogen donator is used up in the process of photochemical CO₂ reduction. For recent discussions of the metabolism of this group, see van Niel (1935), Gaffron (1935), Roelofsen (1935), and French (1937) and for photosynthesis in general Emerson (1936).

It is with the hope of finding a new approach to green plant photosynthesis that several workers are now studying the different kinds of photoassimilation in these bacteria. Probably by defining the differences between green plant and purple bacteria CO₂ assimilation, the chemical mechanism of both will become clearer.

The apparent color of the organisms is due to a mixture of two groups of pigments that are present together, the carotinoids and the bacteriochlorophylls. Both types are similar to, but not identical with, the pigments of green plants, carotene, xanthophyll, and chlorophyll. The bacterial pigments have been studied chemically by van Niel and Smith (1935), and by Schneider (1934 a and b), and Noack and Schneider (1933), Karrer and Solmssen (1936), Fischer and Hasenkamp (1935). Engelmann (1888) and Buder (1919) discovered that the bacteria will collect in a spectrum projected on a liquid culture at the positions corresponding to absorption bands both of the carotinoids and of the bacteriochlorophyll. This fact has been used as an argument that the red pigments can act as a light absorber for photosynthesis. The occurrence of these bacteria in nature under green

algae has also been claimed without justification to show that the red pigment acts as a photosensitizer. These speculations apply by analogy to green plant photosynthesis where the function of the carotinoids is still an unsolved though fundamental question. Gaffron (1934) found that photosynthesis took place rapidly with infrared alone showing that light absorbed only by the green pigment can act photosynthetically as is the case in green plants (Warburg and Negelein, 1923). It is the purpose of this paper to show that only the green pigment, bacteriochlorophyll, is the light absorber for bacterial photosynthesis. In the experiments of Roelofsen, using known intensities a better yield was obtained at the wave length which was absorbed more by the green than by the red substance in his purple sulfur bacteria.

We will discuss first the absorption spectrum of the live bacteria, and notice the location of the bands due to the red and to the green pigments. Then, we will show that the action spectrum for CO₂ assimilation has bands that correspond in position only to those of the bacteriochlorophyll. Thus it becomes very clear that whatever the function of carotinoids, it is not photosensitization for CO₂ reduction.

Principles

The action method of determining the absorption curve of a photosensitizing pigment in cells in thin suspensions has been described by Warburg and Negelein (1928a), in their work on the respiratory enzyme of yeast. Here the same principles are used to study the photosynthetic pigment in purple bacteria.

In a thin layer of homogeneous solution containing a dissolved colored substance, the amount of monochromatic light energy absorbed per unit time is given as follows:

$$-\Delta I = E = I_0 c \beta q \Delta d \tag{1}$$

where I_0 is the incident intensity, c the concentration of the absorbing substance, β its absorption coefficient, q the cross-section area, and Δd the thickness of the layer.

If the molecules undergo a photochemical reaction after absorbing light:

$$\gamma = \frac{E}{W} \tag{2}$$

where E is the energy absorbed expressed in quanta per unit time, W is the number of molecules changed per unit time, γ is then the number of quanta required to change one molecule presumably a constant which is independent of wave length.

In the experiments on *Chlorella* by Warburg and Negelein the quantum yield did not vary appreciably with wave length. A similar case has been found in the activation of O_2 by chlorophyll under the influence of visible light by Gaffron (1927). This assumption is made in the determination of the absorption spectrum of the respiratory enzyme by Warburg and Negelein (1928a) and shown to be correct by their experiments on the dissociation of CO-ferrocystein and of CO-hemochromogen (Warburg and Negelein (1928b)). For the assimilation of CO_2 with H_2 by *Streptococcus varians* $\gamma = 4$ but it has not been determined in *Spirillum rubrum*.

Combining the two expressions:

$$E = \gamma W = I_0 c \beta q \Delta d \tag{3}$$

I_0 being expressed in quanta. If $I' =$ incident intensity in ergs, then:

$$W = \frac{c\beta q I' hC\Delta d}{\gamma \lambda} \tag{4}$$

where h is Plank's constant and C the speed of light.

Evaluating and converting to calories:

$$W = \frac{c\beta q I_1 \Delta d}{\gamma} \times \frac{6.55 \times 10^{-27} \times 3 \times 10^{10}}{\lambda \times 10^{-7} \times 4.18 \times 10^7}$$

$$W = \frac{c\beta q I_1 \Delta d}{\gamma} \times \frac{4.71}{\lambda} \times 10^{-19}$$

where λ is expressed in mμ.

Solving for β

$$\beta = \frac{\gamma W \lambda}{I_1 cq\Delta d} \times 2.13 \times 10^{16}$$

In applying this equation to a thin suspension of bacteria or other cells in water we need only make the assumption that the light in-

tensity is not very different in different parts of a single cell; that is, that a beam of light in passing through one bacterium is not greatly weakened. If Δd is so small that all parts of all the bacteria receive practically equal monochromatic intensities (*i.e.*, small absorption by the suspension as a whole), then the amount of energy absorbed will be equal to the intensity × the exposed area × the thickness × the concentration of pigment in the suspension × the absorption coefficient of the pigment. For the absolute measurement of quantum yields, all these quantities need to be evaluated, but for purposes of comparing the relative absorption coefficients for different wave lengths, it suffices to hold all terms but I and λ constant during one experiment. The measured relative rates at different wave lengths will then be proportional to β (Warburg and Negelein, 1928 *b*).

The expression then reduces to:

$$\beta K' = \frac{W\lambda}{I_1} \text{ or expressing } I_0 \text{ in quanta: } \beta K = \frac{W}{I_0}$$

It has been found experimentally (Figs. 4 and 5) that in the range of intensities used, W is a linear function of I_1 wave length being constant. The intensity, I_1, falling on, and for the most part passing through, the suspension is measured bolometrically. W is determined by the manometric measurements of CO_2 assimilated. Using the assumption that the quantum efficiency, $\frac{1}{\gamma}$ (whatever its value) is constant within the spectral range concerned, $\beta\ K$ is thus measured for a number of wave lengths.

EXPERIMENTAL

The Absorption Spectrum of the Pigments in the Living Bacteria

Pure cultures of *Spirillum rubrum* (strain *S*1), kindly given us by Professor C. B. van Niel were grown in the following medium about 2 days at 35° in the light with 5 per cent CO_2 in argon as described elsewhere (French, 1937).

K H CO₃	0.5	per cent	(0.05 M)
K butyrate	0.126 "	"	(0.01 M)
NH₄Cl	0.1 "	"	
KH₂PO₄	0.05 "	"	
MgCl₂	0.02 "	"	
Yeast autolysate	2.0 "	"	

The culture was centrifuged and the bacteria suspended in tap water. Two identical absorption vessels were filled with a suspension and the absorption of both was found to be identical when measured with a photoelectric spectro-photometer. One vessel kept cool with running water was then placed close to a quartz mercury arc for about an hour to bleach the pigment in the cells. Measurements of absorption of the pigments were then made at various wave lengths
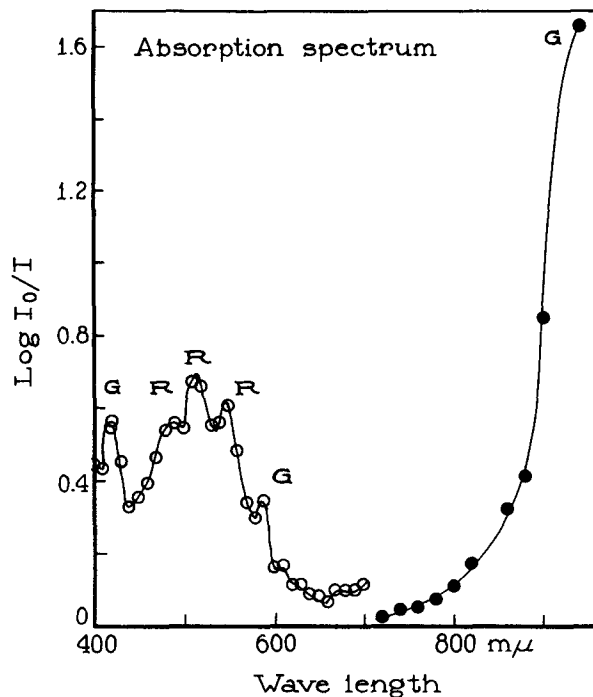
FIG. 1. The relative absorption curve of the pigments of *Spirillum rubrum* in the living bacteria, measured photoelectrically using a scattering control of bleached bacteria. The maxima marked with letter *R* are those of the red pigment, spirilloxanthin, while those labelled *G* are due to the green bacterio-chlorophyll. Infrared wave lengths may be inaccurate due to the small dispersion of glass in this region.

by using the bleached suspension for a scattering control. The vessel was placed directly in front of the photocell to collect a large part of the scattered light. The curve of Fig. 1 presents the combined results of two such experiments. As the monochromators used for this measurement did not have sufficient dispersion for accurate work in infrared, a spectrogram was made in this region to determine more precisely the band position. Fig. 2 shows one prominent band

in the near infrared with a maximum at 880 mμ and suggests a very faint one at 800 mμ. The spectrum of *Streptococcus varians* is also shown for comparison. It has bands at 860 and 800 mμ (French, 1937).

Moist bacteria extracted in the dark at 0° with methyl alcohol give up the bacteriochlorophyll, but retain nearly all the carotinoid which is, however, easily extractable with acetone. In Fig. 3, we see a relative absorption curve of such a bacteriochlorophyll extract prepared in the dark at 0° and measured with very dim light. A few
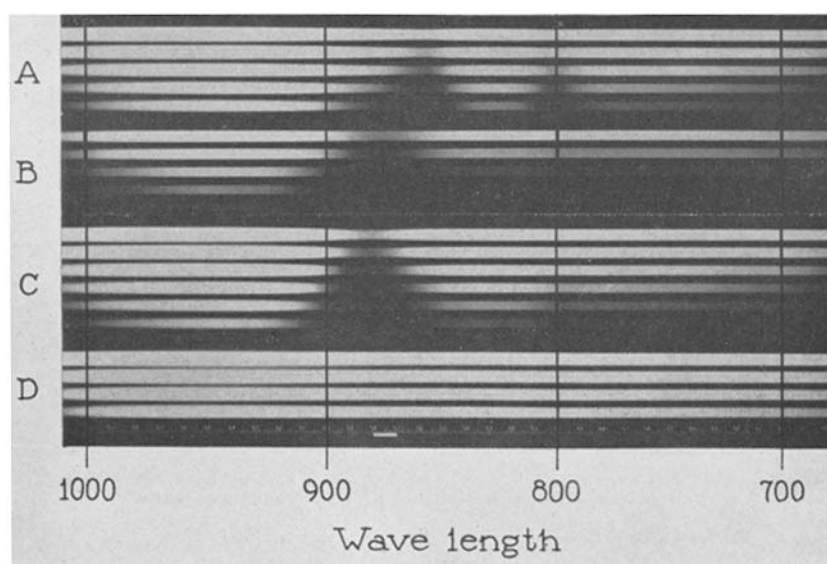
Fig. 2. Infrared spectrograms of living *Spirillum rubrum* (*B* and *C*) as compared with *Streptococcus varians* (*A*). (*D*) is the light alone without any bacteria. Taken with a Zeiss spectrograph for chemists using the grating.

minutes in the ordinary light of a room turns this solution from a clear light green to brown. The large near infrared band is shifted by extraction from 880 mμ in the bacteria to 770 mμ in methyl alcohol. The yellow band is shifted from 590 to 605. It is interesting to note that these bands are not both displaced in the same direction. From this figure, we can identify the bands marked with letter *G* in Fig. 1 which belong to the green pigment. They are at 880, 590, and 420 mμ in the living cells, and 770, 605, and 400 mμ in the methyl alcohol

extract. The bands at 550, 515, 490 mμ, marked R, can easily be identified as belonging to the red pigment described by van Niel and Smith who give an absolute absorption spectrum in CS_2 of the red pigment from this same strain of bacteria.
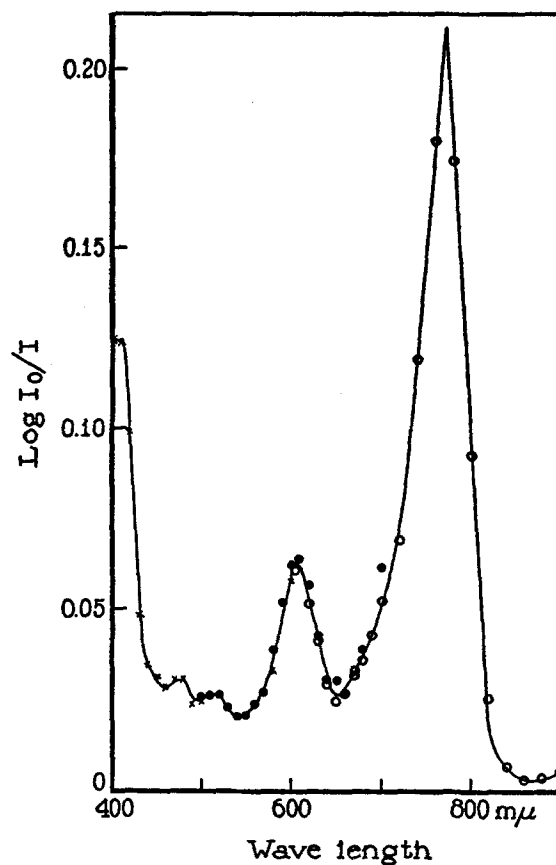
FIG. 3. Relative absorption curve of the green pigment in methyl alcohol. 0.2 cc. moist cells extracted in the dark at 0° with 5.2 cc. absolute methyl alcohol. The extract was kept in the dark and measured at room temperature with very weak light.

Monochromatic Light Sources

The light used in making the photochemical action curve was obtained from a mercury lamp, a sodium lamp, or from a filament lamp in which case the light was dispersed by prisms and certain spectral regions isolated with a slit. With

the metallic vapor lamps, the filters given by Kubowitz and Haas (1932) were used for isolating single lines. Since the experiment was performed, it has appeared that the Osram caesium tube has abundant intensity at 852 and 894 mμ (French, 1937). It may also be possible to use the Na line, 819 mμ, for similar experiments.

The instrument designated in Table II as the two prism monochromator has an opening of 1:1 with usable prism faces of 10 cm. and was built for work in the visible region by B. Halle, Nachfolger, Berlin. The light from the single coil lamp passed through a quartz condenser was thereby made nearly parallel, then converged on the slit with a crown glass lens similar to the collimator inside the instrument. All three of these lenses have an opening of about 1:1. To obtain greater dispersion in the near infrared, the instrument was built over, adding two more prisms and disposing of the entrance slit and the three large aperture lenses. A 160 mm. focus collimator larger than the prisms collected the light from a narrow coil filament placed at its focus. This arrangement was similar in principle to the apparatus used for red light by Warburg and Negelein (1923).

An image of the filament coil was spread over the plane of the curved exit slit by the original telescope lens which was retained in the instrument. The lamp, collimator lens, and first prism were mounted together on an optical bench which was supported by a pivot below the inner corner of the first prism. The other end was supported by the table and carried a pointer sliding over a fixed linear metal scale. The third and fourth prisms were those of the original instrument movable in relation to each other by a screw bearing a drum and scale. Empirically a relationship between the two scales was found which kept the telescope lens evenly illuminated. This was essential as a monochromatic image of it was cast by lenses and mirrors beyond the slit on the plane of the experimental vessel in the thermostat. Wave length calibration was carried out in the visible with a hand spectroscope checked against mercury lines. The scale readings were plotted on dispersion paper and extrapolated to include the infrared. The dispersion then was roughly 546–578, 4.8 mm.; 578–692, 5.2 mm.; 692–773, 4.9 mm.; and the minimal region which could be isolated by an infinitely narrow exit slit at 500, 15 mμ; at 550, 20 mμ; at 600, 23 mμ; at 650, 30 mμ; at 700, 40 mμ; and at 900, 60 mμ.

The region isolated by a definite slit width was taken from the dispersion curve as twice the slit width and is shown by the bars in Fig. 6. The intensity could be diminished by various amounts using neutral glass filters.

Before or after the experiment, the light beam was concentrated into the bolometer by shifting the position of the lenses and the total energy entering the thermostat thus determined. During an experiment, constancy was checked by an ammeter in series with the lamp. The diameter of the light circle at the plane of the manometer vessel was measured by marking in pencil on ground glass held in a brass frame. After correcting for the reflection and water absorption, the total energy divided by the area over which it is spread gives the intensity incident on the bacteria. Water absorption was calculated from the

values given in Landolt-Börnstein which were checked for 850 mμ with water from the thermostat. The length of light path from the quartz entrance window to the vessel was 15 cm. so that about half the light of wave length 850 was absorbed before reaching the suspension.

We then have the intensity:

$$I_1 = \frac{21,300}{\Omega} \times \frac{T_w R}{B} \times 10^{-3} \text{ cals./cm.}^2/\text{min.}$$

$21,300 \times 10^{-3}$ is a constant evaluated in the bolometer calibration, Ω = ohms required to bring the galvanometer pointer back to zero when the bolometer is irradiated, T = fractional transmission of 15 cm. water for the wave length measured, R = reflection, and mirror loss factor = 0.875, B = area of light beam at the position of the vessel.

We may express the light intensity in quanta per minute entering the vessel (I_0) by a conversion factor derived as follows:

$$1 \text{ quantum} = h\nu \text{ ergs} = \frac{hc}{\lambda} \text{ ergs} = \frac{hc}{\lambda \times 4.17 \times 10^7} \text{ cals.}$$

$$= \frac{6.55 \times 10^{-27} \times 3 \times 10^{10}}{\lambda \times 4.18 \times 10^7} \text{ cals.}$$

Converting λ from centimeters to mμ and solving

$$1 \text{ quantum} = \frac{4.70 \times 10^{-17}}{\lambda} \text{ cals.}$$

or $\qquad\qquad 1 \text{ cal.} = \lambda \times 2.13 \times 10^{16} \text{ quanta}$

Since the area of the vessel is 20.5 cm.² the number of quanta entering per minute is:

$$I_0 = I_1 \times 20.5 \times 2.13 \times 10^{16}$$

The Rate of Photosynthesis at Different Wave Lengths

The handling of the cells was fairly similar to the procedure described elsewhere for quantum yield experiments. The same vessels were used, though the control and experimental vessels were interchanged on the manometer arms. For these experiments the bacteria after being centrifuged were suspended in the growth medium
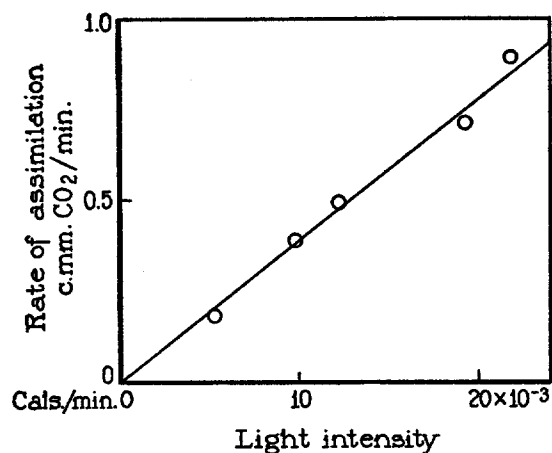
Fig. 4. Rate of CO$_2$ assimilation as a function of light intensity. Large silvered differential manometer, 10 cc. liquid containing 259 c.mm. cells. Gas: 10 per cent CO$_2$ in argon. Wave length band 825-865 mμ isolated with the four prism monochromator. Area of light beam 30.5 cm.^{2}, area of vessel bottom 19.2 cm.^{2} Light intensity given in calories entering the vessel per minute. Assuming total absorption, apparent γ = 17 quanta per CO$_2$ disappearing from the gas phase.
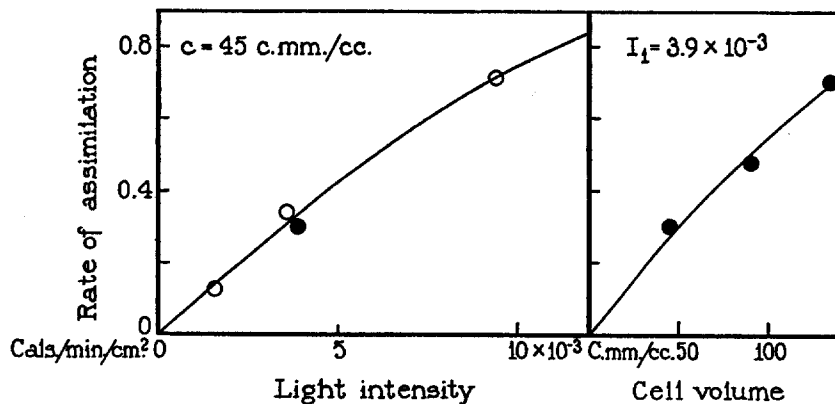
Fig. 5. Rate of CO$_2$ assimilation as a function of visible light intensity and density of suspension. Light from a 10 ampere filament lamp filtered through 6 cm. water + 3 cm. 25 per cent FeSO$_4$ in 10 per cent H$_2$SO$_4$. Cells in 0.033 M KHCO$_3$ + 0.01 M K butyrate in tap water.

at the desired concentration and assimilation of CO_2 measured in an atmosphere of 5 per cent CO_2 in argon.   In the dark, there was a high fermentation rate.   Assimilation was measured as an apparent decrease of this fermentation in the light.   Dark readings were taken between the illumination periods.   The vessel constant k_{CO_2} was 2.16 at the experimental temperature of 25°C. with 6.6 cc. of suspension. The number of molecules of CO_2 removed per minute from the gas phase is given by

$$W = (\Delta h - \Delta h_{dark}) \times \frac{2.16}{5} \times \frac{6.06 \times 10^{23}}{22.4 \times 10^{6}}$$

$$= (\Delta h - \Delta h_{dark}) \times 1.17 \times 10^{16}$$

TABLE I

|	Experiment 1	Experiment 2
Cell volume ($c.v.$)	150 c.mm.	150 c.mm.
Liquid volume (V_2)	6.60 cc.	6.60 cc.
Experimental vessel volume (V)	23.15 cc.	23.15 cc.
Control vessel volume (V')	19.37 cc.	19.37 cc.
Temperature ($t°$)	25.0°C.	25.0°C.
Gas	5 CO_2/argon	5 CO_2/argon
Vessel constant (K_{CO_2})	2.16	2.16
Area of light beam (B)	38.5 cm.^{2}	36.5 cm.^{2}
Area of vessel bottom	20.5 cm.^{2}	20.5 cm.^{2}
Reflection correction factor (R)	1.0	1.0

Approximate initial proportionality between intensity, density of suspension, and rate of assimilation is shown in Figs. 4 and 5.   The experiment summarized in Fig. 5 was performed with Mr. Erwin Haas.

The rate of photosynthesis of a thin suspension was measured with a number of different wave lengths and the mols of CO_2 disappearing from the gas phase per incident quantum tabulated.   No account is taken of the CO_2 change in the solution and the amount of absorption is not known; the data only give the relative absorption spectrum of active pigment and must not be used for efficiency calculations.   The data are presented in Tables I and II, and plotted in Fig. 6.   Repeated attempts with Mr. Haas to measure the absolute quantum yield at 589 mμ by extracting the pigment and measuring its absorption in methyl alcohol were not significant, even when the shift on extraction

TABLE II

Experiment 1
Vapor lamps with filters

t Time	λ Wave length	T water	ω Resistance	I_1 Intensity	Δh Pressure change	Δh dark Dark rate (interpolated)	$\Delta h - \Delta h$ dark Assimilation	I_0 Incident light	W Assimilation	$\beta K = W/I_0$ Light action (relative absorption spectrum)
min.	mμ		ohms	cals./cm.²/min. × 10³	mm./5 min. Ar.	mm./5 min.	mm./5 min.	quanta/min.	molecules/min.	
5 10 15	578 Hg lamp	1	403	1.37	{1.12 1.33 1.20} 1.26	2.37	1.11	3.46×10^{17}	1.30×10^{16}	0.0376
30 35	Dark			0	{2.32 2.18} 2.25					
50 55	546 Hg lamp	1	320	1.70	{1.20 1.21} 1.20	2.22	1.02	4.05×10^{17}	1.19×10^{16}	0.0269
70 75	Dark			0	{2.18 2.19} 2.19					
110 115	436	1	345	1.58	{1.60 1.61} 1.61	2.07	0.46	3.01×10^{17}	0.54×10^{16}	0.0180
130 135 140	Dark			0	{2.04 1.88 1.91} 1.94					
155 160	589 Na lamp	1 Filter: 3 cm. 25 per cent $FeSO_4$ in 10 per cent H_2SO_4	339	1.60	{0.04 0.11} 0.07	1.81	1.74	4.11×10^{17}	2.04×10^{16}	0.0496

175 180	Dark			0	$\{^{1.77}_{1.60}\}1.68$					
195 200	578	1	375	1.45	(0.94) $^{0.74}_{0.71}\}0.73$	1.78	1.05	3.65×10^{17}	1.23×10^{16}	0.0337
205										
220 225 230 235	Dark			0	$\{^{1.99}_{1.87}\}1.89$ $^{1.50}_{1.83}$					
275 280 285	Dark			0	$\{^{1.56}_{1.60}\}1.57$ 1.55					

Two prism monochromator

300 305	500 (470–540)	1	487	1.12	$\{^{1.02}_{1.09}\}1.05$	1.51	0.46	2.44×10^{17}	0.54×10^{16}	0.0221
320 325	Dark				$\{^{1.46}_{1.44}\}1.45$					
340 345	675 (640–710)	Filter: RG2 (Schott) 1	397	1.37	$\{^{0.80}_{0.90}\}0.85$	1.42	0.57	4.04×10^{17}	0.67×10^{16}	0.0166
360 365	Dark				$\{^{1.39}_{1.39}\}1.39$					

TABLE II—*Concluded*

Experiment 2
Four prism monochromator

Time	Wave length	T water	ω Resist-ance	I_1 Intensity	Δh Pressure change	Δh_{dark} Dark rate (inter-polated)	$\Delta h - \Delta h_{dark}$ Assimila-tion	I_0 Incident light	W Assimilation	$\beta K = W/I_0$ Light action (relative absorption spectrum)
min.	*mμ*		*ohms*	*cals./cm.² /min. × 10³*	*mm./5 min. Av.*	*mm./5 min.*	*mm./5 min.*	*quanta/min.*	*molecules/min.*	
5 10	650 (625–680)	1	327	1.78	{2.02 / 2.03} 2.02	2.39	0.37	5.05 × 10⁷	0.43 × 10¹⁶	0.0085
20 25 30	Dark				{2.35 / 2.37 / 2.33} 2.35					
40 45	750 (720–780)	0.65 Filter: *RG2* (Schott)	285	1.33	{1.46 / 1.50} 1.48	2.39	0.91	4.35 × 10⁷	1.06 × 10¹⁶	0.0244
55 60	Dark				{2.36 / 2.47} 2.41					
85 90 95	Dark				{2.46 / 2.50 / 2.38} 2.45					
105 110	900 (865–940)	0.35 Filter: *RG2* (Schott) + 5 cm. water	455	0.45	{1.36 / 1.20} 1.28	2.39	1.11	1.77 × 10⁷	1.30 × 10¹⁶	0.0735
120	Dark				{2.38 / 2.27} 2.33					
135 140	850 (826–863)	0.53 Filter: *RG2* (Schott) + 5 cm. water	555	0.56	{1.14 / 1.15} 1.14	2.39	1.25	2.08 × 10⁷	1.46 × 10¹⁶	0.0700

of the position of the maximum was taken into account. Apparently, large numbers of quanta (about 15) were always required to reduce one CO_2. Probably the high fermentation rate in the dark interfered with this measurement.

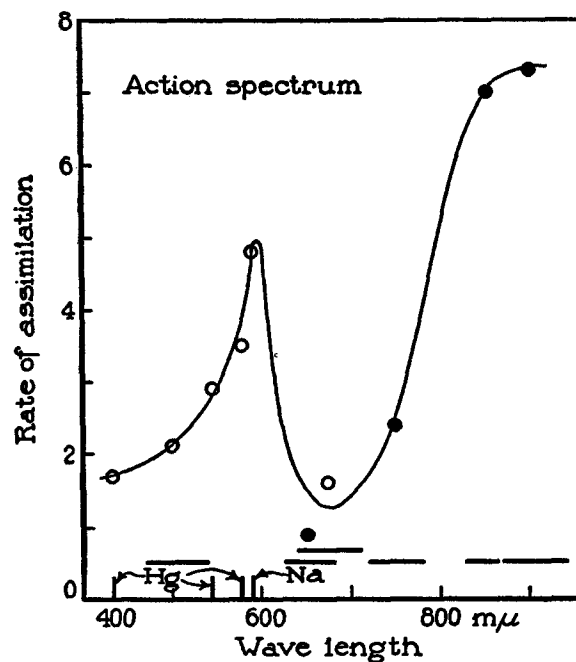FIG. 6. Rate of CO_2 assimilation of a very dilute suspension as a function of wave length of incident light. Rate scale represents molecules CO_2 X 100 per incident quantum. This curve is in effect the relative absorption curve of the photosensitizing pigment.

DISCUSSION

The carotinoids do not play a photosensitizing rôle in bacterial metabolism. Therefore, some other factor than photosynthetic activity must have been the cause of bacteria collecting at the red pigment, as well as at the green pigment, absorption bands in the excellent experiments performed long ago by Engelmann (1888) and confirmed by Buder (1919). There is no doubt as to the correctness of their observations, and apparently the effects observed are due to oriented swimming of the bacteria and not merely to an increased growth rate

in certain wave lengths. Experiments on phototaxis as a function of wave length by Blaauw (1909), Castle (1931), Johnston (1934), and Voerkel (1933), show that for this process, blue light is most effective. It would then be reasonable to expect that in the spectrum projection experiments purple bacteria would collect only at the bands of the carotinoids. In other work with motile photosynthetic green algae, Engelmann (1882) found that the algae moved toward a higher O_2 concentration along a gradient set up by O_2 liberation from the algae themselves when in red light. Thus, an apparent phototaxis to wave lengths of light most useful for photosynthesis turned out to be only a masked chemotaxis having nothing to do with orientation to light. It is perhaps possible that the collection of bacteria in infrared and at their 590 mμ band is nothing more than a chemotaxis in a CO_2 gradient caused by CO_2 utilization in light which is most active for assimilation.

Spirillum rubrum has one infrared band at about 880, and possibly one at 800, while *Streptococcus varians* has one at 860 and another smaller one at 800. Quantitative determinations of the absorption in the near infrared are needed on all available strains of photosynthetic bacteria to find out if these differences indicate different pigments in the various species.

SUMMARY

1. The relative absorption spectrum of the pigments in their natural state in the photosynthetic bacterium *Spirillum rubrum* is given from 400 to 900 mμ. The position of the absorption maxima in the live bacteria due to each of the pigments is: green pigment, 420, 590, 880; red pigment, 490, 510, 550.

2. The relative absorption spectrum of the green pigment in methyl alcohol has been determined from 400 to 900 mμ. Bands at 410, 605, and 770 mμ were found.

3. The wave length sensitivity curve of the photosynthetic mechanism has been determined and shows maxima at 590 and about 900 mμ.

4. It is concluded that the green bacteriochlorophyll alone and not the red pigment can act as a light absorber for photochemical CO_2 reduction.

This work was made possible by Professor Otto Warburg, to whom I wish to express my deepest thanks for the laboratory privileges and for his constant interest and advice. To Mr. Erwin Haas, I am very grateful, for some of this work was done jointly with him and his help many times assured the success of an experiment. It is a pleasure to thank Professors Robert Emerson and C. B. van Niel for their criticism of the manuscript.

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