ENERGY EFFICIENCY OF PHOTOSYNTHESIS BY *CHLORELLA*[*]

by

EDWARD LUNG YUAN, ROBERT W. EVANS AND FARRINGTON DANIELS

Department of Chemistry, University of Wisconsin, Madison, Wisconsin (U.S.A.)

INTRODUCTION

The energy efficiency of photosynthesis was first measured by WARBURG AND NEGELEIN in 1923[1]. Using manometers for measuring the gaseous exchange they reported that under favorable conditions only four quanta of red light are required to fix one molecule of carbon dioxide in *Chlorella*. Measurements of this photosynthetic efficiency were repeated at the University of Wisconsin using several different methods for the analysis of oxygen and carbon dioxide[2,3,4,5,6,7,8]. It was found that about ten quanta of red light were required to fix one molecule of carbon dioxide or oxygen. These later values were also supported by the careful manometric measurements of EMERSON AND LEWIS[9]. WARBURG and his associates repeated his early manometric measurements in 1949 and reported in 1951[10] an even higher yield including a one-quantum process. Values ranging from 8 to 10 photons per molecule have been repeatedly obtained by others. The same variety of algae, *Chlorella pyrenoidosa*, was used in all these experiments.

A review of publications up to 1953 on the energy efficiency has been written[11]. In the present work, separate, specific methods were used for the analysis of carbon dioxide and oxygen and the data were recorded automatically for both gases. The simultaneous recording of both gases not only provides more convincing results, but gives also a direct measure of the ratio of respiration quotient, CO_2/O_2. Such methods, though difficult, are free from assumptions regarding the nature and equilibrium of these gases.

EXPERIMENTAL

Apparatus was developed for the simultaneous measurement of oxygen and carbon dioxide, using magnetic moment for oxygen and infra red absorption for carbon dioxide. The PAULING oxygen meter, manufactured by Arnold O. Beckman, Inc., depends on the principle that oxygen is paramagnetic whereas other common gases are slightly diamagnetic. Infra red absorption apparatus built in this laboratory, was used in preliminary work[6,7,8]. It used a regulated gas flame of methane and oxygen as the source of infra red radiation at 4.2 μ and a thermopile receiver with a photocell amplifier. Although several measurements were made with quantum requirements always greater than 7 photons per molecule, the visual recording of the two galvanometer readings was very difficult and the accuracy was limited. All the measurements described in this investigation were made with recording instruments. The BECKMAN oxygen meter has a range of 20 to 21% oxygen, with 50 divisions and a fraction of the one per cent total deflection is amplified to full scale on a BROWN recorder with a D.C. breaker-type amplifier manufactured by the Liston-Becker Instrument Co.

[*] Further details of this research may be obtained from the Ph.D. thesis of Dr. EDWARD LUNG YUAN, filed in the Library of the University of Wisconsin in 1954.

References p. 193.

The carbon dioxide was measured at 4.2 μ with an infra red gas analyzer manufactured by Sir Howard Grub, Parson and Co. of England. It has a working range between 0 and 2.5% carbon dioxide and at maximum sensitivity, a change of 0.25% carbon dioxide gives a full scale deflection of 100 divisions on the recorder.

The quantity of light absorbed in the photochemical cell was measured with a large area bolometer made by the Lassenwerk Company of Germany. The optical system is arranged so that beams of monochromatic light of desired wave lengths can be obtained by using different interference filters. These interference filters are obtained from the Baird Associates, Inc., and the Farrand Optical Co. A filter of copper sulfate solution and a special glass filter made by Baird Associates, Inc., served to filter out the infra red radiation.

The circulation of the gas in the system is carried out by means of a small aquarium pump of small piston displacement. Tygon tubing, 1/8 inch in diameter, is used for all the connections. The circulation of the gas in the suspension keeps the cells from settling. Fig. 1 shows the circulating system and the arrangement of the apparatus. The gas volume of the whole system is about 125 ml. The reaction vessels are made of lucite, and have the shape as shown in Fig. 1. Two reaction vessels of different volume were used throughout this investigation. The larger vessel has a circular opening of 9.0 cm in diameter, and a total volume of 75 ml. The smaller vessel has a circular opening of 5.0 cm in diameter and a volume of 32 ml.

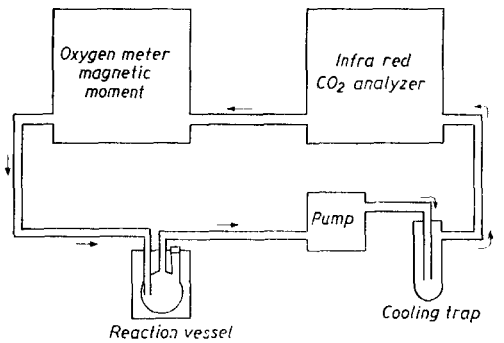

Fig. 1. Circulating system.

The analytical instruments were calibrated by injecting small amounts of the gas, measured with a hypodermic needle, directly into the circulating gas system. The results of such calibrations agreed with less than two per cent uncertainty. The bolometer was calibrated against a standard lamp obtained from the National Bureau of Standards.

A study of light scattering by the *Chlorella* cells was also carried out. During such measurements the bolometer was placed at different angles, three inches away, from the reaction vessel. At each position where the bolometer was placed, the area covering this solid angle on the sphere was measured. The bolometer reading times the area of this particular solid angle gives the amount of light scattering within this solid angle. The position of the bolometer was moved throughout the entire 180°. The sum of the scattered light measured by this process was compared with the total amount of absorption for a particular culture suspension. It was found that if the suspension absorbed more than 70% of the incident light, the amount of scattered light is negligible. When thinner, more transparent, suspensions of algae are used, the scattering corrections may become appreciable and they are different at different light intensities and at different algal suspensions. In order to simplify our calculations, suspensions absorbing 70% or more of the incident light were used in all the experiments described below.

The culture used was a strain of algae, *Chlorella pyrenoidosa*, maintained in pure culture by the Botany Department of the University of Wisconsin. The algae was cultured by the method described by BURK, WARBURG and co-workers[12]. About 10 mm^3 of cells suspended in 250 ml of culture medium is added to each 250 ml Drexel-type, gas washing bottle. The culture medium is:

5 grams	$MgSO_4 \cdot 7H_2O$
2.5 grams	KNO_3
2.5 grams	KH_2PO_4
2 grams	$NaCl$
5 milligrams	$FeSO_4 \cdot 7H_2O$

dissolved in 1000 ml of lake water. The pH of the medium is around 5.0. A stream of gas containing 5% carbon dioxide in air is bubbled through the suspension slowly. The culture is illuminated with a 100 watt tungsten lamp placed about one foot from the bottles. After three to four days, the cells are separated by centrifuging and resuspended in fresh culture medium for experiment.

RESULTS

The experimental data shown below are taken from the recording charts directly. A steady exchange of gases is usually obtained within one or two minutes after each dark

References p. 193.

or light period. The green line at 5461 A and the blue line at 4358 A from a mercury AH-6 lamp were generally used as the light source. This lamp manufactured by the General Electric Co. is a water-cooled, quartz capillary lamp of high intensity. The pH of the suspensions was generally around 5.0 unless otherwise specified.

A 25 watt fluorescent lamp was used occasionally as a compensating light to compensate a part or all of the respiration.

For each dark or light period on the recording chart, a straight line is drawn through the recorded points. In order to standardize the calculations and make them easier to compare, a ten minute period of dark and light was used for all calculations, although the actual recorded time may be longer or shorter than ten minutes. An example of the detailed calculation is shown below, and summaries of results will follow.

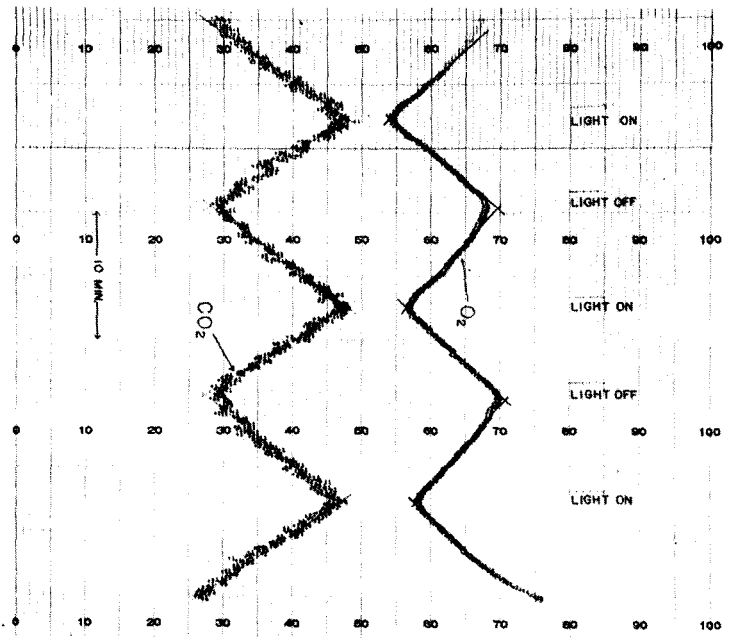

Fig. 2. A sample of recording chart.

Fig. 2 gives an example of the best data obtained under conditions in which the two instruments were adjusted to give nearly equal sensitivities. The following data taken from Fig. 2 illustrate the calculations made throughout the course of this work.

	CO_2 change (Chart division)	*O_2 change (Chart division)*
Dark	28.0	— 19.9
Light	— 23.8	15.9
Dark	29.6	— 19.9
Light	— 24.6	16.6
Dark	28.7	— 22.1
Light	— 21.8	16.9

The calibration of instruments showed each division on the recording chart corresponds

to 0.160 micro mole of carbon dioxide change and 0.227 micro mole of oxygen change respectively.

Taking the average respiration period, which is the average of the dark periods before and after each light period, as the actual dark period during light, the following amount of gas exchanges are obtained for each ten-minute light period.

	CO_2 change (micro mole)	O_2 change (micro mole)
1st light period	8.42	8.07
2nd light period	8.59	8.54
3rd light period	8.08	8.85

The light absorption as measured by the bolometer was 70.2 micro einsteins ($70.2 \times 6.02 \cdot 10^{18}$ photons) per ten minutes.

If we express the quantum efficiency as ϕ (the fraction of a molecule of carbon dioxide or oxygen fixed by the absorption of one light photon), quantum requirement as $1/\phi$ (number of photons required to fix one molecule of carbon dioxide or oxygen), and the ratio of CO_2/O_2 as Q, the results of this experiment may be summarized in the following table.

	ϕ_{O_2}	$1/\phi_{O_2}$	ϕ_{CO_2}	$1/\phi_{CO_2}$	Q
1st light period	0.115	8.7	0.120	8.3	1.04
2nd light period	0.122	8.2	0.122	8.2	1.00
3rd light period	0.126	7.9	0.115	8.7	0.91

The results summarized in Table I are calculated as shown above. The light intensity varied from 0.05 to 0.15 micro einstein per cm^2 per min. The first set of experiments was carried out by using the oxygen meter alone. The fresh culture was saturated with a 5% carbon dioxide-air mixture. The letter G, B, and R listed under light absorption indicates the green, blue and red lights used respectively. Experiments with a * indicate that compensating light was used.

The average value of the quantum requirement of these 14 experiments and 61 determinations in the presence of 5% CO_2 is 8.1 $\pm$ 1.5 photons per molecule.

It should be pointed out that experiments 1–5 and 1–6 showed considerably higher efficiencies than most of the other experiments. These experiments were carried out with rather thick algal suspensions and blue light. The absorption of light was nearly complete. The carbon dioxide concentration was around 5%. Such conditions are favorable for the introduction of induction phenomena and intermittency effects. The continuous stirring of the suspension allows an algal cell to travel from light to dark, and hence introduces an automatic intermittent effect. The effects due to intermittent light will be discussed later. Under these conditions of induction and intermittency, the relation between the rates of gas exchange in the dark and in the light can lead to abnormal results.

The experiments of Table II showed the simultaneous recording of both carbon dioxide and oxygen gas exchanges. The carbon dioxide gas analyzer, as stated above, is only operative with less than 2.5% carbon dioxide in the system. The *Chlorella* suspension,

References p. 193.

TABLE I

QUANTUM EFFICIENCIES AS MEASURED BY OXYGEN EXCHANGE

Experiment	Light abs. (micro einstein)	O_2 change (micro mole)	ø	1/ø	Experiment	Light abs. (micro einstein)	O_2 change (micro mole)	o	1/o
1–1	23.2 (G)	2.25	0.097	10.3		37.8 (B)*	5.80	0.153	6.5
	81.8 (G)	7.64	0.094	10.7		48.6 (G)*	4.84	0.099	10.1
	54.9 (G)	6.16	0.112	9.0		48.6 (G)*	5.13	0.105	9.5
	23.2 (G)	3.21	0.138	7.3					
					1–9	31.0 (G)	3.51	0.113	8.9
1–2	54.9 (G)	6.10	0.111	9.0		31.0 (G)	3.82	0.123	8.1
	34.8 (G)	4.29	0.123	8.1		31.0 (G)	3.64	0.117	8.5
	34.8 (G)	4.36	0.125	8.0		7.9 (G)	1.10	0.139	7.2
						38.4 (B)	5.26	0.137	7.3
1–3	71.2 (G)	7.00	0.098	10.2		38.4 (B)	6.82	0.152	6.6
	44.0 (G)	4.94	0.112	8.9		21.0 (B)	3.14	0.149	6.7
	71.2 (G)	7.70	0.108	9.3		38.4 (B)	5.78	0.150	6.7
	14.5 (G)	1.80	0.124	8.1					
					1–10	12.2 (B)	1.97	0.161	6.3
1–4	44.0 (B)	5.39	0.122	8.2		12.2 (B)*	1.96	0.160	6.3
	71.2 (B)	8.10	0.114	8.8		10.0 (G)	1.56	0.156	6.5
						10.0 (G)*	1.40	0.140	7.2
1–5	46.9 (B)	7.96	0.169	5.9					
	36.1 (B)	6.03	0.167	6.0	1–11	25.4 (R)	3.28	0.129	7.8
	22.0 (B)	3.34	0.151	6.6					
	36.1 (B)	6.35	0.175	5.7	1–12	30.9 (B)*	4.35	0.141	7.1
	46.9 (B)	7.70	0.164	6.1		30.9 (B)	4.72	0.153	6.5
						30.9 (B)	4.35	0.141	7.1
1–6	38.0 (B)	6.22	0.163	6.1		34.7 (G)*	3.28	0.094	10.6
	38.0 (B)	6.35	0.167	6.0		34.7 (G)	3.25	0.094	10.6
	22.4 (B)	3.60	0.161	6.2					
	38.0 (B)	5.78	0.152	6.6					
					1–13	43.2 (B)	7.87	0.179	5.6
1–7	45.0 (B)	5.26	0.117	8.5		43.2 (B)*	5.54	0.128	7.8
	45.0 (B)	6.29	0.139	7.2		24.9 (B)*	3.51	0.141	7.1
	45.0 (B)	5.14	0.114	8.8		24.9 (B)*	4.34	0.130	7.7
	66.0 (G)	6.54	0.099	10.1		24.9 (B)*	2.68	0.108	9.2
	66.0 (G)	6.17	0.094	10.7		10.5 (G)*	1.41	0.134	7.5
	66.0 (G)	6.15	0.094	10.7		10.5 (G)*	1.64	0.156	6.4
1–8	37.8 (B)	5.43	0.143	7.0	1–14**	43.2 (B)	5.80	0.134	7.5
	33.0 (B)	4.50	0.136	7.4		43.2 (B)*	5.57	0.129	7.7
	32.5 (B)	4.04	0.124	8.1		43.2 (B)*	5.96	0.138	7.2
	32.5 (B)	3.71	0.114	8.8		43.2 (B)*	4.91	0.114	8.8

** This experiment was carried out in alkaline solution of pH 8.9. 85% — 15% carbonate-bicarbonate mixture was used as buffer.

therefore, was saturated with 1.0 to 2.0% carbon dioxide for all experiments in this set.

The average value of the quantum requirement (1/ø) for the ten experiments summarized in Table II with forty determinations following the exchange of carbon dioxide gas is 8.7 ± 1.0 photons per molecule. The average value of the quantum requirement from 31 determinations following the exchange of oxygen gas is 9.1 ± 1 2 photons per molecule. The total average value from 71 determinations in this second set of experiments is 8.9 ± 1.0 photons per molecule. The average value of Q, CO_2/O_2, from 31 determinations is 1.02 ± 0.10.

Among the above two sets of experiments we have tried various thickness of chlorella suspensions, different light intensities, above and below the compensation point, and

References p. 193.

different pH, with no appreciable difference in quantum requirement. All of these experiments were carried out at room temperature ranging from 18 to 23° C. The *Chlorella* suspensions were saturated with air containing different concentrations of carbon dioxide gas. No appreciable difference in quantum efficiency was found within the range studied from 1.0% to 5.0% carbon dioxide.

TABLE II

QUANTUM EFFICIENCIES AS MEASURED BY OXYGEN AND CARBON DIOXIDE EXCHANGES

Experiment	*Light abs. (micro einstein)*	*O_2 change (micro mole)*	*CO_2 change (micro mole)*	ϕ_{O_2}	$1/\phi_{O_2}$	ϕ_{CO_2}	$1/\phi_{CO_2}$	Q
2–1	25.5 (G)		3.68			0.144	6.9	
	25.5 (G)*		3.18			0.125	8.0	
	34.4 (B)		5.30			0.154	6.5	
2–2	31.3 (G)		2.87			0.092	10.9	
	31.3 (G)	2.71	3.21	0.087	11.5	0.102	9.8	1.18
	40.6 (B)	3.81	3.68	0.094	10.6	0.091	11.0	0.96
	40.6 (B)	4.24	4.26	0.104	9.5	0.105	9.5	1.00
2–3	41.0 (B)	6.67	5.33	0.163	6.1	0.130	7.7	0.80
	34.1 (B)	3.53	3.81	0.104	9.6	0.111	9.0	1.08
2–4	53.5 (G)	5.19	6.10	0.097	10.3	0.114	8.8	1.18
	53.5 (G)	5.75	6.29	0.107	9.3	0.117	8.5	1.09
2–5	67.9 (B)	6.35	7.30	0.094	10.7	0.108	9.3	1.16
	67.9 (B)*	8.02	8.38	0.118	8.5	0.123	8.2	1.04
	42.4 (B)*	4.84	4.91	0.114	8.7	0.116	8.6	1.01
	40.4 (G)*	5.30	5.05	0.131	7.6	0.125	8.0	0.96
	40.4 (G)	4.63	5.05	0.114	8.7	0.125	8.0	1.09
2–6	59.2 (B)		6.61			0.112	8.9	
	59.2 (B)		5.55			0.094	10.6	
	59.2 (B)		7.28			0.123	8.1	
	50.0 (G)	4.93	5.85	0.099	10.1	0.117	8.5	1.18
	37.5 (G)		4.57			0.122	8.2	
	37.5 (G)		4.21			0.112	8.9	
2–7	33.2 (G)	3.99	4.09	0.120	8.3	0.124	8.1	1.02
	33.2 (G)	3.40	3.13	0.102	9.8	0.095	10.5	0.92
	33.2 (G)	3.71	3.46	0.112	8.9	0.104	9.6	0.93
	33.2 (G)	4.10	4.14	0.124	8.1	0.124	8.1	1.00
	57.0 (B)	5.75	6.19	0.101	9.9	0.108	9.3	1.08
2–8	30.4 (G)	3.57	3.32	0.117	8.5	0.109	9.2	0.93
	30.4 (G)	3.28	3.72	0.108	9.3	0.122	8.2	1.13
	40.7 (G)	4.63	4.70	0.114	8.8	0.115	8.7	1.01
	40.7 (G)	5.00	4.78	0.123	8.1	0.118	8.5	0.96
2–9	48.0 (G)	4.15	5.47	0.087	11.5	0.114	8.8	1.31
	48.0 (G)	6.06	6.69	0.126	7.9	0.139	7.2	1.10
	48.0 (G)	6.11	5.31	0.127	7.9	0.111	9.0	0.87
	48.0 (G)	5.72	4.72	0.119	8.4	0.098	10.2	0.83
	48.0 (G)	7.07	5.76	0.147	6.8	0.122	8.2	0.83
	48.0 (G)	6.51	5.81	0.135	7.4	0.124	8.1	0.89
2–10	44.5 (B)	4.61	4.56	0.104	9.6	0.102	9.8	0.99
	52.0 (B)	6.32	6.30	0.121	8.3	0.120	8.3	1.00
	52.0 (B)	6.33	6.31	0.121	8.3	0.120	8.3	1.00

References p. 193.

The exact amounts of culture used in each experiment were not listed, but they may be found in ref. 2. Generally, the culture respired an amount of gas equivalent to 1.0 to 1.5 times its own volume per hour. We can find no difference in efficiency with respiration rate in our experiments when the cells are respiring at reasonable constant rates.

In order to have a check on the cultures used at different laboratories, we have obtained cultures, *Chlorella pyrenoidosa*, from Prof. ROBERT EMERSON at the University of Illinois, and from Dr. DEAN BURK at the National Institute of Health, Bethesda, Maryland. The absorption spectra in the visible region of these cultures were compared with our own culture. The characteristic peaks of *Chlorella* were exactly the same in the three cultures. The quantum efficiency of each of the three cultures was subsequently measured under substantially the same external conditions. The results are tabulated in Table III. The green line at 5461 A from the mercury AH-6 lamp was used in these experiments.

TABLE III

QUANTUM EFFICIENCIES WITH ALGAE FROM DIFFERENT LABORATORIES

Light abs. (micro einstein)	*O_2 change (micro mole)*	*CO_2 change (micro mole)*	ϕ_{O_2}	$1/\phi_{O_2}$	ϕ_{CO_2}	$1/\phi_{CO_2}$	Q
Wisconsin culture							
50.6	5.66	5.20	0.110	9.1	0.103	9.7	0.93
50.6	5.71	5.97	0.113	8.8	0.118	8.5	1.04
EMERSON's culture							
52.0	5.62	5.67	0.108	9.3	0.109	9.2	1.01
52.0	7.10	5.61	0.136	7.3	0.108	9.3	0.79
BURK's culture							
44.5	4.61	4.55	0.103	9.7	0.102	9.8	0.99
52.0	6.30	6.28	0.121	8.3	0.120	8.3	1.00
52.0	6.26	6.30	0.119	8.4	0.121	8.3	1.01
50.6	6.15	5.39	0.121	8.3	0.106	9.4	0.88
50.6	6.29	5.52	0.124	8.1	0.109	9.1	0.88

EMERSON AND LEWIS have reported a carbon dioxide burst during the first few minutes of illumination[9]. Although the conditions were varied in favor of such a burst, no indication of a burst was found on our recorder. Our system is considerably different from the manometric set up used by EMERSON AND LEWIS. Both the liquid and the gas volumes in our system are considerably larger. Our failure to observe the carbon dioxide burst may be due to the fact that the ratio of water to algal cells in these experiments was large and that quick differences in gas exchanges were flattened out.

Experiments with intermittent light and dark periods were also tried. The length of each period of dark and light depended on the rate of rotation of a sector wheel. Periods ranging from 0.25 second of light and 0.25 second of dark to one minute of light and one minute of dark were tried. The results of these experiments are difficult to interpret. While most of the experiments showed no appreciable difference from the experiments with 10 minute periods, a few of them showed an increase in quantum yield of about 10 to 30% with intermittent light.

References p. 193.

CONCLUSION

This report concludes a long program of research at the University of Wisconsin on the quantitative measurements of the photosynthetic efficiency of *Chlorella*. Thousands of measurements have been made by a dozen different men over a period of more than two decades, using six different types of measuring apparatus. The data reported here with improved apparatus agree with the earlier work of this laboratory and are considered to be the most accurate and reliable. They give an energy efficiency or quantum requirement of 8.9 ± 1.0 photons per molecule when all the results are averaged.

The difference between the approximately eight photons per molecule described here and the less than four reported in many manometric researches of WARBURG AND BURK and their associates cannot be attributed to absolute energy measurements because all the workers have calibrated their thermopiles and bolometer with the same type of carbon filament lamp standardized by the U. S. Bureau of Standards. Moreover, in this laboratory[6] values of about one photon per molecule were obtained for the ethyl chlorophyllide actinometer developed by WARBURG and his associates. This is in close agreement with their values. The bolometer used in the experiment reported here was calibrated both with a standard radiation lamp and with pheophytin a and b kindly given to us by DEAN BURK and used directly in the apparatus described here and measured with the oxygen meter. BURK's value of 0.7 photon per molecule was assumed in this calibration and the data agreed with the calibration by the standard lamp.

The difference cannot be attributed to biological differences and less efficient conditions of culture and growth. The minimum value of about 8 has been obtained uniformly over a twenty year period with many different cultures and biological conditions. These have included algae obtained from Dr. BURK's laboratory and methods of culture which were indentical with those recommended by WARBURG, BURK and their associates.

The most likely cause of discrepancy seems to lie in the difficulty of obtaining equilibrium conditions in the algal suspension just after turning the light on or off. It is important to have steady state conditions in both dark and light for the calculation of the quantum requirement. A detailed interpretation of the manometric data has been given by EMERSON[13]. A reinterpretation of the high efficiencies of WARBURG AND BURK has been given by FRANCK[11].

It is concluded that *the normal maximum efficiency of photosynthesis in Chlorella pyrenoidosa is about eight photons per molecule*. This corresponds in green light 5461 A to an energy storage of 27% of the absorbed light, and in red light of 6500 A it is 32%. No other algae or plant has yet been reported to give a greater photosynthetic efficiency than *Chlorella**.

ACKNOWLEDGMENT

The authors wish to thank the Research Committee of the Graduate School of the University of Wisconsin for long continued support of this research, with funds from the Wisconsin Alumni Research Foundation.

* Quantum requirements measured on other algae under the same conditions are being reported elsewhere.

References p. 193.

SUMMARY

The quantum efficiency of photosynthesis by *Chlorella pyrenoidosa* was determined by following the gas exchanges between oxygen and carbon dioxide, using a magnetic oxygen meter and an infrared carbon dioxide gas analyzer. It was found that on the average, 8.9 ± 1.0 photons are required to fix one molecule of oxygen or carbon dioxide. Cultures from different laboratories showed no appreciable difference in yields.

RÉSUMÉ

Le rendement quantique de la photosynthèse chez *Chlorella pyrenoidosa* a été déterminé en suivant les échanges gazeux entre l'oxygène et le gaz carbonique, en utilisant un oxygénomètre magnétique et un analyseur à infrarouge pour le gaz carbonique. En moyenne 8.9 ± 1.0 photons sont nécessaires pour fixer une molécule d'oxygène ou de gaz carbonique. Des cultures provenant de différents laboratoires ne présentent pas de différences appréciables de rendements.

ZUSAMMENFASSUNG

Die Quantumausbeute der Photosynthese von *Chlorella pyrenoidosa* wurde mit Hilfe einer Methode gemessen, welche es erlaubt, den Gasaustausch von Sauerstoff und Kohlendioxyd mit einem magnetischen Sauerstoffmessapparat und einem infraroten Kohlendioxyd-Gasanalysator zu verfolgen. Es wurde festgestellt, dass im Durchschnitt 8.9 ± 1.0 Photons gebraucht werden, um ein Molekül Sauerstoff oder Kohlendioxyd zu binden. Kulturen aus verschiedenen Laboratorien zeigten keine merklichen Unterschiede in ihrer Ausbeute.

REFERENCES

[1] O. WARBURG AND E. NEGELEIN, *Physik. Chem.*, 106 (1923) 191.
[2] From the Ph.D. thesis of EDWARD LUNG YUAN, University of Wisconsin, submitted August, 1954.
[3] J. L. MAGEE, T. W. DEWITT, E. G. SMITH AND F. DANIELS, *J. Am. Chem. Soc.*, 61 (1939) 3529.
[4] H. G. PETERING, B. M. DUGGAR AND F. DANIELS, *J. Am. Chem. Soc.*, 61 (1939) 3525.
[5] M. W. MANNING, J. F. STAUFFER, B. M. DUGGAR AND F. DANIELS, *J. Am. Chem. Soc.*, 60 (1938) 266.
[6] R. W. EVANS, *Ph.D. thesis*; University of Wisconsin (1951).
[7] R. E. WILFONG, *M.S. thesis*; University of Wisconsin (1942).
[8] W. O. ERICKSON, *B.S. thesis*; University of Wisconsin (1943).
[9] R. EMERSON AND C. M. LEWIS, *Am. J. Botan.*, 28 (1941) 789.
[10] D. BURK AND O. WARBURG, *Z. Naturforsch.*, 6b (1951) 12.
[11] F. DANIELS, *Energy Efficiency in Photosynthesis, Radiation and Biology*, HOLLAENDER, McGraw Hill Book Co., Vol. III (1955).
[12] D. BURK, S. HENDRICKS, M. KORSENOVSKY, V. SCHOCKEN AND O. WARBURG, *Science*, 110 (1949) 225.
[13] Meeting of the National Academy of Sciences, Washington, D.C., April 26, 1954.
[14] J. FRANCK, *Arch. Biochem. Biophys.*, 45 (1953) 190.

Received December 10th, 1954