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PHOTOSYNTHETIC WATER SPLITTING*

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DISCLAIMER

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This report is organized according to the following outline:

1. INTRODUCTION AND BACKGROUND

In 1942, Gaffron and Rubin [1] performed experiments which indicated that certain green algae are capable of producing molecular hydrogen both upon irradiation with visible light as well as by fermentation in the dark. They placed the alga *Scenedesmus* in a nitrogen atmosphere which was devoid of oxygen and CO_2. Under these conditions, one can ask what molecular species serves as the terminal-electron acceptor. Carbon dioxide, the normal terminal electron acceptor of photosynthesis is unavailable. Lacking the basic carbon source, no new plant matter can be synthesized. Gaffron and Rubin made the remarkable discovery that under anaerobic conditions certain green algae can synthesize hydrogenase, an enzyme capable of accepting electrons at low oxidation/reduction potential, and, together with available protons, produce molecular hydrogen:

$$2e^- + 2H^+ \xrightarrow{\text{hydrogenase}} H_2$$

Much has been learned about the structural and bioenergetic aspects of photosynthesis since the pioneering work of Gaffron and Rubin. In particular, the concept of photosynthesis as a process involving two light reactions in series has evolved: the Z scheme of photosynthesis. The two light reactions (PSI and PS II) are connected by an electron-transport chain of dark biochemical reactions. Using the Z scheme, we can estimate the maximum theoretical efficiency of photosynthesis.

For the half reaction

$$2H_2O \rightleftarrows O_2 + 4H^+ + 4e^-$$

the midpoint versus SHE is +0.8V at pH = 7 [2]. Since this number is the reversible thermodynamic value, the actual molecular species that is responsible for the oxidation of water must have an effective midpoint potential of at least +0.8 V. (This assumes that the internal pH of the cell is close to 7.) In practice, the actual effective midpoint potential will be even greater (i.e., more oxidizing) due to irreversible losses. By adding artificial electron donors and acceptors of known midpoint potentials to whole cells and isolated chloroplasts, it has been determined that both PSI and PS II are capable of spanning potential differences of about IV each. The movement of electrons on the oxidizing side of PS II (P_{680}) to X on the reducing side of PS I spans a potential difference of approximately 1.2V. That is, the thermodynamically uphill movement of electrons through the photosynthetic electron-transport chain from H_2O to X results in an increase of energy of 1.2 electron volts (eV) per electron transferred (27.7 kcal/mol of electrons transferred). This energetically uphill process is driven, of course, by the absorption of visible light quanta in the photosynthetic reaction centers. It is generally assumed that the primary process of photosynthesis is such that the absorption of one quantum in a photosynthetic reaction center results in the transfer of one electron. Since there are two photoreactions in series, it takes the absorption of two quanta to move one electron through the electron-transport chain of photosynthesis. The photosynthetically active radiation is in the wavelength range 400-700 nm (3.1-1.8 eV). This wavelength interval contains about 47% of the power in the solar-emission spectrum. The primary event of photosynthesis is a quantum conversion process which, presumably, takes place from the lowest excited singlet state of reaction-center chlorophyll (about 1.8 eV above ground state). From the point of view of solar energy conversion and storage, absorption of a 3.1-eV photon is no more effective than a 1.8-eV photon since thermal equilibration times in a condensed phase take place on a subpicosecond time scale. Similar considerations apply to all solar energy conversion schemes, such as those that are purely photochemical and photophysical. The maximum theoretical efficiency of energy conversion by the photosynthetic apparatus is, therefore,

$$\frac{1.2\ eV}{2\ X\ 1.8\ eV}\ X\ 40\% \simeq 13\%$$

This efficiency is not as high as the maximum theoretical efficiency of electricity generation by silicon photovoltaic cells. It is, however, important to bear in mind that the end product of photosynthesis consists of storable, transportable energy-rich molecules. In addition, the process works quite well in a relatively impure environment.

The results of Gaffron and Rubin can be interpreted in terms of the Z scheme. Reducing equivalents generated by PS I are eventually taken up by hydrogenase and evolved as molecular hydrogen. The question of the source of electrons has been the cause of continuing controversy. Gaffron and Rubin did not observe any oxygen along with their hydrogen. They recognized that the photoproduction of hydrogen was most likely

representative of an anaerobic photooxidation of some unknown intermediate formed in fermentation. Recently, the fermentative metabolism of *Chlamydomonas moewusii* has been examined by Klein and Betz [3]. They came to the important conclusion that starch is the substrate for a number of products of anaerobic metabolism, including molecular hydrogen.

Since the pioneering work of Gaffron and Rubin [1], other photosynthetic systems have been shown to be capable of producing hydrogen. These include the blue-green algae [4] and the chloroplast-ferredoxin-hydrogenase system [5-17]. The coupling of spinach chloroplast PS I to a clostridial hydrogenase with ferrodoxin was noted by Arnon, Mitsui and Paneque [18]. An excellent review of the field of hydrogen production by photosynthetic organisms has been given by Weaver, Lien, and Seibert [19].

The ability of algae and chloroplast systems to photoproduce molecular hydrogen and/or oxygen raises the possibility of using the photochemical machinery of photosynthesis to split water into hydrogen and oxygen in stoichiometric ratios of 2:1. Measurements on the simultaneous photoproduction of hydrogen and oxygen have been relatively few in number compared to those on hydrogen production alone. The pioneering effort on simultaneous photoproduction of hydrogen and oxygen was made by Spruit [20]. Spruit developed a novel two-electrode polarographic technique for the simultaneous measurement of photoproduced hydrogen and oxygen by *Chlorella*. The principle conclusion that he came to was that hydrogen and oxygen metabolisms are closely related and that both gases are ultimately given off during illumination from the same source, namely water. Later work by Bishop and Gaffron [21] indicated that the light-dependent evolution of hydrogen appeared to require both photosystems. However, two schools of thought prevail concerning both the nature of the substance dehydrogenated during photohydrogen production and the photosystems utilized. In the original research of Gaffron and Rubin, the substrate was postulated to be an organic donor since the addition of glucose caused an increase in the amount of hydrogen evolved (see also Kaltwasser, Stuart, and Gaffron [22] and Stuart and Gaffron [23]. Bishop, Frick, and Jones [24] have applied a two-electrode polarographic technique for measuring the amount of gas produced in a confined volume. Due to the buildup of hydrogen and oxygen, with subsequent inhibition, these reactions could only be followed for several minutes.

In this report we will summarize the current status of the SERI contract Photosynthetic Water Splitting. We will describe previous research, recent results and future plans.

2. PREVIOUS WORK

Most of this work has been published. We will briefly summarize the highlights and significance of this work.

2.1 The Photosynthetic Unit of Hydrogen Evolution (Refs. 25 and 26).

We have designed and built an original analytical measuring system which has the capability of detecting the absolute yield of hydrogen

or oxygen per saturating single-turnover flash of light. This instrumentation has been used to perform the first measurement of the photosynthetic unit size of hydrogen production. The significant aspect of this work is that it demonstrated that the photosynthetic unit size for hydrogen evolution is comparable to that for oxygen evolution. This result implies that the photoreaction for hydrogen evolution is not a trivial side reaction of photosynthesis but that in fact the electrons for photoproduced equivalents for hydrogen evolution are derived from the mainstream of the electron transport chain of photosynthesis.

2.2 The Turnover Time of Photosynthetic Hydrogen Production (Ref. 27).

An important consideration relating to photosynthetic systems and hydrogen production is the ability of the hydrogen photoapparatus to keep pace with incident light quanta. We have performed the first measurement of the turnover time of photosynthetic hydrogen production. This measurement was done in two ways. First, individual flash pair yields were detected. This method gives a value of about 1 millisecond. Second, we have driven the algae into the steady state by repetitive flash illumination of varying frequency. The details of this work are reported below. This method gives a value of 5-10 milliseconds. The significance of these numbers is discussed below in the section on recent results (3.2).

2.3 Hydrogenic Photosynthesis (Ref. 28)

An intriguing aspect of photosynthetic hydrogen production is the simultaneous photoproduction of hydrogen and oxygen with visible radiation. This is an artificial type of photosynthesis in which molecular oxygen is evolved and hydrogen ions are reduced to molecular hydrogen (as opposed to the production of a carbon dioxide fixation compound). There is no doubt that anaerobically adapted algae can perform hydrogenic photosynthesis. The process is, however, complex and further study is needed in this area.

3. RECENT RESULTS

3.1 Simultaneous Photoproduction of Hydrogen and Oxygen

One of the objectives of this research program is to make a quantitative assessment of the potential for using marine algae for producing hydrogen and oxygen from sea water. Our main experimental approach is to screen selected species of green algae for simultaneous photoproduction of hydrogen and oxygen. Prior to this work, there have been no reports in the literature on simultaneous photoproduction of hydrogen and oxygen by any *marine* photosynthetic organism. We identified six marine green algae that have this property.

The selection of marine algae was motivated by our previous work and by what is known in the published literature on hydrogen production by freshwater algae. Hydrogen production by freshwater systems has been studied in much greater detail than marine systems. Of all the green algae surveyed, about 50% of them possess the ability to synthesize the hydrogenase enzyme. In particular, we have determined that the freshwater green alga *Chlamydomonas reinhardtii* possesses attractive

biophysical parameters for hydrogen photoproduction (photosynthetic unit size, turnover time, etc.). We therefore, decided to investigate marine species of *Chlamydomonas* and other green algae. These algae were isolated by R. R. L. Guillard from waters of the Great Harbor Area, Woods Hole, Mass. A summary of organisms chosen for study as well as the results obtained are presented in Table I.

Table I. Summary of results on simultaneous photoproduction of hydrogen and oxygen in selected marine green algae

Alga	Strain	H_2	O_2
Chlamydomonas	11/35	+	+
Chlamydomonas	D	+	+
Chlamydomonas	0-5	+	+
Chlamydomonas	f-9	+	+
Chlamydomonas	f-17	+	+
Chlamydomonas	CP	-	+
Chorella	580	trace	+
Chlorella sp	0-17	-	+
Halochlorocococcum	fla-9	+	+

In these experiments, time did not permit a systematic study of hydrogen and oxygen production for a given alga. Basically, we were interested in establishing a first demonstration of simultaneous photoproduction of hydrogen and oxygen in marine algae. We were able to observe simultaneous photoproduction of hydrogen and oxygen in six of the algae listed in Table I - five *Chlamydomonas* and one *Halochlorocococcum*. In particular one of these organisms, *Chlamydomonas* f-9, is quite interesting. The time rate profile for *Chlamydomonas* f-9 is illustrated in Figure 1. It can be seen in Figure 1 that the steady state rates of hydrogen and oxygen production are very close to the ideal ratio of 2:1. This result strongly suggests that *Chlamydomonas* f-9 might be capable of performing true photosynthetic water splitting. The initial burst of hydrogen production in Figure 1 can be explained in terms of the depletion of the pool of electron carriers in the plastoquinone pool of the electron transport chain linking the two photosystems of photosynthesis.

The role of photosystem II of photosynthesis in providing reducing equivalents which are eventually evolved as molecular hydrogen has been a continuing controversy since the original discovery of algal hydrogen evolution by Gaffron and Rubin [1]. In this status report we provide further evidence for the hypothesis that reducing equivalents for the photoevolution of molecular hydrogen can be derived from at least two distinct sources: (a) via photosystem II in a water splitting photoreaction and (b) via the photooxidation of endogenous reductants that interact, presumably directly with the electron transport chain linking the two photosystems of photosynthesis.

In Fig. 2 the simultaneous photoevolution of hydrogen and oxygen from anaerobically adapted *Chlamydomonas reinhardtii* is illustrated. These organisms were illuminated with a single stroboscopic light source (GenRad 1539A) at a flash repetition rate of approximately 10 Hz. (One lamp is approximately 80% saturating.) Both the stoichiometric ratios and time duration of H_2 and O_2 photoevolution are consistent with the hypothesis stated above regarding the source of reducing equivalents for evolution of molecular hydrogen.

In addition to *Chlamydomonas* we have investigated the species *Scenedesmus quad.* In this strain of *Scenedesmus* the pattern of hydrogen and oxygen photoevolution is very different from that of *Chlamydomonas.* Oxygen is evolved at a relatively steady rate, whereas hydrogen is evolved in a burst and decays to a very low value with the light still on. After a period of darkness, the pattern is repeated. We interpret this pattern as follows. During the course of O_2 evolution in which very little H_2 is evolved, an electron carrier is reduced and can be transformed into a photooxidizable substrate in the dark. This is another observation which supports the idea of photosystem II providing reducing equivalents for H_2 evolution, although in this example it appears that a dark intermediate step is necessary. It would be most interesting to be able to identify this intermediate.

3.2 Kinetic Studies

An important parameter in understanding the limiting steps of algal hydrogen production is the turnover time. We have previously measured his parameter for a variety of adaptable freshwater green algae [27]. In the work of reference [27], however, individual flash yields were resolved and the algae were not driven into the steady state. In this report, Fig. 3 is the first simultaneous measurement of the turnover times of steady-state photosynthetic hydrogen and oxygen production. The significance of the steady state data is that they should bear directly on the interpretation of data obtained by continuous wave illumination. Although the steady state values are somewhat slower than the values obtained by resolving individual flash yields, they are still rapid. In Fig. 3 the steady state turnover times are 9 msec for O_2 and 6 msec for H_2. The values for individual flash yields are about 1 msec for H_2 and O_2. These values are in the range of excitation rates of photosynthetic reaction centers in normal sunlight.

3.3 Macroscopic Marine Algae - Seaweeds

This research was performed in collaboration with Professor J. Ramus of the Duke University Marine Laboratory.

There are reports in the published literature of macroscopic marine algae possessing an adaptable hydrogenase [29]. All of the claimed hydrogenase activity, however, was measured by photoreduction not hydrogen evolution. Photoreduction was a term coined by Gaffron to describe the anaerobic photoreduction of CO_2 using molecular hydrogen as the electron donor. This reaction is believed to be associated

with photosystem I only and uses the enzyme hydrogenase to activate the molecular hydrogen. *Ulva lactuca*, according to reference [29] is a macroscopic marine alga which can be anaerobically adapted as measured by photoreduction. We, therefore, thought that *Ulva* would be an excellent candidate in which to observe the photoproduction of molecular hydrogen. We could not, however, observe any hydrogen evolution in *Ulva*. Nor did we observe photoevolution of hydrogen in any other of the macroscopic algae studied except for a single observation on *Sargussum* which was probably contaminated with microscopic algae. It is our belief that, as of this writing, there is not a single example of hydrogen photoproduction by a macroscopic marine photosynthetic organism. There are two possible explanations for this result: (1) macroscopic algae, in the course of evolution, have lost the ability to synthesize hydrogenase under anaerobic conditions or (2) competing pathways for reducing equivalents from photosystem I prevent the generation of H_2. This latter aspect will be discussed more fully in the following subsection.

3.4 Oxygen Profiles

3.4.1 Light saturation curve. The detailed shape of the light saturation curve of photosynthesis can be used to deduce certain information concerning the kinetics and mechanism of the photosynthetic process. A textbook discussion of the light saturation curve of photosynthesis usually describes it as "linear at low light intensities and saturating out at higher light intensities." This statement is generally true for normal aerobic photosynthesis. It is not true for anaerobic photosynthesis.

In Fig. 4 the light saturation curve of the macroscopic marine alga *Padina* is illustrated. Two points are worthy of mention: First, the light saturation curve at low light intensities is non-linear. This observation is analogous to the data of Diner and Mauzerall [30] who showed that the light saturation curve of the fresh water green alga, *Chlorella* was also non-linear at low light intensities. They interpreted this non-linearity as a competitive reductive loss with the oxygen evolving apparatus of photosystem II. Such an explanation would appear to be consistent with our data on *Padina*. Second, photosynthesis saturates at relatively low light intensities. In the data of Fig. 4 one could estimate that oxygen evolution is over 90% saturated at $50 Wm^{-2}$. This corresponds to only 5% of the peak solar irradiance (AM1 at noon time) which is about $1 KWm^{-2}$. This low saturation probably reflects the fact that *Padina* is accustomed to growing in marine environments where it does not normally get exposed to high light intensities.

3.4.2 Oxygen vs. time. In order to survey the selected seaweeds for hydrogen production capability we sought to place them in a situation in which they would be deprived of their natural electron acceptors (CO_2 or bicarbonate). We therefore, prepared CO_2-and bicarbonate-free sea water from natural sea water. This preparation was used as our reaction medium. As was mentioned earlier in this report, no hydrogen is claimed to have been observed from any of the seaweeds

studied. However, oxygen production was easily observed and could persist for hours. (See Fig. 5 for *Sargassum* as an example). Clearly an interesting question that can be asked at this point is: What is the electron acceptor? One possibility could be that macroscopic marine algae have the ability to sequester CO_2 in the form of bicarbonate or carbonate and use this for photosynthesis in a "CO_2-free reaction medium. If this is the case, then it could be argued that the reason H_2 was not observed isn't because these organisms can't synthesize hydrogenase but because the natural pathway of CO_2 fixation is preferred to that of hydrogen photoevolution.

Further analysis and discussion of these data are being written up in collaboration with Professor Ramus and will be submitted to a peer review journal.

4. CONCLUSIONS

In conclusion, it is felt that photobiological production of hydrogen is a significant area of research for studying the potential of biological systems in solar energy conversion and storage. We feel that the results that have been obtained both by ourselves and others are promising and that the SERI Solar Hydrogen Production Program should be continued and strengthened.

5. ACKNOWLEDGMENTS

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6. REFERENCES

[1] H. Gaffron and J. Rubin, *J. Gen. Physiol., 26,* 219 (1942).
[2] G. Milazzo and S. Caroli, *Tables of Standard Electrode Potentials* (Wiley, New York, 1978), p. 229.
[3] U. Klein and A. Betz, *Plant Physiol., 61,* 953 (1978).
[4] J. R. Benemann and N. M. Weare, *Science, 184,* 174 (1974).
[5] J. R. Benemann, J. A. Berenson, N. O. Kaplan, and M. D. Kamen, *Proc. Natl. Acad. Sci. U.S.A., 70,* 2317 (1973).
[6] L. O. Krampitz, in *An Inquiry Into Biological Energy Conversion.* A. Hollender *et al.,* Eds. (The University of Tennessee, Knoxville, 1972), p. 22.
[7] A. Ben-Amotz and M. Gibbs, *Biochem. Biophys. Res. Commun., 64,* 355 (1975).
[8] A. A. Krasnovsky, V. V. Nikandrof, G. P. Brin, I. N. Gogotov, and V. P. Oshchepkov, *Dokl. Biochem., 225,* 509 (1975).
[9] K. K. Rao, L. Rosa, and D. O. Hall, *Biochem. Biophys. Res. Commun., 68,* 21 (1976).
[10] S. G. Reeves, K. K. Rao, L. Rosa, and D. O. Hall, in *Microbial Energy Conversion,* H. G. Schlegel and J. Barnea, Eds. (Erich Kolbe KG., Göttingen, 1976), pp. 235-243.

[11] I. Fry, G. Papageorgiou, E. Tel-Or, and L. Packer, *Z. Naturforsch. A, 32c,* 110 (1977).
[12] D. Hoffmann, R. Thauer, and A. Trebst, *Z. Naturforsch. A, 32c,* 257 (1977).
[13] A. A. Krasnovsky, in *Research in Photobiology,* A. Castellani, Ed. (Plenum, New York, 1977), pp. 361-370.
[14] L. O. Krampitz, in *Clean Fuels From Biomass and Wastes.* W. W. Waterman, Ed. (Institute of Gas Technology, 1977).
[15] L. Packer and W. Cullingford, *Z. Naturforsch. A, 33c,* 113 (1978).
[16] K. K. Rao, I. N. Gogotov, and D. O. Hall, *Biochimie, 60,* 291 (1978).
[17] B. Z. Egan and C. D. Scott, *Biotechnol. Bioeng. Symp., 8,* 489-500 (1978).
[18] D. Arnon, A. Mitsui, and A. Paneque, *Science, 134,* 1425 (1961).
[19] P. Weaver, S. Lien, and M. Seibert, *Photobiological Production of Hydrogen—A Solar Energy Conversion Option,* Solar Energy Research Institute, SERI/TR-33-122, January 1979.
[20] C. J. P. Spruit, *Mededel. Landbouwhogeschool, Wageningen, 58,* 1 (1958).
[21] N. I. Bishop and H. Gaffron, in *Photosynthetic Mechanisms in Green Plants,* B. Kok and A. T. Jagendorf, Eds. (Natl. Acad. Sci.-Natl. Res. Council, Washington, D. C., 1963), pp. 441-451.
[22] H. Kaltwasser, T. S. Stuart, and H. Gaffron, *Planta, 89,* 309 (1969).
[23] T. S. Stuart and H. Gaffron, *Planta, 100,* 228 (1971).
[24] N. I. Bishop, M. Frick, and L. W. Jones, in *Biological Solar Energy Conversion,* A. Mitsui, S. Miyachi, A. San Pietro, and S. Tamura, Eds. (Academic, New York, 1977), pp. 3-22.
[25] E. Greenbaum, *Science, 196,* 878 (1977).
[26] E. Greenbaum, in *Biological Solar Energy Conversion,* A. Mitsui, S. Miyachi, A. San Pietro, and S. Tamura, Eds. (Academic, New York, 1977), pp. 101-107.
[27] E. Greenbaum, *Solar Energy, 23,* 315 (1979).
[28] E. Greenbaum, *Biotech. Bioeng. Symp. 10,* 1 (1980).
[29] A. W. Frenkel and C. Rieger, *Nature 167,* 1030 (1957).
[30] B. Diner and D. Mauzerall, *Biochim. Biophys. Acta 305,* 329 (1973).

7.0 FIGURE LEGENDS

Figure 1. *Chlamydomonas f-9.* In these experiments, the following protocol was established for each of the algae listed. The algae were placed under anaerobic conditions (in darkness) for a period of 2-4 hours to induce the *de novo* synthesis of the hydrogenase enzyme. At the end of the induction period, the light (tungsten filament) was turned on and the simultaneous photoproduction of hydrogen and oxygen was measured.

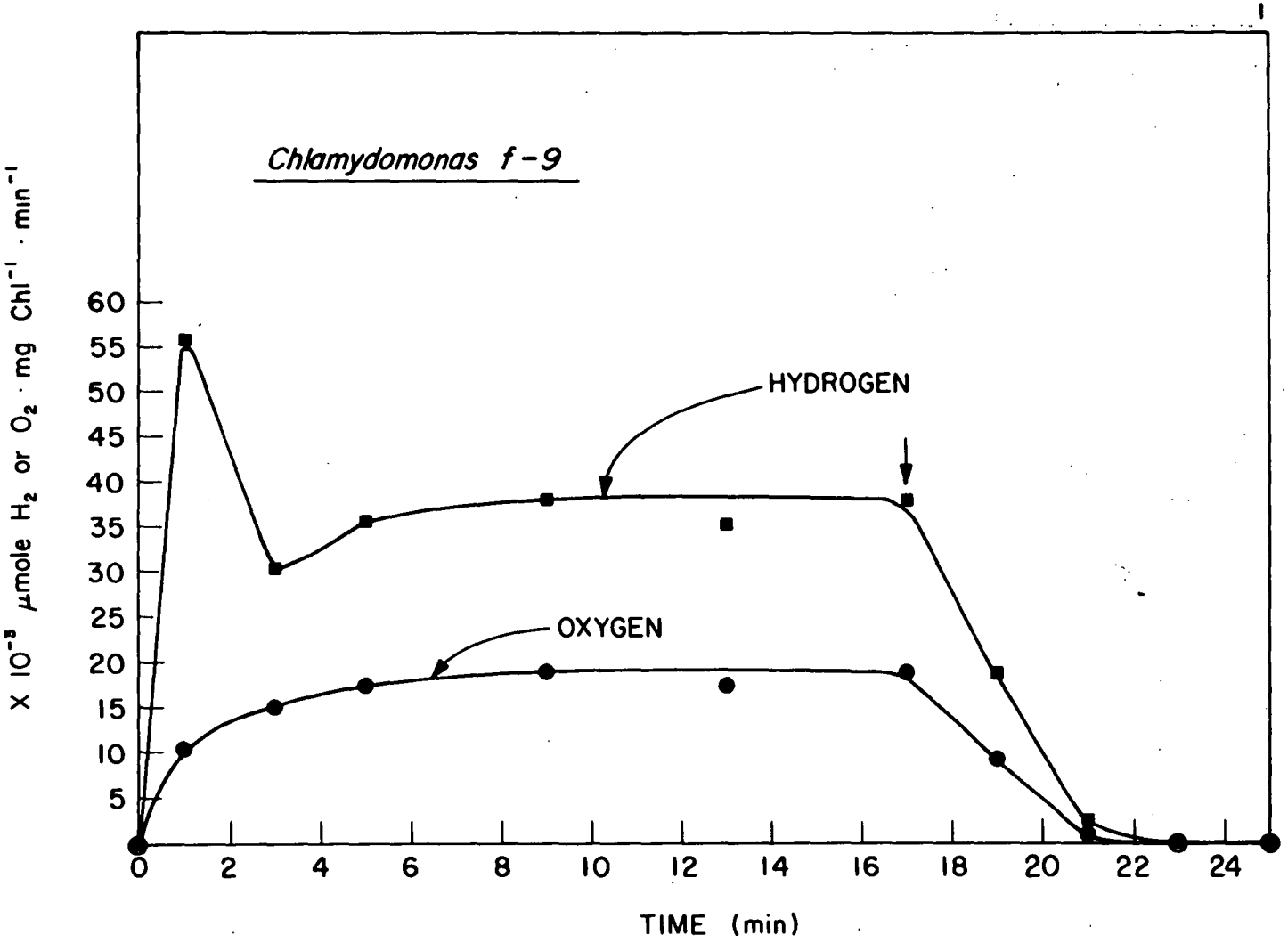
Figure 2. Simultaneous photoproduction of hydrogen and oxygen by *Chlamydomonas reinhardtii* under repetitive flash illumination at 10 Hz.

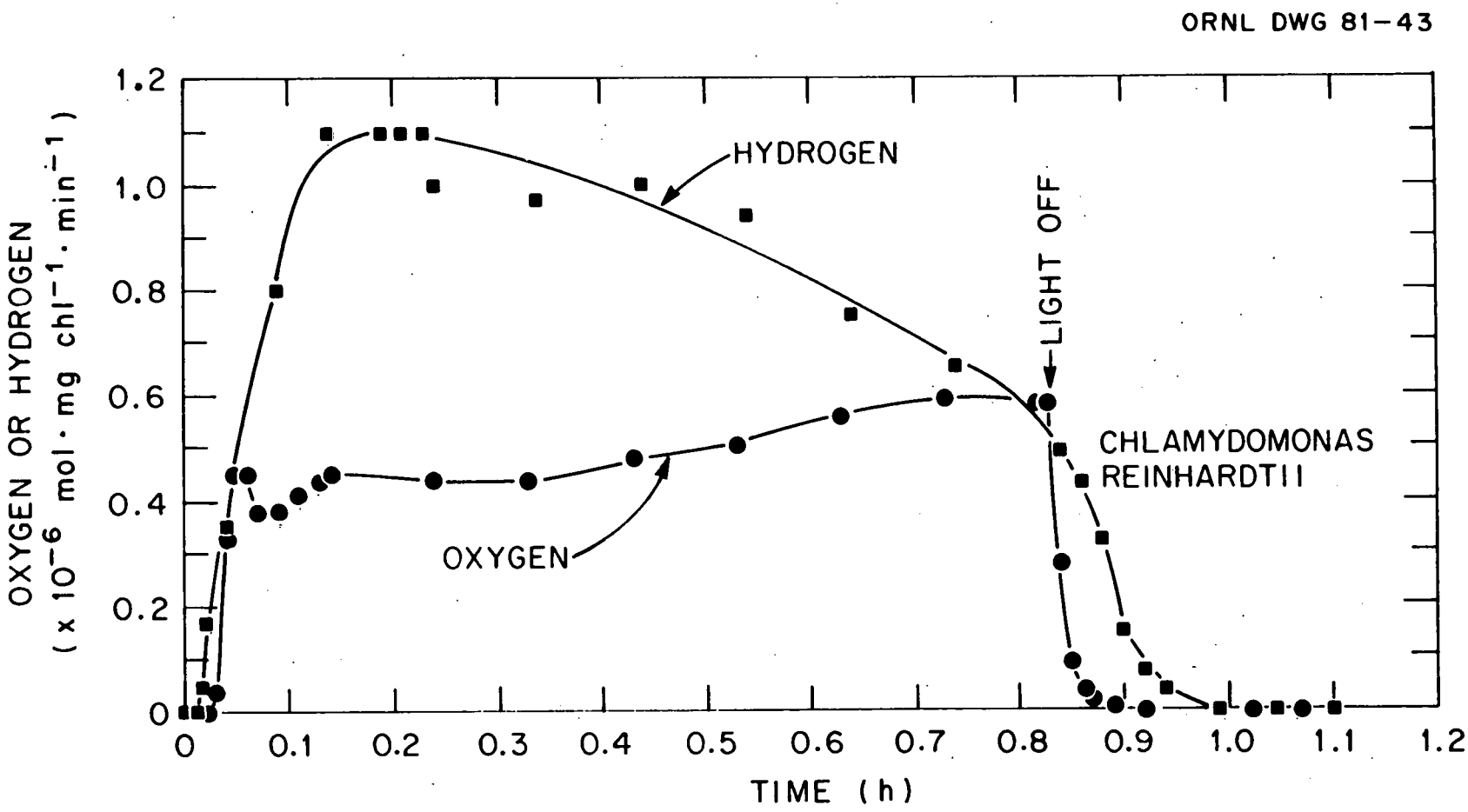
Figure 3. Pulsed frequency response of the hydrogen and oxygen

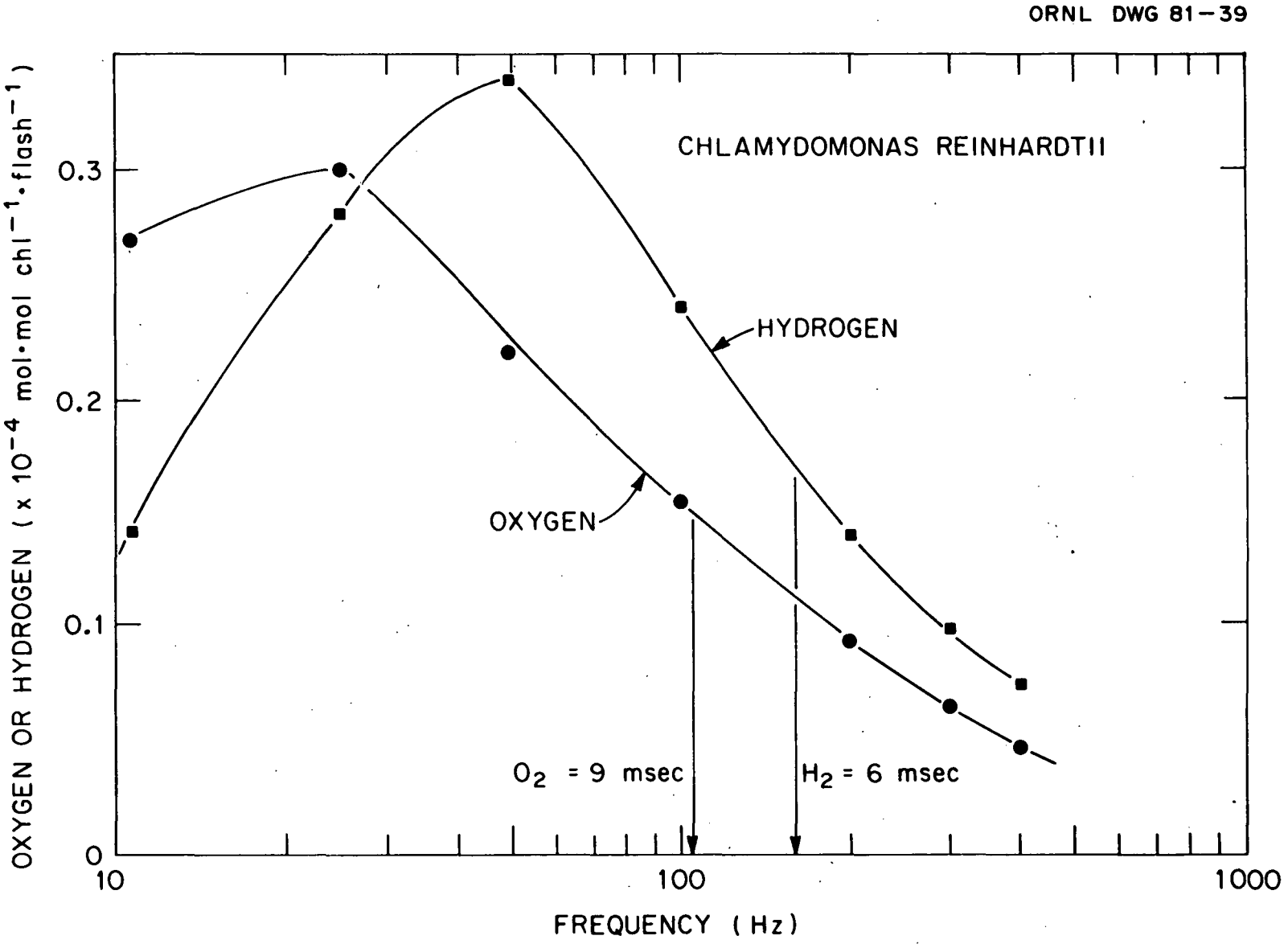
photoreactions of anaerobically adapted *Chlamydomonas*. The steady state turnover times determined by this experiment are $T(O_2)$ = 9 msec and $T(H_2)$ = 6 msec.

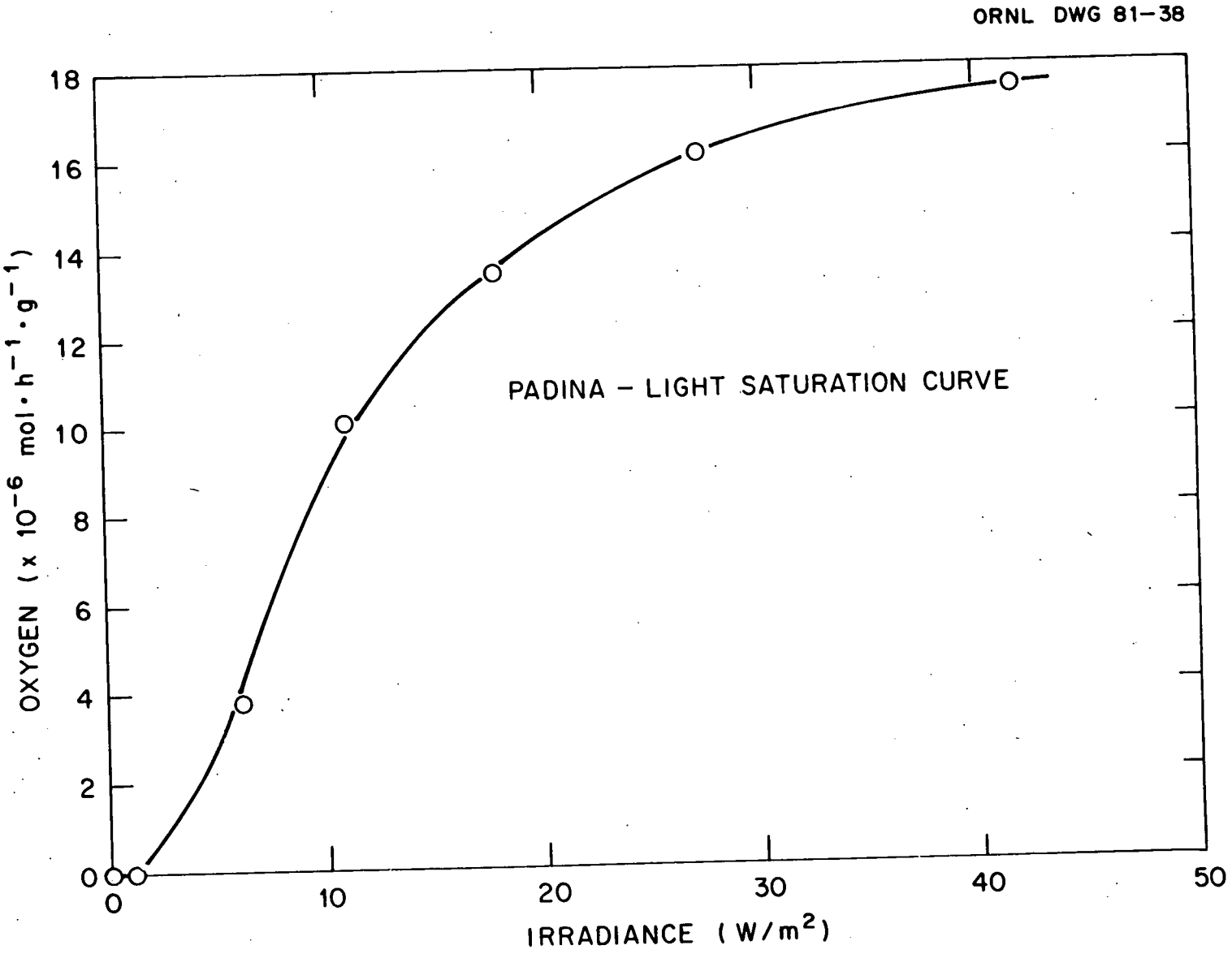
Figure 4. The light saturation curve of anaerobic photosynthesis for the macroscopic marine alga *Padina*.

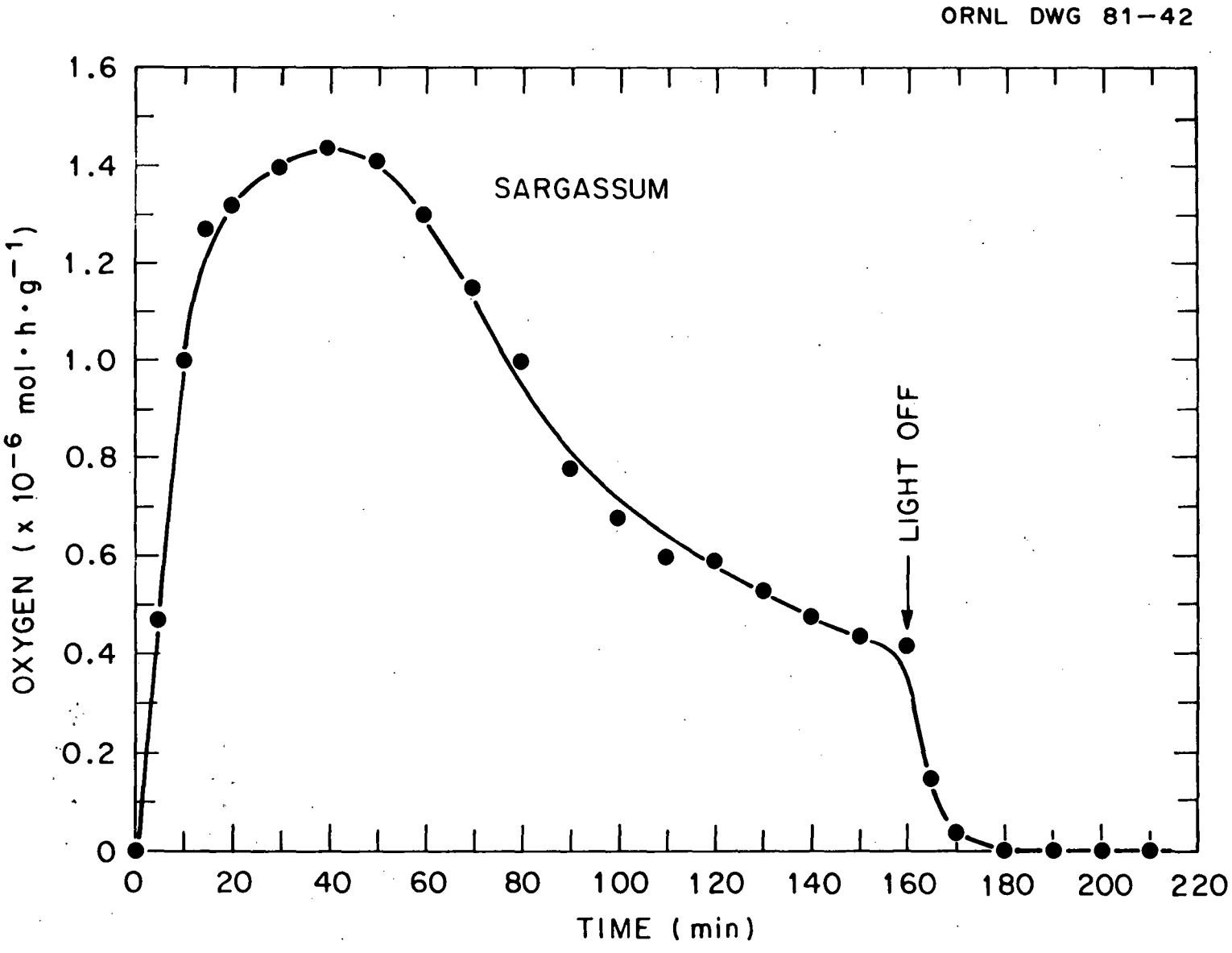
Figure 5. Oxygen versus time profile in the macroscopic marine alga *Sargassum*.


Chlamydomonas f-9
HYDROGEN
OXYGEN
× 10⁻³ μmole H₂ or O₂ · mg Chl⁻¹ · min⁻¹
TIME (min)
0
2
4
6
8
10
12
14
16
18
20
22
24
5
10
15
20
25
30
35
40
45
50
55
60


ORNL DWG 81-43
OXYGEN OR HYDROGEN
(x 10⁻⁶ mol · mg chl⁻¹ · min⁻¹)
1.2
1.0
0.8
0.6
0.4
0.2
0
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
TIME (h)
HYDROGEN
OXYGEN
LIGHT OFF
CHLAMYDOMONAS
REINHARDTII


ORNL DWG 81-39
CHLAMYDOMONAS REINHARDTII
HYDROGEN
OXYGEN
O_2 = 9 msec
H_2 = 6 msec
OXYGEN OR HYDROGEN (x 10^{-4} mol·mol chl^{-1}·flash^{-1})
0
0.1
0.2
0.3
10
100
1000
FREQUENCY (Hz)


ORNL DWG 81-38
PADINA – LIGHT SATURATION CURVE
OXYGEN (x 10⁻⁶ mol • h⁻¹ • g⁻¹)
IRRADIANCE (W/m²)
0
2
4
6
8
10
12
14
16
18
0
10
20
30
40
50


ORNL DWG 81-42
SARGASSUM
LIGHT OFF
OXYGEN (x 10⁻⁶ mol · h · g⁻¹)
TIME (min)
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
0
20
40
60
80
100
120
140
160
180
200
220