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The respiration of photosynthetic carbon in eutrophic areas of the ocean

by Walker O. Smith, Jr.[1,2]

ABSTRACT

The respiration of photosynthetic carbon by phytoplankton populations from upwelling regions was calculated from the difference in 6- and 24-h productivity incubations after the light intensity received in the 6-h incubations had been normalized to the light intensity received in 24 h. The results indicate that the phytoplankton off Northwest Africa respired 13.4% of the previously fixed photosynthetic carbon. A direct experimental test of the results confirms the calculations. A similar analysis of data from the coast of Peru indicated that respiratory losses averaged 78.4% of the observed carbon increase. Daily production values were similar in both regions. The waters off Peru were characterized by blooms of the motile dinoflagellate *Gymnodinium splendens*, while NW Africa was a diatom-dominated assemblage. The large difference in respiratory carbon loss seemed to be due to the observed species differences in the two regions. The data indicate that motility and/or the specialized conditions necessary for dinoflagellate blooms in upwelling regions may impose serious respiratory demands on phytoplankton, but that advantages arising from motility outweigh any carbon losses.

1. Introduction

The loss of previously fixed organic material during an incubation using the radio-active tracer ^{14}C introduces considerable uncertainty into the interpretation of aquatic productivity measurements. Early workers paid great attention to possible artifacts and errors (e.g. Vollenweider, 1969), yet quantifying the loss of carbon either through excretion or respiration was never successfully completed. Recent investigations have indicated that the release of dissolved organic carbon is a small fraction (10% or less) of the total carbon budget of a population (Berman and Holm-Hansen, 1974; Smith *et al.,* 1977). Other investigations have indicated that phytoplankton may oxidize more material in the light than in the dark due to photo-respiration (Tolbert, 1974). However, the respiratory loss of carbon and the magnitude of this loss in various regions of the world's oceans remains a matter of controversy.

Ryther (1954, 1956) attributed the difference he detected between the oxygen

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and ^{14}C methods for measuring primary productivity to the respiration of labeled metabolites. He noted in his experiments a decline in the ratio of gross photosynthesis to respiration with culture age. This implies that respiration increased relative to carbon fixation as the growth rate decreased. Eppley and Sharp (1976) found in oligotrophic areas that 50% of the previously fixed carbon was lost in a 12-h dark period, which represented a serious source of carbon loss to the populations. Laws and Caperon (1976), using batch cultures of *Monochrysis lutheri,* found that growth rate and respiratory rate were positively correlated, and at high growth rates the respiration accounted for 10.5% of the maximum photosynthetic rate. Cells with low growth rates (i.e. those typical of oligotrophic areas) respired a still smaller proportion of their total carbon fixed (at zero growth rate respiration was 3.4% of p_{max}). These results are quantitatively similar to the findings of Steeman Nielsen and Hansen (1959), whose measured respiratory rates differed only slightly between eutrophic or oligotrophic regions.

The purpose of this study was to provide data to establish the carbon budget of a eutrophic, upwelling region and to determine whether the amount of material respired in darkness constituted a major loss of carbon from phytoplankton populations. The regions studied had a widely differing phytoplankton species composition and conclusions concerning respiration relative to these differences are offered.

2. Materials and methods

Part of the biological measurements were carried out on the JOINT-I expedition to Northwest Africa (R. V. *Atlantis* Cruise A-82) from March through May, 1974. The area studied was the region off the coast of Cap Blanc, known to be an area of intense upwelling (Wooster *et al.,* 1976) in which large gradients in phytoplankton productivity and biomass are observed (Estrada, 1974). Additional measurements were conducted off the coast of San Juan, Peru, during March-April, 1976. Exact locations of the stations off NW Africa are given in Smith *et al.* (1977). The stations occupied in the Peruvian upwelling system were all at 15° 6'S, 75° 31.2'W. Additional experiments were carried out during Reise 36 of the F. S. *Meteor* during January-February, 1975 off the coast of NW Africa.

Measurements of productivity (particulate and dissolved) were conducted at sea using ^{14}C techniques. Thirty-eight stations were completed off Cap Blanc and fourteen off San Juan. Each station had two incubations. One lasted 6 h and was centered around local noon (0900 to 1500) and the other lasted 24 h, from 0900 to 0900 the next day. Details of the procedures used are given elsewhere (Smith *et al.,* 1977).

Respiration was calculated using the methods of Eppley and Sharp (1976) with slight modifications. They estimated respiration by doubling the carbon fixed in a 6-h, noon-sunset incubation and subtracting the carbon fixed in a 24-h incubation, reasoning that the difference represented carbon respired in the dark. This assumes
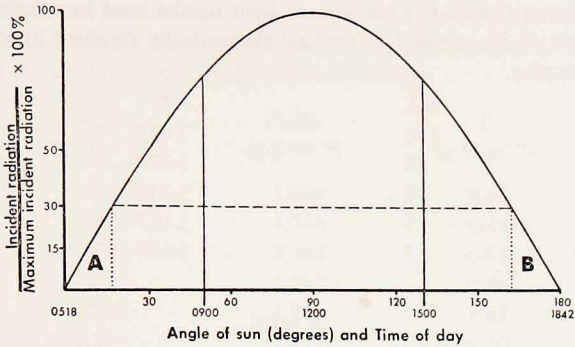
Figure 1. The path of the sun over a 13.4 h day. The area under the curve represents the total daily radiation; if the depth of maximum productivity occurs at the 30% light level, the curve is truncated and the area under 0.3 (dashed line) calculated as the amount of photosynthetically "useful" radiation.

that photosynthesis in the morning equals that in the afternoon, and that carbon fixation in the water column is proportional to light intensity. To calculate respiration and to facilitate comparison of incubations carried out in Africa and Peru, I used the following procedure. Since a 24-h incubation received more sunlight than did a 6-h incubation, the production at each 6-h incubation was multiplied by a factor F to normalize for the amount of light received in each incubation. This factor is the ratio between the radiation received in a 24-h incubation and that received in a 6-h incubation, and assumes that incident radiation followed a sinusoidal path (Fig. 1). When production throughout the water column increased as light intensity increased, F equaled the ratio of the total amount of light received in a 24-h period to that between 0900 and 1500. If, however, additional light produced no corresponding increase in carbon fixation (i.e. light saturation of photosynthesis occurred at some depth below the surface), the light was considered "excess" and the curve truncated at the depth of maximum productivity. Operationally this meant that if the depth of maximum production occurred at the depth to which 30% of the incident radiation penetrated, then only the area of the curve under 0.3 was used for 6- and 24-h incubations in the calculation of F (Fig. 1). If p_{max} occurred at the 30% light level, the total area is the sum of areas A, B, and the area under 30% and between the angle of the sun (θ) at which the incident radiation is 30% of the maximum (i.e. $\sin^{-1}\theta = .3$; therefore, for $p_{max} = .3$, $\theta = 0.31$ radians). Since area A equals area B, the total area can be computed by

$$I_{24} = 2 \int_{0}^{0.31} \sin \theta + (.3) (\pi - 2\theta)$$

$$= 2 \left.\vphantom{\int} \right|_{0}^{0.31} (-\cos \theta) + (.3) (2.532)$$

Table 1. The calculated factors (F) for various light depths used in calculation of respiratory rates. F is the ratio of the amount of sunlight theoretically received in a 24-h incubation to that in a 6-h incubation.

$\% I_0$	F
100	1.425
50	1.870
30	2.018
15	2.127
5	2.199

$$= 0.85$$

where I_{24} is the radiation received in a 24-h incubation and θ the angle of the sun in radians. Similarly,

$$I_6 = (.3)(2.27 - 0.87) = 0.42$$

where I_6 is the total radiation in a 6-h incubation. Therefore,

$$F = I_{24}/I_6 = 2.02.$$

Values for F at the depths to which 100, 50, 30, 15 and 5% of the incident light penetrated to give the maximum production are shown in Table 1.

Respiration in a 24-h incubation (R) for each station was calculated as the difference between the amount fixed in the 6-h incubations (P_6) normalized to total radiation received and the carbon fixed in the 24-h incubations (P_{24}), or

$$R = (F)(P_6) - P_{24}.$$

No correction for loss of photosynthetic carbon by excretion is made. The percent excretion measured in 6- and 24-h incubations is similar (Smith et al., 1977).

3. Results

The results of the carbon studies off NW Africa show that losses due to respiration in the 24-h incubations averaged 0.262 g C m^{-2} d^{-1} (Table 2). This represents an average of 13.4% of the total carbon fixed in the 24-h incubations, and is a small fraction of the daily carbon flux. It appears that in eutrophic upwelling areas such as NW Africa the contribution of respiration to losses of carbon from the phytoplankton carbon pool is of minor importance. For comparison, the loss of carbon due to release of dissolved organic matter in a 24-h incubation was measured for the same set of stations and averaged 8.16 mg C m^{-2} h^{-1} or 0.196 g C m^{-2} d^{-1} (Smith et al., 1977). This represents a loss of carbon which is 75% of the calculated respiratory loss. The respiratory losses from the phytoplankton from Peru indicate that the populations respired a much higher percentage of the carbon fixed photosynthetically than those in NW Africa, averaging 1.45 g C m^{-2} d^{-1} or 74.6% of the carbon fixed in the light (Table 3).

Table 2. The results of the incubations from Northwest Africa. $P(6)$ is the total carbon fixed in a 6-h incubation, $P(24)$ the carbon fixed in 24 h, L the calculated carbon loss, and $\%L$ the percentage of the total daily carbon fixed lost $(L/P(24))$.

Station	$P(6)$ (g C m^{-2})	$P(24)$ (g C m^{-2})	L (g C m^{-2})	$\%L$
6	1.999	2.935	0.86	27.4
13	0.723	1.766	−0.41	−23.4
14	0.098	0.246	−0.05	−19.6
18	1.026	1.566	0.50	32.2
23	0.753	1.249	0.27	21.7
30	0.614	1.137	0.10	9.0
31	0.429	0.763	0.10	13.5
36	1.386	2.423	0.53	21.7
37	1.238	2.513	−0.20	− 7.9
38	1.322	2.376	0.10	4.0
44	0.616	0.866	0.38	43.5
52	0.888	2.238	−0.45	−19.9
53	1.436	2.068	0.83	40.1
55	1.545	2.018	1.10	54.5
62	3.244	5.005	1.06	21.2
70	1.439	2.436	0.47	19.2
85	1.838	2.732	0.71	25.8
89	1.472	2.112	0.64	30.3
99	0.917	1.677	0.17	10.3
104	1.937	4.163	−0.04	− 1.0
105	1.458	2.179	0.55	25.1
112	0.807	1.536	0.09	6.0
119	0.573	1.004	0.07	6.7
120	1.696	4.222	−0.80	−18.9
122	1.071	2.049	0.11	5.5
127	1.261	1.906	0.45	23.7
128	0.373	0.641	0.11	17.4
129	1.393	2.235	0.58	25.8
135	0.357	0.581	0.09	14.9
136	0.996	1.642	0.48	29.0
137	1.019	1.554	0.50	32.3
138	1.072	1.889	0.27	14.5
139	1.382	2.378	−0.41	−17.1
147	1.127	1.776	0.33	18.7
153	1.623	2.735	0.54	19.8
164	0.987	1.659	0.33	20.1
171	0.800	1.805	−0.19	−10.6
175	0.322	0.452	0.20	43.8
Mean	1.138 ± 1.293	1.961 ± 2.236	.262 ± .492	13.4

Table 3. The results of incubations from Peru. Notation as in Table 2. Losses greater than 100% do not indicate a decrease in particulate carbon, but indicate that respiratory carbon loss equaled the observed particulate carbon increase.

Station	P(6)	P(24)	L	%L
8	0.768	1.383	0.31	22.1
9	1.759	3.961	−0.22	− 5.5
10	0.859	1.544	0.34	22.3
11	0.761	2.240	−1.16	−51.6
12	1.092	1.796	0.41	22.7
13	1.559	2.204	0.71	32.3
17	1.585	2.399	0.37	40.5
18	3.524	2.739	3.85	140.5
22	1.455	1.229	1.71	138.3
24	2.660	1.889	3.96	209.6
26	0.581	0.449	0.72	161.1
27	2.526	1.661	3.06	184.4
29	3.390	2.660	4.55	121.1
31	1.234	0.981	1.64	167.6
Mean	1.697 ± .968	1.938 ± .869	1.45 ± 1.75	74.6

An experiment conducted off NW Africa directly measured the decrease in previously fixed carbon in a 12-h dark period. The release of dissolved organic carbon was simultaneously measured (Table 4). The respiration rate can be directly determined by calculating the loss of particulate carbon in the dark period after correcting for the loss of the material released as dissolved organic matter. The calculated respiration rate (the particulate carbon change after the correction for excretion) is 0.6 mg C m^{-3} h^{-1}, or 4.7% of the measured photosynthetic rate.

4. Discussion

The respiratory loss of carbon in NW Africa was small, averaging 13.4%, while the loss in Peru was 74.6% of the carbon fixed in the light. The explanation for the difference between the two regions may be in the species composition of each area's populations. NW Africa was dominated by nonmotile forms throughout the entire study period (the diatoms *Leptocylindrus danicus, L. minimus, Chaetoceros socialis,* and *Thalassiosira partheneia*; T. Cowles, personal communication), whereas the Peruvian region was completely dominated by the motile dinoflagellate *Gymnodinium splendens*. The high respiratory rates measured in Peru may be the result of the high metabolic costs of motility. Moshkina (1961) measured the respiration of *Gymnodinium wulfii* in laboratory experiments and found an average respiratory loss of 57.8%. Thus the energy needed for motility may result in high respiration rates and in the observed decrease in carbon. It is also possible that the nutrient conditions encountered in Peru (i.e. nutrients depleted at the surface but abundant

Table 4. An experiment designed to measure loss of photosynthetic carbon in darkness. Station location was 21° 16.2'N, 17° 04.5'W. Sample depth 5 m; date January 30, 1975 during Reise 36, F. S. *Meteor*. The light period lasted 8 h and the dark period 12 h. Values in parentheses are the hourly rates.

Particulate Carbon After Light Period	Particulate Carbon After Dark Period	Excreted Carbon After Light Period
106.2 mg C m^{-3}	94.9 mg C m^{-3}	4.5 mg C m^{-3}
(13.3 mg C m^{-3} h^{-1})	(−1.0 mg C m^{-3} h^{-1})	(0.6 mg C m^{-3} h^{-1})

Excreted Carbon After Dark Period	Particulate Carbon Change (Corrected for Excretion)
8.2 mg C m^{-3}	7.6 mg C m^{-3}
(0.3 mg C m^{-3} h^{-1})	(0.6 mg C m^{-3} h^{-1})

at depth) maintained the dinoflagellate population in more or less constant physiologically stressed condition which resulted in increased respiratory rates. However, the high loss of photosynthetic carbon observed is probably counterbalanced by the advantages of motility, such as the ability to migrate to depth to obtain nutrients during periods of relaxed or no upwelling.

The data show a large degree of variability, including "negative" respiration values. The large negative values (Stations 13, 37, 52, 120, 139, and 171 in NW Africa and Station 11 in Peru) may have been the result of populations which exhibited strong circadian rhythms, therefore incorporating more carbon in the early or late hours of the day. Such photosynthetic rhythms have been observed with natural populations of phytoplankton (Yentsch and Ryther, 1956). This would cause an increase in the 24-h incubation relative to the 6-h determination and reduce the calculated respiration. The small negative values for some stations probably result from the method's insensitivity. The large respiration rates observed (St. 44, 53, 55, 175) also may have resulted from reduced photosynthesis in the 24-h incubations caused by hazy conditions in the early and late hours. Shipboard measurements indicated that the light which reached the surface during these periods was only 25% of that calculated from Figure 1; therefore, respiration would be slightly overestimated. Also, if long term incubations underestimate productivity as has been suggested by limnological work (Gelin, 1975), then the calculated respiration would be overestimated due to the observed depression in the 24-h incubation.

The loss of carbon measured directly (Table 4) agrees closely with the average calculated respiratory loss in NW Africa, especially since no correction for a dark loss of dissolved organic carbon was made in the calculations. Comparison of Table 4 with Eppley and Sharp's (1976) data indicates that the absolute rate of carbon fixed h^{-1} in the light varied almost 500-fold (13.3 in NW Africa compared to 0.03 in the central Pacific). The absolute rate of dark loss was 0.6 mg C m^{-2} h^{-1} in NW

Africa to 0.0095 mg C m^{-2} h^{-1} in the central Pacific, only a 63-fold difference. Therefore, the relative amount of carbon lost through respiration (neglecting excretion) appears to be of greater importance in oligotrophic regions than in eutrophic areas of the ocean as a result of the larger variations in the absolute rate of photosynthesis.

Photorespiration, the light enhanced oxidation of organic material and release of CO_2, probably occurs to some extent in phytoplankton (Tolbert, 1974). Because a light incubation using ^{14}C measures net uptake, the effects of photorespiration on 6-h incubations and on the calculations of total respiration cannot be determined. Further work and improved techniques are needed to assess accurately the magnitude of this phenomenon and its effect on the carbon budget of phytoplankton populations.

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