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Physiology of carbon photoassimilation by *Oscillatoria thiebautii* in the Caribbean Sea[1]

W. K. W. Li[2], *H. E. Glover, and I. Morris*
Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, Maine 04575

Abstract

Surface populations of *Oscillatoria thiebautii* (Gom.) Geitler in the Caribbean Sea are exposed to photoinhibiting irradiances throughout most of the 12-h light period. Oxygen inhibition of carbon assimilation at high irradiance suggested that photoinhibition was partly due to photorespiration.

The pattern of carbon flow into the major end products of photosynthesis appeared to be the same for a given photosynthetic rate regardless of irradiance level. At one station, enhanced relative rates of protein synthesis were observed at low rates of photosynthesis. At another station, this effect was not observed but the proportion of ^{14}C in polysaccharide was low while that in metabolites was high. On the basis of previous findings, colonies at the second station were interpreted to have been in a nutritionally poor state. The rates at which intracellular macromolecular pools approached saturation seemed to depend on the rate of photosynthesis.

Diel estimates of in situ carbon photoassimilation rates and dark carbon loss rate lead to an estimate of carbon doubling time for surface *Oscillatoria* populations of 18 days.

The planktonic cyanophyte *Oscillatoria* is capable of N_2 fixation and therefore introduces new, combined nitrogen to the euphotic zone of tropical and subtropical seas. Most investigators of *Oscillatoria* have emphasized aspects of nitrogen nutrition in an attempt to assess the importance of N_2 fixation relative to uptake of combined nitrogen (Goering et al. 1966; Mague et al. 1974, 1977; Carpenter and McCarthy 1975). Relatively little is known about the physiology of carbon photoassimilation by *Oscillatoria* although this single genus may account for 60% of the phytoplankton chlorophyll *a* and 20% of the primary productivity in the eastern Caribbean Sea (Carpenter and Price 1977). We present here the results of a study of carbon photoassimilation by *Oscillatoria thiebautii* in the Caribbean Sea.

Our previous work with other phytoplankton suggests that certain physiological and biochemical characteristics of photosynthesis may be useful in identifying the mechanisms of CO_2 fixation and physiological state of algae. We investigated some of these characteristics in *Oscillatoria*; in particular, the pattern of ^{14}C incorporated into the major end products of photosynthesis (cf. Morris et al. 1974; Morris and Skea 1978; Smith and Morris 1980), the activities of ribulose-1,5-bisphosphate carboxylase (RUBPCase) and phosphoenolpyruvate carboxylase (PEPCase) (cf. Morris et al. 1978; Glover and Morris 1979) and also the sensitivity of photosynthesis to oxygen (Beardall and Morris 1975).

We thank A. Smith for helpful discussions concerning the cellular fractionation procedure.

Methods

Samples were collected on cruise 34 of the RV *Endeavor* between 22 March and 16 April 1979 in the eastern Caribbean Sea. *Oscillatoria thiebautii* was collected from surface waters with a 183-μm-mesh net (0.75-m mouth diameter) with nonfiltering cod end. Colonies from 10- and 20-m depths (corresponding to depths receiving about 57 and 32% of incident surface irradiance) were collected with Clarke-Bumpus nets of 64-μm nylon mesh (loaned by E. J. Carpenter).

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[2] Present address: Marine Ecology Laboratory BIO, Dartmouth, Nova Scotia B2Y 4A2.

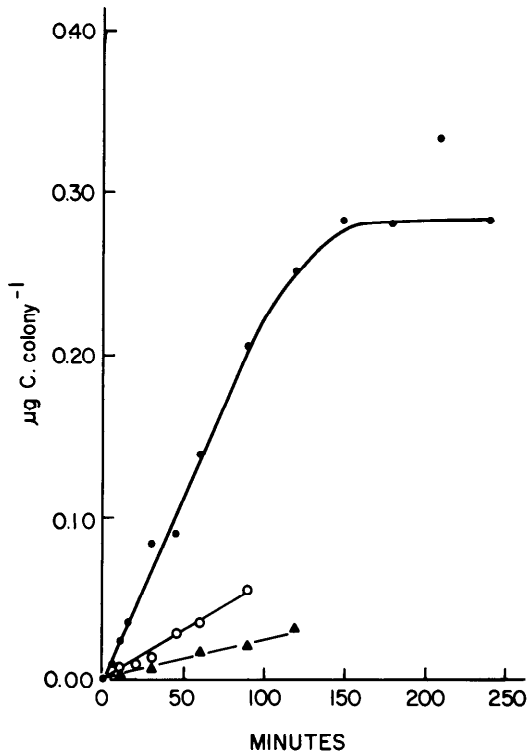

Fig. 1. Time-course of ^{14}C assimilation. *Oscillatoria* collected from surface waters at station 4 (16°08'N,66°50.3'W, 26 March 1979) and incubated at 50 (●), 220 (○), and 2,200 μEinst·m^{-2}·s^{-1} (▲).

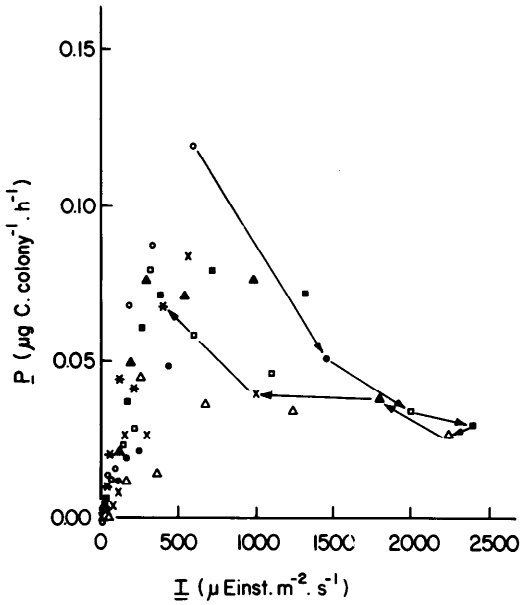

Fig. 2. Rate of ^{14}C assimilation as a function of irradiance. *Oscillatoria* collected from surface waters at station 28 (13 April 1979) and incubated for 1.5 h starting at 0630 (○), 0800 (●), 0930 (□), 1100 (■), 1230 (△), 1400 (▲), 1530 (×), and 1700 (*) hours. Arrows indicate diel progression of ^{14}C assimilation rate of *Oscillatoria* incubated at 100% irradiance.

Colonies consisting of fusiform or radial trichomes were hand picked with Pasteur pipettes. For whole cell carbon assimilation rate experiments, five colonies were placed in a 16- × 100-mm Pyrex screwcapped test tube and filtered surface seawater was added to a final volume of 5 ml. One-tenth milliliter of $NaH^{14}CO_3^-$ solution (50 μCi·ml^{-1}) was added to the tube contents to give a specific activity of 0.5 μCi·μmol^{-1} (assuming HCO_3^- concentration in seawater to be 2 mM). For ^{14}C fractionation experiments, 10 colonies were suspended in 10 ml of filtered seawater and 0.2 ml of $NaH^{14}CO_3^-$ (50 μCi·ml^{-1}) was added to give the same specific activity. For oxygen inhibition experiments, 8 ml of filtered seawater in 20-ml serum bottles were bubbled with N_2, O_2, or air. After bubbling for 5 min, 1 ml of filtered seawater containing five colonies and 1 ml of $NaH^{14}CO_3^-$ solution (5 μCi·ml^{-1}) were added to the bottles.

Incubations were carried out under natural illumination in a deck incubator cooled by flowing surface seawater. Light was attenuated with neutral density filters of plastic screening. Solar irradiance was measured with a quantum meter (LI-170, Lambda Instr. Corp.).

^{14}C assimilation experiments were terminated by filtering entire test tube or serum bottle contents onto Gelman A/E glass-fiber filters. The filters were rinsed thoroughly with filtered seawater and placed in scintillation vials with 10 ml of scintillation fluid (Handifluor, Mallinckrodt). Radioactivity was determined on board ship in a Beckman LS-100C liquid scintillation counter. Quench correction was by the external standards method.

The cellular fractionation procedure was modified from that of Smith and Morris (1980). Filters with colonies were

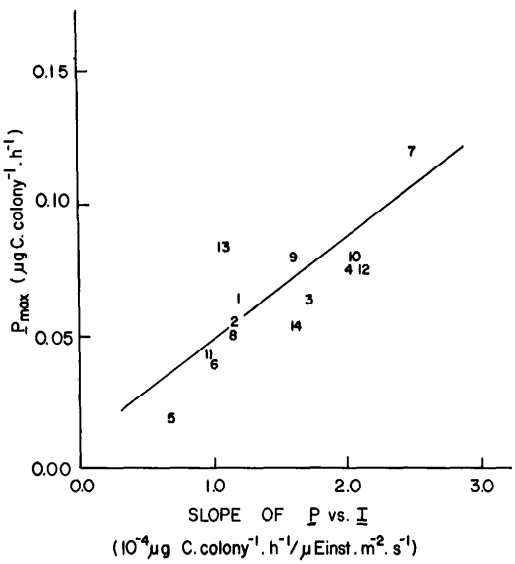

Fig. 3. Relationship between P_{max} and slope of P vs. I curve. Symbols coded as follows: *s/z/t, Oscillatoria* collected at station *s* from depth *z* (m) and incubation started at time *t*. 23/0/1030 (1), 25/0/1130 (2), 26/0/1130 (3), 27/0/1230 (4), 27/10/1230 (5), 27/20/1230 (6), 28/0/0630 (7), 28/0/0800 (8), 28/0/0930 (9), 28/0/1100 (10), 28/0/1230 (11), 28/0/1400 (12), 28/0/1530 (13), 28/0/1700 (14). Station locations: 23 (10°25.0′N,60°10.0′W), 25 (13°28.5′N,61°08.5′W), 26 (14°19.0′N,62°30.0′W), 27 (14°15.9′N,62°15.3′W), and 28 (14°17.4′N,62°16.5′W).

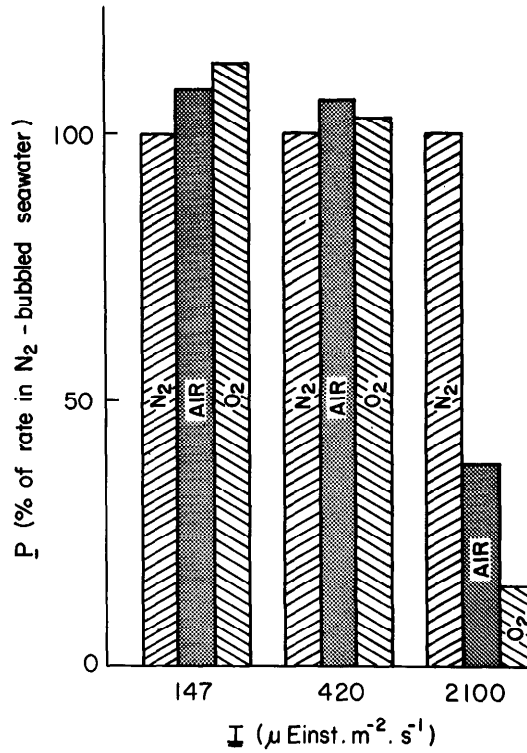

Fig. 4. Effect of oxygen on rate of ^{14}C assimilation (P) at limiting (147 μEinst·m^{-2}·s^{-1}), near optimal (420 μEinst·m^{-2}·s^{-1}), and inhibiting (2,100 μEinst·m^{-2}·s^{-1}) irradiances. Results expressed as percentages of rates measured in N_2-bubbled seawater.

stored frozen in 1.2 ml of distilled water until analysis. After filters were thawed, 1.5 ml of chloroform and 3.0 ml of methanol were added. The suspension was Vortex-mixed vigorously for 1 min, placed at 4°C for 10 min, and then filtered through a glass-fiber filter (Gelman A/E). After the filter was washed with 1.5 ml of chloroform, 1.5 ml of distilled water was added to the combined filtrate. The mixture was Vortex-mixed vigorously for 1 min and then centrifuged at 800–1,000 × *g* for 10 min. The lower chloroform layer was removed with a Pasteur pipette and an aliquot dried in a scintillation vial. Scintillation fluid was added directly to the dry residue and also to an aliquot of the upper methanol-water layer. The filter was resuspended in 4 ml of 5% trichloroacetic acid (TCA) and heated at 95°C for 30 min. The suspension was filtered through another glass-fiber filter (Gelman A/E) with a further 4 ml of 5% TCA for wash and an aliquot of the combined filtrate dried in a scintillation vial. The dry residue was resuspended in 1 ml of distilled water before scintillation fluid was added. TCA-insoluble material collected on the filter was placed directly into a vial and scintillation fluid added. In this procedure, we refer to the chloroform fraction as lipid, the methanol-water fraction as small molecular weight metabolites, the hot TCA-insoluble fraction as protein, and the hot TCA-soluble fraction as polysaccharide (although this fraction also contains nucleic acids).

RUBPCase and PEPCase activities were assayed from samples of 12 colonies each as described by Glover and Morris (1979). Chlorophyll *a* was determined on samples of 100 colonies each by the spec-

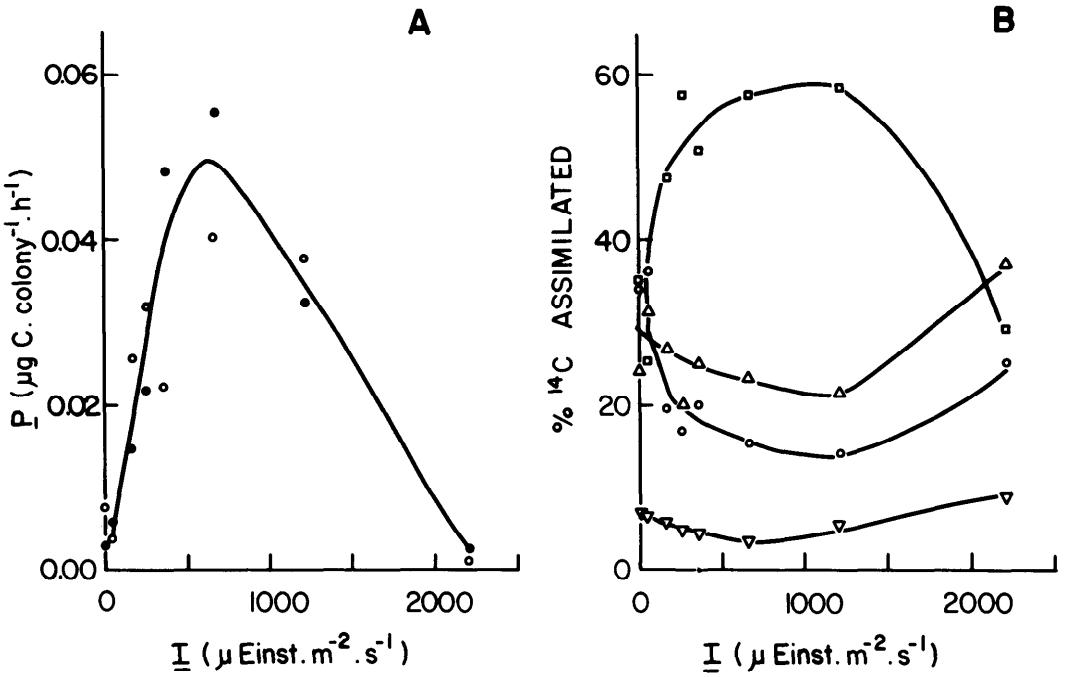

Fig. 5. A. *P* vs. *I* curve for *Oscillatoria* collected from surface waters at station 25 (10 April 1979). Rates obtained from measurements of whole cells (●) and from summation of intracellular pool measurements (○); 2-h incubation. B. Percentages of ^{14}C assimilated into protein (○), polysaccharide (□), lipid (▽), and metabolites (△).

trophotometric method of Strickland and Parsons (1972).

Results

Time-course of carbon assimilation—The rate of $H^{14}CO_3^-$ assimilation by *Oscillatoria* was constant during the first 2 h of incubation but decreased thereafter (Fig. 1); this kinetic pattern was observed in cells incubated over a wide range of irradiances (50–2,200 μEinst·m^{-2}·s^{-1}). Thus, the inhibition by high irradiances did not result from prolonged incubations but could be observed after a time as short as 5 min. In the remaining experiments described here, incubation times of 1.5–2 h were used.

Diel variation of carbon assimilation—Although there was variation in *P* values for any given *I* value, there was no discernible systematic diel trend in *P* vs. *I* curves of populations sampled at different times of day (Fig. 2). A plot of maximum values of *P* (P_{max}) vs. photosynthetic efficiency (slope of *P* vs. *I* curve at low *I* values) (Fig. 3) indicates a positive linear correlation between the two parameters (cf. Harris 1978). Data for colonies collected at other stations and depths are also included. The value of I_k (Talling 1957) estimated from the slope of the least-squares best-fit line was 358 ± 166 μEinst·m^{-2}·s^{-1} (95% confidence limit). Estimated in situ photosynthetic rates for the surface *Oscillatoria* population during the course of the 12-h light period are shown as the trajectory in Fig. 2. The hysteresis in the trajectory from rising to falling light regime is mainly due to the single high rate measured in the 0600–0830-hour incubation. There was no variation in chlorophyll *a* content (0.02 μg Chl *a*·colony^{-1}) over the course of the light day.

Oxygen inhibition of carbon assimilation—Carbon assimilation at an irradiance of 2,100 μEinst·m^{-2}·s^{-1} was severely inhibited by oxygen at atmospheric

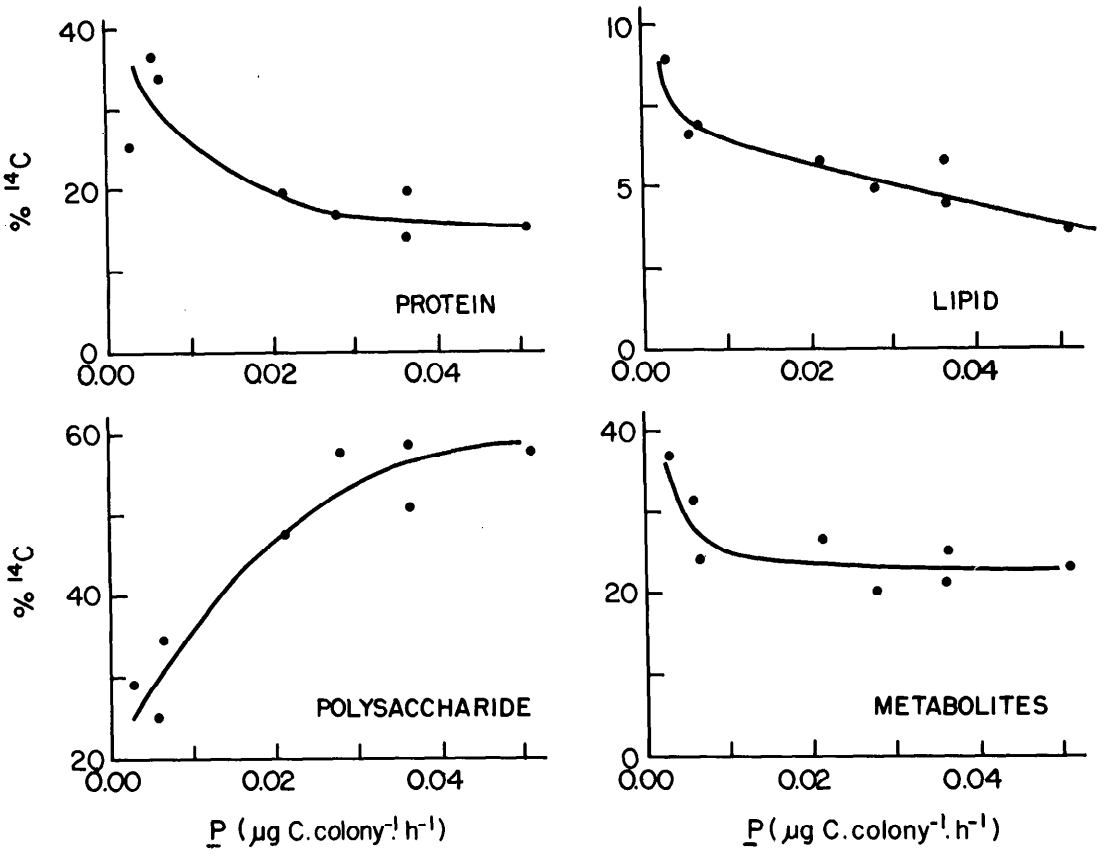

Fig. 6. Percentages of ^{14}C assimilated into intracellular pools as a function of whole cell photosynthetic rate; station 25 *Oscillatoria* incubated 2 h.

concentration (62% inhibition) and 84% O_2 (85% inhibition). There was no evidence of O_2 inhibition at nonphotoinhibiting irradiances (Fig. 4).

Pattern of ^{14}C in macromolecules—Incorporation of $H^{14}CO_3^-$ into whole cells, protein, polysaccharide, lipid, and soluble metabolites was measured after 2-h deck incubations. Duplicate tubes were incubated in parallel. Whole cell assimilation was determined from one of these and macromolecular assimilation from the other. The sum of ^{14}C in fractions averaged 110% of that in whole cells (Fig. 5A).

The percentage of ^{14}C in polysaccharide was high (50–60%) at irradiances near I_k and less at both higher and lower irradiances (Fig. 5B). The patterns of ^{14}C in protein, lipid, and metabolites were the converse of that in polysaccharide; percentages were least at irradiances near I_k and greatest at both higher and lower irradiances. Although the underlying mechanisms leading to decreased photosynthetic rates are different at irradiances lower and higher than I_k, the observed gross pattern of ^{14}C in major end products is similar for a given photosynthetic rate—whether this arises from light limitation or from light inhibition (Fig. 6).

There was some variability in the gross pattern of photosynthesis from one population to the other. For example, the data in Fig. 6 were taken from a station (25) near the eastern end of the St. Lucia channel (13°28.5'N,61°08.5'W, 10 April)

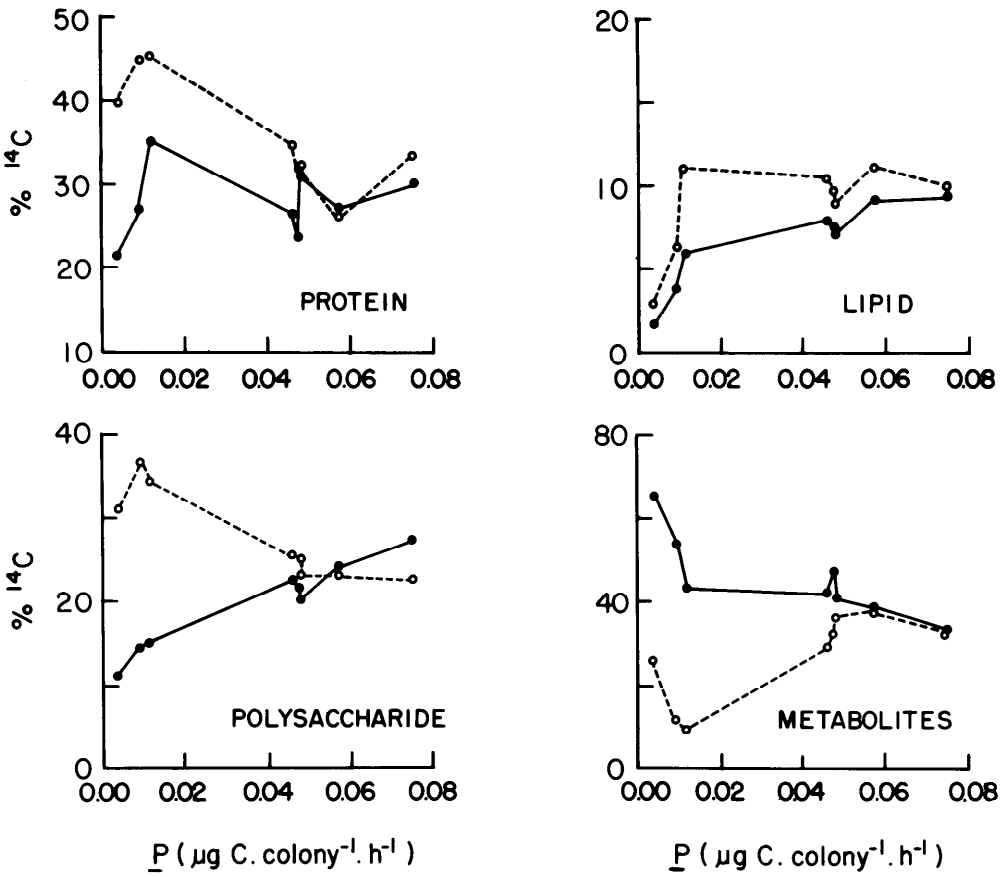

Fig. 7. Percentages of ^{14}C assimilated into intracellular pools as a function of whole cell photosynthetic rate; station 27 *Oscillatoria* incubated 2 h (●) and 4 h (○).

and showed the proportion of ^{14}C incorporated into protein at optimal irradiance levels to be about 17%. At station 27 (14°15.9'N,62°15.3'W, 12 April) due west of station 25, as much as 25% of the ^{14}C was incorporated into protein at optimal irradiances and this was little affected by lower or higher irradiances (Fig. 7).

Given that the total amount of ^{14}C incorporated by *Oscillatoria* did not increase substantially from 2 h to 4 h (Fig. 1), it seemed of interest to ask whether there would be any difference in distribution of ^{14}C among the various intracellular pools between 2 and 4 h. The gross pattern of photosynthesis at 4 h was substantially different from that at 2 h. At low and moderate photosynthetic rates, there was a loss of ^{14}C from the metabolite pool and increases in the protein and polysaccharide pools. There were no net changes in any of these three pools at high photosynthetic rates. The proportion of ^{14}C in lipids increased slightly at all photosynthetic rates although, even at 4 h, its proportion of the total remained relatively small (Fig. 7).

Dark loss of ^{14}C—The rate of ^{14}C dark loss was estimated from the decrease in particulate ^{14}C in a 2-h dark incubation after a 2-h light incubation. This rate varied with the irradiance to which colonies had previously been exposed during the first 2 h (Fig. 8A). Rates of dark loss and photoassimilation were positively correlated ($r = 0.72$; $P < 0.05$).

At high and low irradiances, most of the ^{14}C lost derived from the metabolite

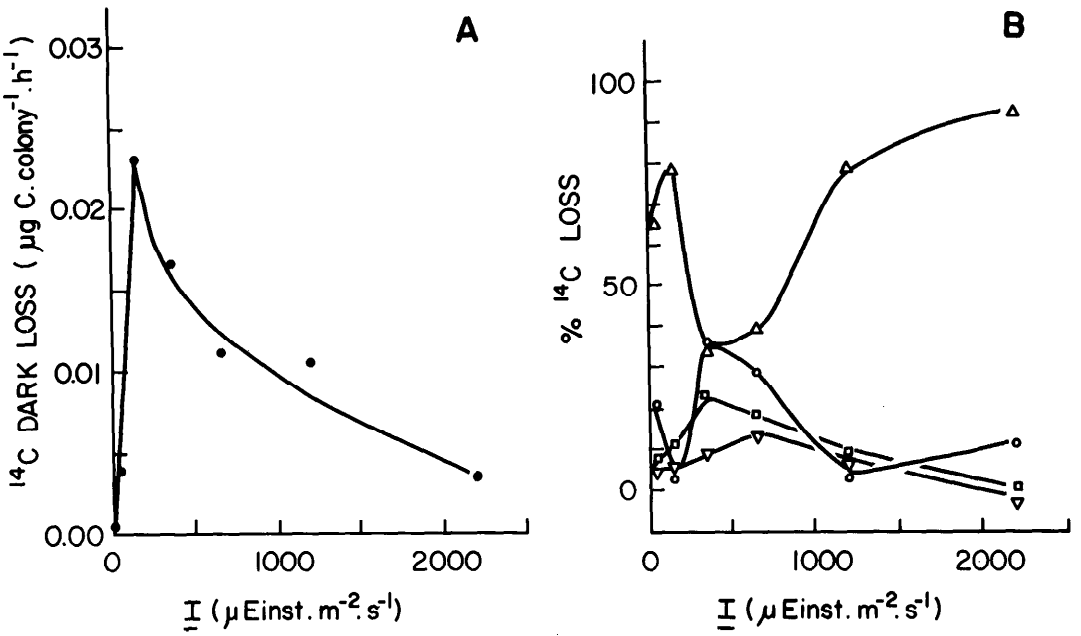

Fig. 8. A. Rate of dark loss of ^{14}C as a function of irradiance during initial 2-h light period. B. Dark loss of ^{14}C from protein (○), polysaccharide (□), lipid (▽), and metabolites (△) expressed as a percentage of total dark ^{14}C loss.

pool. At irradiances near I_k, there were greater contributions from the macromolecular pools—in the order protein > polysaccharide > lipid (Fig. 8B).

Carboxylase activities—The measured combined activities of RUBPCase and PEPCase were sufficient to account for the rate of photosynthesis observed at most stations. For example, from 17 observations, the mean carboxylase activity was 0.078 (extremes: 0.013–0.169) µg C·colony^{-1}·h^{-1} and, from 7 measurements, the mean P_{max} value was 0.074 (extremes: 0.036–0.120) µg C·colony^{-1}·h^{-1}. The apparent extreme variability in carboxylase activity was caused largely by the low values (0.013–0.022) from one station. Activities from the other 13 measurements varied from 0.037 to 0.169 and gave a mean of 0.097 µg C·colony^{-1}·h^{-1}.

From Fig. 9, we see that the mean ratio of RUBPCase : PEPCase was 0.76. Most measurements varied between 0.057 and 1.55, although data from one station (showing low carboxylase activities) varied between 7.57 and 18.29). Although there are too few data to relate the variation in carboxylase activities to environmental or physiological conditions, one observation is of possible interest: the ratio of RUBPCase : PEPCase at station 25 was higher than that at 27 (1.30 and 0.57). This compares with the greater relative synthesis of protein at station 27 (*see above*).

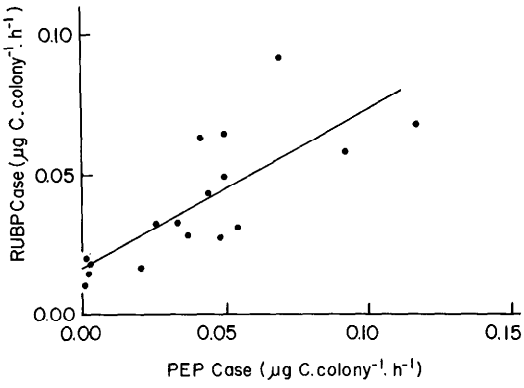

Fig. 9. Correlation of RUBPCase and PEPCase activities. Assays performed on *Oscillatoria* collected at various stations, depths, and times.

Discussion

In our attempts to relate physiological aspects of photosynthesis to growth of phytoplankton populations in the sea, we have investigated the effects of temperature, light, nutrient deficiency, and oxygen on patterns and mechanisms of carbon assimilation (e.g. Morris and Glover 1974; Glover et al. 1975; Beardall and Morris 1976; Morris and Skea 1978; Smith and Morris 1980). Our present results for *Oscillatoria* extend our earlier studies to include physiological stress induced by photoinhibiting irradiances.

Our results (Figs. 2, 5A) confirm the observations of McCarthy and Carpenter (1979) that optimum photosynthesis in *O. thiebautii* does not extend over a range of irradiances and that there is severe photoinhibition at sea surface irradiances. Harris and Piccinin (1977) considered photoinhibition to be most likely the result of two processes: photorespiration and photochemical inhibition of electron transport. Excretion of dissolved organic ^{14}C did not seem to be important in their experiments.

The inhibition of photosynthesis by O_2 was first observed by Warburg (1920) and it is now generally thought that photorespiration is responsible for this effect (Gibbs 1969). Photorespiration is defined as a light-dependent O_2 uptake and CO_2 release occurring during photosynthesis. Whatever the reactions involving light-dependent O_2 uptake, be they those of glycolate synthesis and metabolism (Tolbert 1974) or that involving photosystem I in a Mehler-type process leading to peroxide formation (Harris 1978), there is a resultant decrease in net carbon dioxide fixation. Tolbert (1974) emphasized that photorespiration is favored under conditions of high irradiance, high temperature, and high O_2 concentration; these are the conditions prevailing at the surface of low-latitude seas. At midday sea surface irradiance, *Oscillatoria* photosynthesis was inhibited by the atmospheric O_2 concentration and even more inhibited as the O_2 concentration was increased (Fig. 4). Zelitch (1971) summarized data that show photosynthetic inhibition at atmospheric O_2 levels to be associated with C-3 metabolism. In this respect, *O. thiebautii* resembles *Dunaliella tertiolecta* and *Gonyaulax* sp. (Beardall et al. 1976).

The photochemical inhibition of photosystems I and II leads to a decrease in gross photosynthetic rate (Harris 1978). This should be reflected in a decrease in the initial slope of the P vs. I curve in photoinhibited cells and also a decrease in P_{max}. Our results show that this is indeed so for *Oscillatoria* (Fig. 3). The fact that we obtained a single value of I_k for spatially and temporally distinct populations suggests that the observed variations in photosynthetic rates are due to this common mechanism which affects the light and dark reactions equally. Harris (1978) described situations in which diatoms, green algae, and blue-green algae exhibit similar responses.

Harris and Piccinin (1977) observed that at photoinhibiting irradiances there was an initial induction period during which the rate of photosynthesis was high and after which the rate declined. Our time-course experiments with *Oscillatoria* showed no evidence of an initial transient increase in carbon assimilation rate (Fig. 1). Although the colonies were not darkened before we began the time-course, they were prepared for the experiment under subdued fluorescent light in the laboratory.

Surface populations of *Oscillatoria* are exposed to photoinhibiting irradiances for almost the entire 12-h light period of the day. In the diel experiment (Fig. 2), only colonies collected at dawn (0600 hours) had not been previously exposed to high irradiances. It is significant that these cells had the highest rate of photosynthesis. Under the falling light regime of late afternoon, the effects of photoinhibition were apparently not completely reversed; this produces the asymmetric P vs. I curve (Fig. 2) that has been reported by others (Harris and Lott 1973). The recovery from photochemical photoinhibition takes several hours (Harris and Piccinin 1977).

Carbon doubling times can be calculated for surface populations by using the estimated in situ diel carbon assimilation rates (Fig. 2), dark ^{14}C loss rate (Fig. 8), and McCarthy and Carpenter's (1979) carbon content value of 11.3 μg C·colony^{-1}. Net carbon assimilated per colony during the 12-h light period (0.606 μg C·colony^{-1}) was calculated by summing the amount of carbon assimilated over eight successive 1.5-h incubations from dawn to dusk (values linked by arrows in Fig. 2). A night loss rate of 0.015 μg C·colony^{-1} is assumed. This is the value *Oscillatoria* would have (Fig. 8A) during a dusk incubation (1700–1830 hours) on the basis of a mean irradiance of 400 μEinst·m^{-2}·s^{-1} during this period. Total carbon loss for the 12-h night would then be 0.180 μg C·colony^{-1}. Net carbon gain in 24 h is 0.426 μg C·colony^{-1}. Carbon doubling time is thus calculated to be 18 days. This is a short time compared to many estimates, based on either C or N (Goering et al. 1966; Carpenter and McCarthy 1975; McCarthy and Carpenter 1979) but is similar to an estimate of 15 days based on both N and C from ATP values (Mague et al. 1977).

Except in the case of phytoplankton from very cold waters (Smith and Morris 1980), our previous work indicates that the proportion of carbon assimilated into protein is increased in cells subject to stresses of low irradiance, low temperature, and nutrient limitation (Morris et al. 1974; Glover 1977; Morris and Skea 1978). The increased relative rate of protein synthesis is generally accompanied by a reduced proportion of carbon incorporated into polysaccharide. This pattern is also shown by *Oscillatoria* during active photosynthesis, i.e. in 2-h incubations (Fig. 5B). In terms of the flow of carbon into major end products, the stress of photoinhibition resembles that of low light (Fig. 6).

The photosynthetic pattern of *Oscillatoria* collected at station 27 differed from that described above for colonies from station 25. The major differences after 2-h incubations were that there was no enhanced relative rate of protein synthesis at low photosynthetic rates and there were low percentages of carbon in polysaccharide (11–27%), high percentages of carbon in the metabolite pool (33–66%), and a depressed relative rate of lipid synthesis at low photosynthetic rates. Morris and Skea (1978) found that summer populations from water containing low concentrations of nutrient did not show an enhanced relative rate of protein synthesis at reduced irradiances as did populations from nutrient-rich waters. Glover (1977) found that for *Isochrysis galbana* and *Phaeodactylum tricornutum* grown in nutrient-limited chemostats, the percentage of carbon incorporated in polysaccharide was low (12–45%) while that in the metabolite pool was high (29–70%). It therefore seems that the *Oscillatoria* at station 27 was in a nutritionally poor state.

Since fixation of both N_2 and CO_2 demands energy and reductant generated by light processes, it is possible that the decreased rate of carbon assimilation after 2 h (Fig. 1) is due to an increased rate of N_2 fixation. However this does not seem to be the case since the time-course for N_2 fixation by *O. thiebautii* (McCarthy and Carpenter 1979) is almost identical to that for CO_2 fixation.

Despite the lack of significant net carbon incorporation from 2 to 4 h, there was a shift of ^{14}C from the metabolite pool to macromolecules in cells that photosynthesized at low and moderate rates (Fig. 7). In other words, these cells initially accumulated ^{14}C in their metabolite pool in excess of steady state level. Cells that photosynthesized at high rates had apparently achieved steady state labeling of their pools by 2 h (Fig. 7). Saturation of intracellular pools at rates that depend on the photosynthetic rate further complicates the assessment of cellular carbon loss by ^{14}C techniques. It would be incorrect to attribute cellular carbon loss at low photosynthetic rates primarily to metabolite losses (Fig. 8B) if there had been significant losses of unlabeled macromolecules. As shown by the ^{14}C methodology used here, appreciable contribution to dark carbon loss by macromolecules oc-

curred only at irradiances that allowed steady state labeling by 2 h (Fig. 8B).

In the laboratory unialgal populations reported by Glover and Morris (1979), high rates of photosynthesis were associated with high RUBPCase : PEPCase values. Most of the measurements reported here show PEPCase activity to be greater than that of RUBPCase. We are not certain that this observation can be compared with that earlier work. If such a comparison were valid, the enzyme ratio would suggest that most populations of *Oscillatoria* are not healthy.

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