TO THE GRADUATE SCHOOL:

The members of the Committee approve the thesis of Thomas C. Hohman presented November 27, 1972.

James A Marsh Jr
J. A. Marsh, Jr., Chairman

Stuart F. Hayes
S. Hays

Neil C. Cheney
D. P. Cheney

Roy T. Tsuda
R. T. Tsuda

ACCEPTED:

James A. McDonough
J. A. McDonough
Dean of the Graduate School

AN ABSTRACT OF THE THESIS OF Thomas C. Hohman for the Master of Science in Biology presented November 27, 1972.

Title: Diurnal Periodicity in the Photosynthetic Activity of *Caulerpa racemosa* (Forsskal) J. Agardh

Approved: James A. Marsh, Jr.
J. A. Marsh, Jr., Chairman, Thesis Committee

Oxygen evolution of the green alga *Caulerpa racemosa* was measured at two-hour intervals for 24- and 48-hours under constant temperature and light conditions. Plants exhibited a unimodal periodicity in photosynthetic activity similar to that previously reported in phytoplankton. Holding the plants under high-light intensity erased the photosynthetic rhythm.

DIURNAL PERIODICITY IN THE PHOTOSYNTHETIC ACTIVITY OF CAULERPA RACEMOSA (FORSSKAL) J. AGARDH

by

THOMAS C. HOHMAN

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE
in
BIOLOGY

University of Guam

1972

TABLE OF CONTENTS

	PAGE
LIST OF FIGURES	ii
INTRODUCTION	1
METHODS AND MATERIALS	5
RESULTS AND DISCUSSION	9
LITERATURE CITED	42

LIST OF FIGURES

FIGURE		PAGE
1.	Caulerpa racemosa growing in the field	20
2.	Control chamber	21
3.	Net productivity curve of Caulerpa collected 12 hours before initiation of the experiment	22
4.	Productivity and respiration curves of Caulerpa collected 12 hours before initiation of the experiment .	24
5.	Productivity and respiration curves of Caulerpa collected 60 hours before initiation of the experiment and held in outdoor aquaria	26
6.	Productivity and respiration curves of Caulerpa collected 60 hours before initiation of the experiment and held 12 hours in outdoor aquaria and 48 hours in the laboratory at light intensity of 3000 ft-c. . . .	28
7.	Productivity and respiration curves of Caulerpa collected 60 hours before initiation of the experiment and held 12 hours in outdoor aquaria and 48 hours in the laboratory at light intensity of 1500 ft-c. . . .	30
8.	Productivity and respiration curves of freshly collected plants and plants held for 12 hours before initiation of the experiment which began at 1200.	32
9.	Productivity and respiration curves of freshly collected plants and plants held for 12 hours before initiation of the experiment which began at 1200.	34
10.	Productivity and respiration curves of freshly collected plants and plants held for 12 hours before initiation of the experiments which began at 1800	36
11.	Productivity and respiration curves of freshly collected plants and plants held for 12 hours before initiation of the experiments which began at 1800	38
12.	Productivity and respiration curves of Caulerpa collected 12 hours before initiation of the experiment. Measurements were made at 1500 ft-c	40

INTRODUCTION

Experiments measuring productivity of aquatic plants usually determine changes in pH, radioactive carbon dioxide assimilation, or oxygen production for short periods of time. These short-term values are then projected to give daily or other long-term values (Maguire and Neill 1971). However, extrapolating a short-term productivity value to give a daily or longer-term value does not take periodicity of productivity into consideration (Doty et al. 1967).

A diurnal difference in productivity of aquatic plants was first observed in a population of marine phytoplankton by Doty and Oguri (1957). This phenomenon was later confirmed by other investigators in populations of both fresh water and marine phytoplankton (Yentsch and Ryther 1957; Shimada 1958; Lorenzen 1963). When productivity was measured under constant light intensity and temperature, the highest point in productivity always occurred at midday, and the lowest point in productivity always occurred during the night hours. Belikov and Motorina (1961) reported a similar periodicity in productivity of the stringless Saks bean. The existence of a similar diurnal productivity rhythm in these two extremely different groups of plants suggests its possible existence in all plants.

Several investigators have attempted to determine the presence of a diurnal periodicity in productivity in macroscopic algae. Conflicting data have resulted from these studies, however. Sweeney and Haxo (1961) in their study of Acetabularia major detected a

diurnal difference in oxygen production in plants measured under a light intensity of 1500 foot candles at 1200 and 2400 hours, and subjected to either constant light or alternating light and dark. The higher point in productivity was consistently at 1200.

There are several hypotheses which can be proposed to explain the differences in the activity of the plants at these different hours. One hypothesis is that the change in the photosynthetic rate is a result of a change in the respiration rate. It is possible that the photosynthetic rate at 2400 is lower than the rate at 1200 because the respiration rate at 2400 is greater than the rate at 1200. Possibly the gross productivity, which is the sum of net productivity and respiration, is constant throughout the day, but its component parts have synchronized alternating rapid and slow rates. From the study by Sweeney and Haxo, it is unknown if the respiration rate at 2400 is different from that at 1200 since no respiration measurements were made. Another hypothesis which might explain the difference in productivity rates between the hours of 1200 and 2400 is that rapid rates in productivity might alternate with slower ones. Since only two measurements were made in a 24 hour period, the productivity is not proved to be diurnal.

Blinks and Givan (1961) attempted to look for the existence of a rhythm in productivity by monitoring oxygen production in 12 species of temperate marine algae. The productivity measurements were all made during the daylight hours at a light intensity of 900 ft-c. The investigators reported that they were unable to find a diurnal

periodicity in any of the 12 species. Several possible explanations can be proposed to account for their results. In the studies which have reported a productivity rhythm, the rhythm was in photosynthetic capacity. The photosynthetic capacity of a plant is the rate of photosynthesis which takes place under conditions in which the biochemical apparatus of the plants is the limiting factor. To measure the photosynthetic capacity, the light intensity must be above the saturation point of the plants, which is thought to be 1500 ft-c. Since the light intensity in this experiment was well below 1500 ft-c, the photosynthetic capacity was not measured. In this study by Blinks and Givan, where light is the limiting factor for photosynthesis, productivity might be expected to be constant throughout the day. Only when the biochemical apparatus is the limiting factor in photosynthesis should a rhythm in productivity be expected. In the studies which have reported a diurnal rhythm in productivity, the low point in productivity occurred during the night hours, and the peak occurred during midday. By the selection of their sampling times, Blinks and Givan may have failed to observe a productivity rhythm. The times selected for observations may have been on opposite sides of a peak or low point in productivity, thus depicting similar rates.

Buggeln (1965) reported a diurnal periodicity in oxygen production of the brown alga Padina crassa. In this study the plants were incubated for 60 minutes at a light intensity of 1200 ft-c. Measurements made at one-hour intervals demonstrate a peak in productivity at midday and a low point in productivity during the middle of the

dark period. Respiration measurements were made in this study. Three sets of plants were used on an alternating basis to make the observations. Two plants from each set were used for the oxygen production observations, and the third plant from each set was used for the respiration observations. In order to use this technique, it is necessary to assume that all of the plants have the same activity rate. This assumption has not been shown to be correct by the investigator.

An interesting phenomenon reported in the periodicity studies of several investigators is the inhibition of the rhythm by exposing the plants to a constant light intensity. This reaction has been reported by Warren and Wilkins (1961) in the rhythm of radioactive carbon dioxide assimilation of excised leaves of Bryophyllum fedschenkoi, which is inhibited by constant exposure to a light intensity of about 300 ft-c. This same phenomenon was also reported (Hastings, Astrachan, and Sweeney 1961) in the dinoflagellate Gonyaulax when exposed to a constant light intensity of 1500 ft-c. This phenomenon has not been reported in an intact macroscopis alga to the knowledge of the author.

The diurnal periodicity in the photosynthetic capacity of Caulerpa racemosa is examined in this study. Caulerpa racemosa (Figure 1) is a green siphonaceous alga which is found in almost all tropical or subtropical waters (Dawson 1966). This plant was selected for the study because of its abundance on the reefs of Guam, the ease with which it could be used in the techniques of the experiments, and background information provided by previous studies (Peterson 1971).

METHODS AND MATERIALS

The photosynthetic capacity of Caulerpa racemosa was measured by monitoring oxygen exchange at two-hour intervals for 24 and 48 hour periods. The productivity of the plants is most frequently given in terms of gross productivity, which is the sum of net productivity (oxygen production of plants incubated in clear bottles) and respiration (oxygen uptake of plants incubated in darkened bottles). Dissolved oxygen was measured using the azide modification of the Winkler technique (APHA 1965).

In order to test for a diurnal periodicity in photosynthetic capacity, it was necessary to monitor productivity under controlled conditions for at least 24 hours. In this work, temperature and light intensity were controlled in a chamber which was supplied with flowing sea water and banks of fluorescent and incandescent lights. Each plant was exposed to two banks of fluorescent lights and one bank of incandescent lights. Except when noted otherwise the light intensity, as measured by a GE type 213 photometer, was 3000 ft-c; hence, photosynthetic capacity was the variable being examined. By regulating the rate of flow of sea water through the chamber, it was possible to limit the temperature rise in the water bath to an increase of one degree Celsius from ambient temperature (29^{o}C) during the incubation period.

The control chamber was also equipped with an agitating apparatus which supplied constant motion to the incubation bottles. Preliminary

work confirmed that plants subjected to constant motion exhibited a greater rate of productivity than plants with no motion.

All specimens of Caulerpa racemosa used in this study were collected from the same field population during the months of February through April, 1972. This population was growing on coral heads exposed to full sunlight in 1.5 meters of water at high tide, ten meters from shore at San Vitores Beach, Guam. Immediately after collection, the plants were taken to the laboratory where all visible epiphytes were removed. Some specimens were held before the initiation of the experiment in outdoor aquaria supplied with fresh flowing sea water and were exposed to the natural photoperiod and light intensity. The holding duration ranged from 12 to 48 hours, depending upon the particular experiment. Other samples were used for experimentation immediately after collection.

Upon initiation of an experiment, specimens measuring between 20 and 25 centimeters from the apical end to the severed end, and therefore of comparable age, were placed in 435-ml blackened incubation bottles (dark bottles) with rubber stoppers. Five replicate blackened bottles and a control (bottle with no plant) were filled with membrane filtered sea water collected from behind the surge at high tide. Vacuum filtering sea water at a pressure of 8 mm of mercury decreased the oxygen concentration by 20%. When the blackened incubation bottles and control were filled, a water sample was also taken for immediate oxygen determination. The five dark bottles and control were then placed in the incubation chamber for 30 minutes.

Prior experiments with incubation periods of 15, 30, 45, and 60 minutes showed that a 30 minute incubation was sufficient to observe a noticeable change in oxygen concentration without demonstrating a bottle effect. Upon completion of the incubation period, the water was siphoned without bubbling from the incubation bottles into 300-ml BOD bottles for oxygen determination. The plants were then immediately transferred to a set of clear incubation bottles (light bottles) and the process was repeated. At the completion of each light and dark run, the clear incubation bottles still containing the plants were filled with sea water and stored under a low light intensity of 400 ft-c until the experiment was repeated an hour later. During each run all of the plants were exposed to three different light intensities: 0 ft-c during the respiration measurements, 3000 ft-c during the net productivity measurements, and 400 ft-c during the holding time between runs. The light intensities of 0 ft-c and 3000 ft-c both lasted 30 minutes, while the light intensity of 400 ft-c lasted 60 minutes.

Upon termination of each complete experiment, the plants were placed in pre-weighed containers and stored in a drying oven at 105°C. After a drying period of 14 hours, the dry weights of the plants were determined to the nearest .001 gram. These values were used to correct differences in biomass of each plant; thus, final productivity calculations were in terms of milligrams of oxygen per gram of dry weight per hour. Preliminary results indicated that 14 hours was sufficient time for the samples to reach a constant weight. The final productivity calculations were plotted on graphs versus time. The net

productivity measurements, which began on the even hours of the experiments and continued for 30 minutes were plotted on the graphs at the even hours. The respiration measurements, which began 30 minutes before the even hours of the experiments, were also plotted on the graphs at the even hours.

To reduce experimental uncertainty, replicate titrations were performed on each of the water samples. Fewer than 20% of the replicate titrations showed greater than a 3% variation in the amount of dissolved oxygen. The variation was never greater than 5%. When the concentration of dissolved oxygen in the control bottles after incubation was compared with the concentration of dissolved oxygen in the initial samples, only 10% of the bottles were found to have any variation. This variation was never greater than 7% and did not show a consistent increase or decrease.

RESULTS AND DISCUSSION

In the initial experiment net productivity was measured in plants which had been held overnight in outdoor aquaria for 12 hours prior to the initiation of the experiment. The experiment began at 0800 and continued for 48 hours. During the first 24 hours of the experiment, the highest point in productivity (3.0 milligrams of dissolved oxygen per gram dry weight per hour) occurred at 1400; the lowest point in productivity (0.9 mg O_2/g/hr) occurred at 0400. During the second 24 hours of the experiment, there was an increase in productivity from 0800 to 1400. The productivity, which was 3.4 mg O_2/g/hr at 1400, showed little variation for the remainder of the experiment. The data in Figure 3 show that productivity varies with time. There was a diurnal rhythm in oxygen production during the first day of the experiment, but no rhythm was evident during the second day. The change in the rhythm from day one to day two of the experiment might be explained by several hypotheses. One hypothesis is that the change in net productivity rhythm was a result of a change in the respiration rhythm. The second experiment was designed to test this hypothesis.

Plants for the second experiment (Figure 4) were again collected and held in outdoor aquaria for 12 hours before the initiation of the experiment. Respiration and net productivity measurements began at 0730 and 0800, respectively, and continued for 48 hours. During the first 24 hours of the experiment, the highest point in productivity (3.4 mg O_2/g/hr) again occurred at 1400, and the lowest point

(1.7 mg O_2/g/hr) again occurred at 0400. During the second 24 hours of the experiment, productivity increased from 0800 until 1000 with little variation from this productivity level (3.6 mg O_2/g/hr) for the remainder of the experiment. Likewise, the highest point in respiration (1.2 mg O_2/g/hr) occurred at 1400 on the first day, and the lowest point (0.4 mg O_2/g/hr) occurred at 0400. On the second day, respiration increased from 0800 to 1000. Respiration for the remainder of the experiment varied only slightly from the 1000 value of 1.2 mg O_2/g/hr. Thus, a diurnal rhythm in respiration was evident for the first day but was erased during the second day.

While there was a change in the respiration rhythm from day one to day two of the experiment, this change in respiration does not account for the change in net productivity. The third curve of this experiment illustrates that gross productivity of the plants is not constant throughout the day, but parallels the rhythms in net productivity and respiration. In both experiments, a diurnal periodicity is seen during the first day of the experiment, but not for the second day. One explanation for this observation is that plants under conditions of stress, i.e., held under laboratory conditions, demonstrate altered photosynthetic and respiration rates. The plant rhythms disappear after 42 hours.

In order to test this hypothesis, the plants of the third experiment (Figure 5) were collected 60 hours before the experiment began and were held in the ourdoor aquaria. Both respiration and net productivity measurements began at 0730 and 0800, respectively, and continued for 48 hours. During the first 24 hours of the experiment, the highest point

in net productivity (3.0 mg O_2/g/hr) occurred at 1400; the lowest point (0.9 mg O_2/g/hr) occurred at 0400. On the second day of the experiment, there was an increase in net productivity until 1200. There was little variation from this 1200 value of 3.4 mg O_2/g/hr for the remainder of the experiment. The respiration curve and the gross productivity curve paralleled the net productivity curve. If the results of the second and third experiments are compared, it can be seen that regardless of the length of the holding period, the change in the activity rates always occurs after the first 24 hours of the experiment. This observation suggests that it is not the stress of holding the plants which causes the change in the activity rates, but some other stress factor. The plants of the three experiments had been exposed to a light intensity of 3000 ft-c during the last 48 hours of each experiment. The change in the plant rhythms from day one to day two of the experiments might be a response to the stress condition imposed by a constant light intensity.

To test this hypothesis, the plants of the fourth experiment (Figure 6) were collected 60 hours before the experiment began and were held for 12 hours overnight in outdoor aquaria, followed by 48 hours in the laboratory under a constant light intensity of 3000 ft-c. Respiration and net productivity measurements began at 0730 and 0800, respectively, and continued for 26 hours. The initial net productivity value for the first day of the experiment was 1.35 mg O_2/g/hr. There was little variation from this productivity value for the duration of the experiment. The respiration rhythm, which paralleled the net productivity rhythm, also failed to exhibit a diurnal periodicity in

activity. The results of this experiment indicate that the diurnal rhythms in productivity and respiration have been erased by the constant exposure of the plants to the light intensity of 3000 ft-c for 48 hours.

The activity rhythms of the plants in experiments one through four were all erased when the plants were exposed to a constant light intensity of 3000 ft-c for at least 42 hours. The change in the rhythms, however, might be a result of the light intensity to which the plants were exposed, or it could could be a result of the duration of the exposure. To determine which of these variables influenced the changes in the activity rhythms of the plants, the plants of the fifth experiment (Figure 7) were collected 60 hours before the beginning of the experiment and were held for 12 hours overnight in outdoor aquaria, followed by holding for 48 hours in the laboratory under a constant light intensity of 1500 ft-c. Measurements began at 0730 and continued for 28 hours. During the first day of the experiment, the highest point in net productivity (2.0 mg O_2/g/hr) occurred at 1400; the lowest point (0.7 mg O_2/g/hr) occurred at 0400. There was a diurnal rhythm in net productivity and respiration during the first day of the experiment. Exposing the plants to a constant light intensity of 1500 ft-c did not erase the periodicity. Apparently periodicity is erased only when the plants are subjected to a constant light intensity higher than 1500 ft-c.

When the results of the first five experiments are compared, it can be seen that rhythms in respiration and productivity can be erased

by exposure to a constant light intensity of 3000 ft-c, but not 1500 ft-c. These experiments, however, have not shown whether the plant rhythms are a naturally occurring phenomenon or whether they are induced in the plants by the techniques of the experiments.

The plant rhythms in four of the experiments are similar. If the plant rhythms are induced by the techniques of the experiments, then the similarities in the rhythms of the experiments might be explained as a result of the similarities in the techniques. One similarity in the experimental techniques was that all of the plants used in the experiments were collected at approximately the same time of day. Another similarity was that all of the experiments began at the same time of day. The similarity in plant rhythms could be a result of a response of the plants initiated by either collection time or initiation time of the experiments. If the plant rhythms are dependent upon the time of collection or the initiation time of the experiments, then the highest and lowest points in activity should be independent of the time of day, but dependent upon the length of time since the experiment began or the length of time since the plants were collected.

Experiments six through nine were designed to measure the productivity differences between freshly collected algae and algae which had been held for 12 hours overnight in outdoor aquaria. If the plant rhythms are induced by collection time, then the rhythms of freshly collected plants should be 12 hours out of phase from the rhythms of plants which had been held for 12 hours before the initiation of the experiment.

Experiments six (Figure 8) and seven (Figure 9) were conducted under identical laboratory conditions but on different dates. In both experiments, three samples of freshly collected plants and three samples of plants held for 12 hours overnight were used for the respiration and net productivity measurements, which began at 1130 and 1200, respectively, and continued for 24 hours. Experiments eight (Figure 10) and nine (Figure 11) were also conducted under identical laboratory conditions, but on different dates. Again three samples of freshly collected plants and three samples of plants held for 12 hours overnight were used for the respiration and net productivity measurements, which began at 1730 and 1800, respectively, and continued for 24 hours. If the plant rhythms are initiated at the start of each of the experiments, then the plant rhythms of experiments six and seven would be expected to be six hours out of phase with the plant rhythms of experiments eight and nine.

In all four of the experiments, the productivity and respiration measurements of freshly collected algae were averaged together with the productivity and respiration measurements of plants which had been held for 12 hours before the initiation of the experiment. Plus and minus one standard deviation is given for the mean of the six separate plants at each data point on the graphs. If the standard deviations from Figures 8-11 are compared with the standard deviations of the previous figures, it can be seen that the variation in productivity and respiration between freshly collected plants and plants held for 12 hours before the initiation of the experiment in experiments six

through nine is no greater than the variation in productivity and respiration of the plants in the previous experiments. From this observation it can be seen that there is no measurable difference in either net productivity or respiration between freshly collected plants and plants held for 12 hours.

In all four of the experiments, the highest point in net productivity occurred at 1400 and the lowest point at 0400. The respiration curve paralleled the net productivity curve in all of the experiments. The peaks in respiration occurred at 1400, and the low points occurred at 0400. Regardless of when the plants were collected or when the experiments began, the rhythms were the same. The results of these experiments indicate that the plant rhythms are dependent upon the time of day.

Rhythms in respiration and productivity were not observed in any of the plants during the second 24 hours of any of the experiments. Experiment four demonstrated that the periodicity could be erased by exposure to a light intensity of 3000 ft-c. Another hypothesis could also explain the lack of rhythm during the second day of the experiments. Some investigators state that plant rhythms are exogenous--that is, caused by external stimuli such as tides (Bruchner 1932). According to this theory, plant rhythms disappear when the plants are isolated from the stimuli. The rhythms of the plants used in this project disappear after the first 24 hours of the experiment, possibly because the plants have been isolated from the external stimuli which initiated the rhythm. Experiment ten was designed to test this hypothesis.

The plants of experiment ten (Figure 12) were collected 12 hours before the initiation of the experiment and were held overnight in outdoor aquaria. Both respiration and net productivity measurements, beginning at 0730 and 0800, respectively, and continuing for 48 hours, were made under a constant light intensity of 1500 ft-c. During the first 24 hours of the experiment, the highest point in productivity (4.1 mg O_2/g/hr) occurred at 1400, and the lowest point (1.8 mg O_2/g/hr) occurred at 0400. During the second 24 hours of the experiment, the highest point in productivity (4.2 mg O_2/g/hr) occurred at 1400, and the lowest point (1.8 mg O_2/g/hr) again occurred at 0400. In this experiment a diurnal periodicity is evident in both respiration and net productivity for both days of the experiment. Apparently the plant rhythms in all of the previous experiments were erased by the exposure to the constant light intensity of 3000 ft-c. The disappearance of the rhythm in these experiments cannot be explained by the concept of exogenous rhythms.

If the results of the ten experiments of this study are compared, it can be seen that the green alga Caulerpa racemosa demonstrates a diurnal periodicity in oxygen production when the plants are incubated under a constant light intensity of 1500 ft-c. The experiments also show that this periodicity in oxygen evolution is independent of the tested experimental techniques, but is dependent upon the time of day. Neither holding plants under the natural photoperiod and illumination for periods lasting from 0 to 48 hours nor holding the plants under a constant light intensity of 1500 ft-c alters the productivity rhythm.

Holding the plants under a constant light intensity of 3000 ft-c, however, does erase the productivity rhythm.

In all of the experiments, the respiration curve parallels the net productivity curve, with the highest point in net productivity and respiration of the first day always occurring at 1400. The lowest point in net productivity and respiration occurs at 0400 in all of the experiments. Gross productivity, which is the sum of respiration and net productivity, has the same curve as its component parts. While the plant rhythms of all of the experiments were similar, the amplitudes were not always the same. The high points in net productivity in the experiments ranged from 1.2 mg O_2/g/hr to 4.1 mg O_2/g/hr. Some investigators have interpreted similar data as evidence for a lunar periodicity in plant activity (Brown 1962). While this explanation is possible, it does not seem probable, since the variation in amplitude of the productivity curves did not follow a lunar pattern. The differences in the amplitudes of the productivity curves can probably best be explained as being a result of individual differences among the plants.

The results of this study are similar to the results of several other studies in that diurnal changes were observed (Sweeney 1961; Buggeln 1965). One difference between the present study and the studies previously mentioned is that the peaks and low points in productivity do not occur at the same time of day. The peaks in productivity of Caulerpa racemosa occur at 1400, and the low points occur at 0400, while the peaks in the rhythms observed by Sweeney and

Buggeln occur at 1200, and the low points in productivity occur at 2400. The differences in the timing of these rhythms could be due to species differences in plants. These timing differences in the rhythms could also be due to the locations of the experimental sites within their time zones. The hours recorded in all of the studies were not the correct time as measured by the location of the sun, but were the approximate times of the individual time zones.

It was not the purpose of this study to determine whether the observed periodicity was an endogenous or exogenous rhythm, since it was impossible to eliminate all external stimuli from the experiment. Several questions concerning rhythms in plants remain unanswered. Do all plants have productivity rhythms? While rhythms have been found in a wide variety of plants, not all of the groups of plants have yet been studied. Some investigators have stated that certain plants do not have rhythms (Sweeney 1963). It is possible that these plants do have rhythms, but that the investigators were unable to measure the rhythms because of the experimental conditions employed.

Several suggestions have been proposed to explain the significance of these rhythms to the plants. These proposals suggest that the rhythms synchronize cell division and plant growth and also allow for better utilization of the biochemical apparatus (Sweeney 1963; Cumming and Wagner 1968). Probably the importance of the rhythm is not yet fully understood.

It was not the intent of this study to examine the significance of the diurnal rhythm of productivity, but to determine the presence and factors affecting a productivity rhythm in a macroscopic algae.

With the productivity rhythm being reported in Caulerpa racemosa in addition to those plants in which a rhythm was previously reported, the suggestion can again be made that a productivity rhythm exists in many, if not all, plants. Thus, all previous productivity studies should be re-examined to determine if a periodicity of productivity was taken into consideration when hourly rates were converted into daily or other long-term productivity values.

Figure 1. Caulerpa racemosa growing in the field

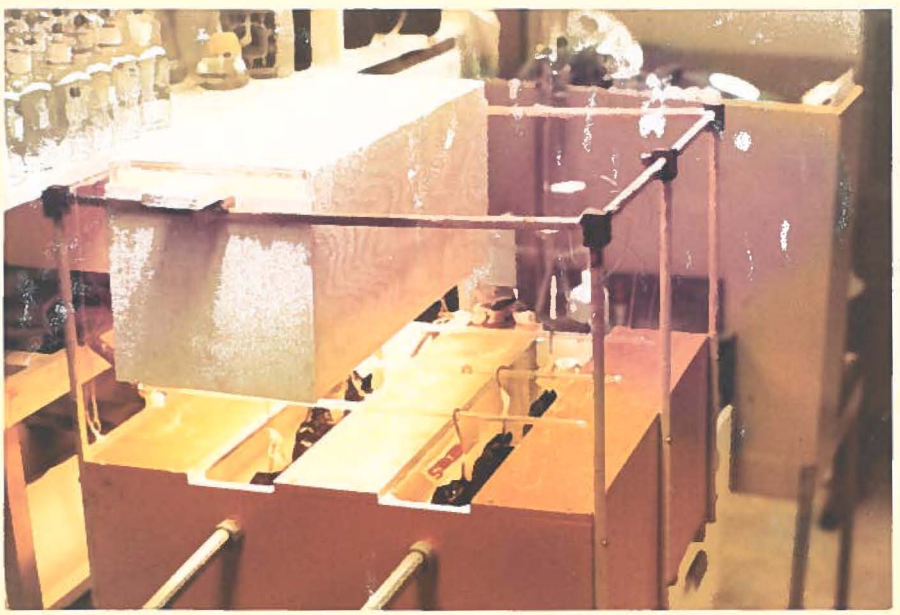

Figure 2. Control chamber

NET P
TIME OF DAY

Figure 3. Net productivity curve of Caulerpa collected and held 12 hours in outdoor aquaria before initiation of the experiment. Measurements were made at 3000 ft-c. Each vertical line represents ± 1 s.d. from the mean of five separate plants.

GROSS P
NET P
FEED
TIME OF DAY

Figure 4. Gross productivity, net productivity, and respiration curves of Caulerpa collected and held in outdoor aquaria 12 hours before initiation of the experiment. Measurements were made at 3000 ft-c. Each vertical line represents ± 1 s.d. from the mean of five separate plants.

mg O2/hour/g dry weight
4.0
3.0
2.0
1.0
GROSS P
NET P
RESP
TIME OF DAY

Figure 5. Gross productivity, net productivity, and respiration curves of Caulerpa collected and held in outdoor aquaria for 60 hours before the initiation of the experiment. Measurements were made at 3000 ft-c. Each vertical line represents ± 1 s.d. from the mean of five separate plants.

GROSS P
NET P
RESP
2.0
1.0
mg O2/hour/ dry weight
1200
2400
TIME OF DAY

Figure 6. Gross productivity, net productivity, and respiration curves of Caulerpa collected 60 hours before the initiation of the experiment and stored 12 hours in outdoor aquaria and 48 hours in the laboratory at a light intensity of 3000 ft-c. Measurements were made at 3000 ft-c. Each vertical line represents ± 1 s.d. from the mean of five separate plants.

3.0
2.0
1.0
GROSS P
NET P
RESP
1200
2400
1200
TIME OF DAY

Figure 7. Gross productivity, net productivity, and respiration curves of *Caulerpa* collected 60 hours before the initiation of the experiment and stored 12 hours in outdoor aquaria and 48 hours in the laboratory at a light intensity of 1500 ft-c. Measurements were made at 3000 ft-c. Each vertical line represents ± 1 s.d. from the mean of five separate plants.

GROSS P
NET P
RESP
4.0
3.0
2.0
1.0
1200
2400
1200
TIME OF DAY
mg O2/hour/g dry weight

Figure 8. Gross productivity, net productivity, and respiration curves of the average of two sets of plants. One set of plants was freshly collected and the other set was plants which had been collected 12 hours before the initiation of the experiment and held in outdoor aquaria. Measurements were made at 3000 ft-c and began at 1200 hours. Each vertical line represents ± 1 s.d. from the mean of six separate plants.

GROSS P
NET P
RESP
TIME OF DAY

Figure 9. Gross productivity, net productivity, and respiration curves of the average of two sets of plants. One set of plants was freshly collected and the other set was plants which had been collected 12 hours before the initiation of the experiments and held in outdoor aquaria. Measurements were made at 3000 ft-c and began at 1200 hours. Each vertical line represents $\pm$ 1 s.d. from the mean of six separate plants.

3.0
1.0
GROSS P
NET P
RESP
1200
2400
1200
TIME OF DAY

Figure 10. Gross productivity, net productivity, and respiration curves of the average of two sets of plants. One set of plants was freshly collected and the other set was plants which had been collected 12 hours before the initiation of the experiment and held in outdoor aquaria. Measurements were made at 3000 ft-c and began at 1800 hours. Each vertical line represents $\pm$ 1 s.d. from the mean of six separate plants.

mg O_2/hour/g. dry weight
3.0
2.0
1.0
GROSS P
NET P
RESP
1200
2400
1200
TIME OF DAY

Figure 11. Gross productivity, net productivity, and respiration curves of the average of two sets of plants. One set of plants was freshly collected and the other set was plants which had been collected 12 hours before the initiation of the experiments and held in outdoor aquaria. Measurements were made at 3000 ft-c and began at 1800 hours. Each vertical line represents ± 1 s.d. from the mean of six separate pl

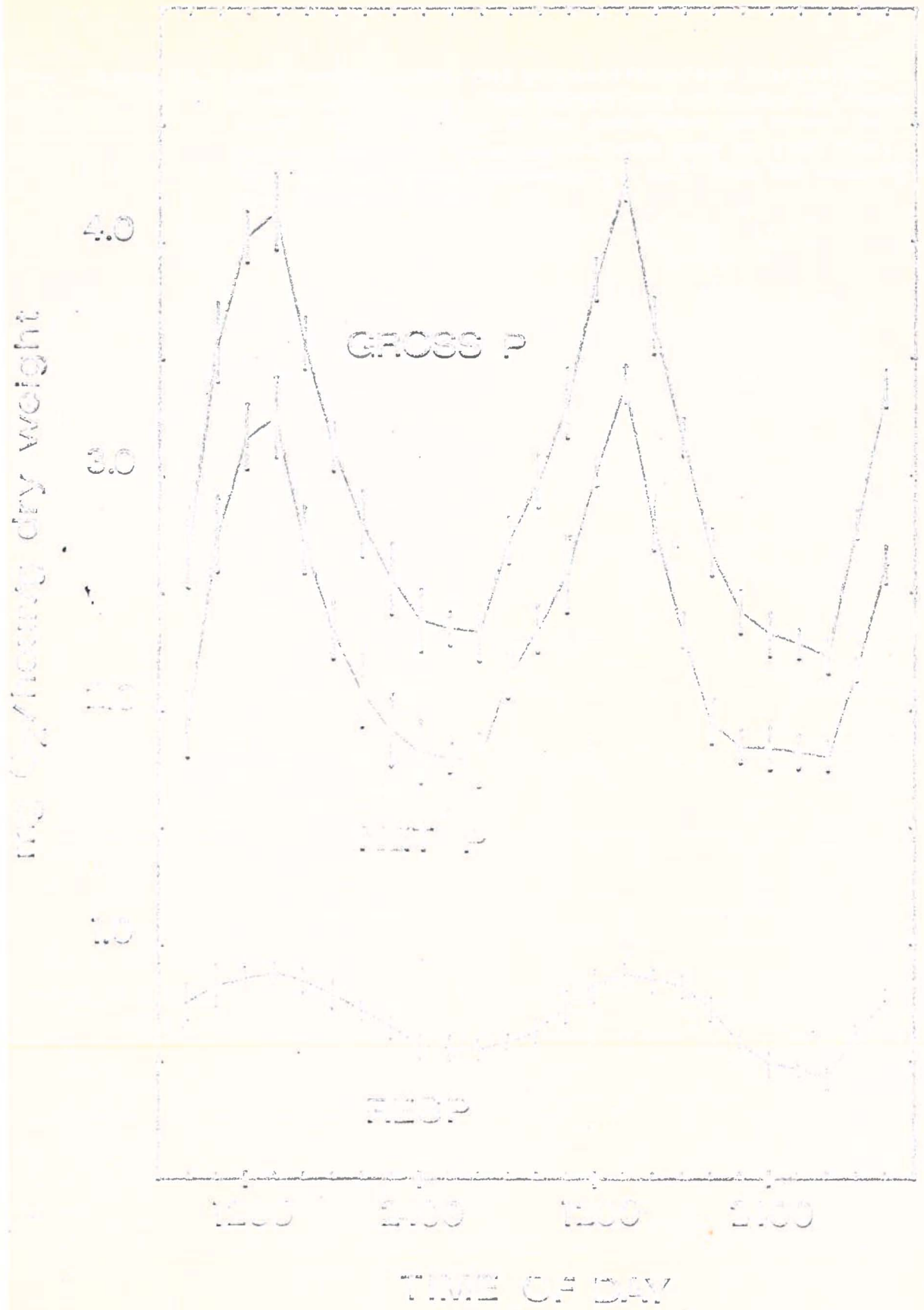
4.0
3.0
GROSS P
NET P
RESP
TIME OF DAY

Figure 12. Gross productivity, net productivity, and respiration curves of Caulerpa. The plants were collected 12 hours before the initiation of the experiment and stored in outdoor aquaria. Measurements were made at 1500 ft-c. Each vertical line represents ± 1 s.d. from the mean of five separate plants.

LITERATURE CITED

American Public Health Association. 1965. Standard methods for the examination of water, sewage, and industrial wastes (12th ed.) A.P.H.A., New York. 769 p.

Bolikov, P. and M. Kotorina. 1958. Daily rhythms of photosynthesis. Dokl. Botan. Sci. Sect. (Eng. Trans.) 123:267-70.

Blinks, L. and C. Given. 1961. The absence of daily photosynthetic rhythms in some littoral marine algae. Biol. Bull. 121:230-33.

Bracher, R. 1932. The light relations of *Euglena limosa* Gard. Part I. The influence of intensity and quality of light on phototaxy. J. Linn. Soc. Bot. London. 51:23-42.

Brown, F. 1962. Extrinsic rhythmicality: A reference frame for biological rhythms under so-called constant conditions. Ann. New York Acad. Sci. [illegible]

[illegible] periodicity in the photosynthetic capacity of the [illegible] marine algae, [illegible]

Cumming, B. and E. Wagner. 1968. Rhythmic processes in plants. Ann. Rev. Plant Physiol. 19:382-416.

Dawson, E. 1966. Marine Botany. Holt, Rinehart, and Winston, Inc. New York. 371 p.

Doty, M.S., J. Newhouse, and R. T. Tsuda. 1967. Daily phytoplankton primary productivity relative to hourly rates. Arch. Oceanogr. Limnol. 15:1-9.

Doty, M.S. and M. Oguri. 1957. Evidence for a photosynthetic daily periodicity. Limnol. Oceanogr. 2:37-40.

Hastings, W., L. Astrachan, and B. Sweeney. 1961. A persistent daily rhythm in photosynthesis. J. Gen. Physiol. 45(1):69-76.

Lorenzen, C. J. 1963. Diurnal variations in photosynthetic activity of natural plankton populations. Limnol. Oceanogr. 8(1):56-62.

Macguire, B. and W. Neill. 1971. Species and individual productivity in phytoplankton communities. Ecology. 52(5):903-07.

Peterson, R. 1971. Effects of light intensity on the morphology and productivity of [illegible] (Hudson) J. Ag. Master thesis, Univ. of Connecticut, Storrs, Conn. 40 p.

Schon, W. 1955. Periodische schwankungen der photosynthese und atmung bei *Hydrodictyon* . (Engl. trans.) Flora. 142:347-80.

Shimada, B. 1958. Diurnal fluctuations in photosynthetic rate and chlorophyll a content of phytoplankton from Eastern Pacific waters. Limnol. Oceanogr. 3:336-39.

Sweeney, B. 1963. Biological clocks in plants. Ann. Rev. Plant Physiol. 14:411-40.

Sweeney, B. and J. Haxo. 1961. Persistence of a photosynthetic rhythm in enucleated *Acetabularia*. Science. 134(3487):1361-63.

Warren, D. and M. Wilkins. 1961. An endogenous rhythm in the rate of dark-fixation of carbon dioxide in the leaves of *Bryophyllum fedtschenkoi*. Nature. 191:686-88.

Yentsch, C. and J. Ryther. 1957. Short term variation in phytoplankton chlorophyll and their significance. Limnol. Oceanogr. 2(2):140-42.