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Title LABORATORY STUDIES OF PERIPHYTON PRODUCTION AND COMMUNITY METABOLISM IN LOTIC ENVIRONMENTS

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Laboratory streams and a photosynthesis-respiration chamber were employed to study periphyton production and community metabolism in lotic environments. Periphyton communities developed under 550 foot candles of illumination from warm white, fluorescent tubes were designated as "light-adapted" communities and those developed under 225 foot candles as "shade-adapted" communities.

Curves relating illumination intensity to primary production obtained for the light-adapted periphyton communities, in general, were characterized by a linear range extending to between 100 and 200 foot candles, a compensation point attained at approximately 50 foot candles, and a saturating intensity in the vicinity of 2000 foot candles. Similar curves for the shade-adapted communities exhibited a steep initial slope, a short linear range not extending beyond 100 foot candles, a long and gradual inflection from the linear segment toward the horizontal, and a saturating intensity only slightly less than that observed with respect to the light-adapted communities. Primary production-light intensity curves

determined for the light-adapted communities could be characterized by the mathematical equation:

$$KI = P(P_m^2 - P^2)^{-\frac{1}{2}}$$

where P is the photosynthetic rate, I the light intensity, P_m the asymptotic maximum rate, and K a constant that locates the curve on the scale of light intensity; while curves for the shade-adapted communities could not be expressed mathematically in this manner.

Primary production in the light-adapted periphyton community was continuously enhanced by increasing the supply of molecular carbon dioxide to concentrations as high as 45 mg/l; no significant enhancement was found in the shade-adapted community.

The laboratory periphyton communities could be characterized as autotrophic communities with gross production-community respiration ratios normally ranging from about 1.3 to 2.5. Gross primary production was 1.7 - 4.1 g O_2/m^2/day for the shade-grown community and 2.5 - 6.4 g O_2/m^2/day for the light-grown community. In general, gross production in the laboratory steams was slightly greater than that normally reported for eutrophic lakes and oceanic waters and more characteristic of the least-productive flowing water systems.

Export of periphyton from the streams was greatly enhanced by turbid water conditions.

The efficiency of fixation of light energy as organic matter was 12.8 percent for the light-grown community and 22.7 percent for the shade-grown community. The efficiencies of the laboratory communities were considerably higher than efficiencies estimated for

most natural ecosystems and appeared to resemble more closely those for small cultures of Chlorella.

The concentration of chlorophyll a in the laboratory communities was usually slightly higher than that normally found in the majority of shallow, flowing water environments. The chlorophyll a content of the light-grown periphyton community varied between 0.48 and 2.01 g/m^2 and that of the shade-grown community between 0.14 and 1.30 g/m^2.

The gross primary production-chlorophyll a ratios found for the laboratory communities varied from 0.2 to 1.4 milligrams of oxygen per hour per milligram of chlorophyll a. Ratios obtained for the light-grown community became relatively constant during the fifth month of the study, while the ratios for the shade-adapted community were erratic until the ninth month of the study.

In the stream subjected to the higher light intensity, the community was well established and reasonably stable by the end of the third month of the investigation, with species of green algae supplementing an ever-present diatom flora during the warmer months. Community succession in the shade-grown community was a much slower process, and stability was not achieved until near the end of the study, when the species of blue-green algae Phormidium retzii and P. tenue almost covered the entire available substrate.

LABORATORY STUDIES OF PERIPHYTON PRODUCTION AND COMMUNITY METABOLISM IN LOTIC ENVIRONMENTS

by

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INTRODUCTION

Two general approaches to the study of ecological problems are available to the investigator: the field approach and the laboratory approach. Although the field study is probably the most realistic approach, the investigation of complex ecosystems in nature, if carried on effectively, usually involves a large personnel and requires the collection and processing of large quantities of data. In spite of an intensive effort on the part of competent research personnel, it is sometimes difficult to arrive at a satisfactory understanding of the complex natural system under investigation, and often the presentations of the end results are restricted to elaborate statistical demonstrations, which may or may not be entirely adequate. At times, it has been rewarding for the ecologist to bring a segment of nature into the laboratory where it can be examined in simplified and controlled systems. The principal disadvantage of such laboratory investigations is that artificial systems are frequently so far removed from reality that it is difficult to apply information obtained to natural ecosystems.

Measurement of primary production and community metabolism has been popular in the investigation of various aquatic ecosystems, particularly since Lindeman (15) introduced his concept of "trophic dynamics." The study of the rates of energy fixation by the autotrophic constituents of an aquatic community along with the assessment of the energy losses from the community provide a fundamental

understanding of the productive capacity of the environment. Field methods of estimating primary production and community respiration in different types of aquatic communities have been discussed by Ryther (39), Verduin (54), Penfound (34), and Odum (21). Some investigators, notably Lindeman (14), Teal (52), and Odum (22), have utilized primary production and community respiration data as a basis for the study of the transfer, or "flow," of energy from the primary producers to the higher "trophic levels" and have attempted to compute the efficiency of energy conversion from one group of organisms to another. Unfortunately, however, only very limited data are available on the energetics of periphyton communities inhabiting lotic, or flowing-water, environments, as measurements of metabolic rates in such systems are very difficult. McConnell and Sigler (18), Grzenda and Brehmer (10), and Waters (57) have tried to determine quantitatively the production of stream periphyton by measuring pigment concentrations, but their results, thus far, have not been too encouraging.

One of the first attempts to study periphyton communities in the laboratory was that of Odum and Hoskin (23) who constructed a small, flowing water microcosm from a glass condenser tube. Although some interesting data were obtained from these experiments, the microcosm was a very artificial system, and the results were limited in value. McConnell (17) studied communities in carboy microcosms and noted that such microcosms may differ from natural habitats in having unusual concentrations of metabolic gases, low rates of bacterial

activity, and accumulations of biotic substances which may be inhibitory to primary and secondary production.

The work reported in this thesis was concerned primarily with the development and utilization of methods for the accurate estimation of periphyton production and community metabolism in laboratory streams. A photosynthesis-respiration chamber was used in conjunction with the laboratory streams to study the effects of illumination intensity and carbon dioxide concentration on periphyton production. A long term experiment was carried out to determine the seasonal fluctuations in periphyton production at two light intensities and to examine carefully some of the relationships between primary production, community respiration, biomass, chlorophyll, and community structure. Some of the facilities described here have been successfully employed by Davis (7) to study trophic relations of simplified animal communities.

EXPERIMENTAL APPARATUS AND METHODS

Laboratory Stream Apparatus

The six laboratory streams were housed in a concrete block building, 25 feet long and 20 feet wide. Each stream (Figure 1) consisted of a pair of parallel wooden troughs each of which measured 3 meters long, 25 centimeters wide and 20 centimeters deep. An opening in adjacent sides at each end of the troughs allowed complete circulation of water through both troughs. The troughs were finished with a non-toxic white waterproof enamel. The bottom material placed in each laboratory stream was taken from a nearby stream and consisted of approximately 40 liters of smooth water-worn rubble, 5 to 15 centimeters in diameter, and smaller gravel.

The source of the water for the laboratory streams was a small stream near the laboratory. Wooden flumes conducted the water to wooden storage tanks. From these tanks, the water was passed through a sand filter and then through polyethylene pipe to the laboratory streams. The coarse sand filter removed sticks, leaves, and some of the larger suspended particles. The rate of flow of water entering each stream was regulated by a gate valve placed in the water line in front of the flow meter for that stream. The depth of water in the streams was regulated by the height of overflow standpipes. Circulation and mixing of the water in the streams was accomplished by variable-speed paddle wheels or by the jet action of centrifugal pumps. An arrangement for filling sample bottles with influent or effluent

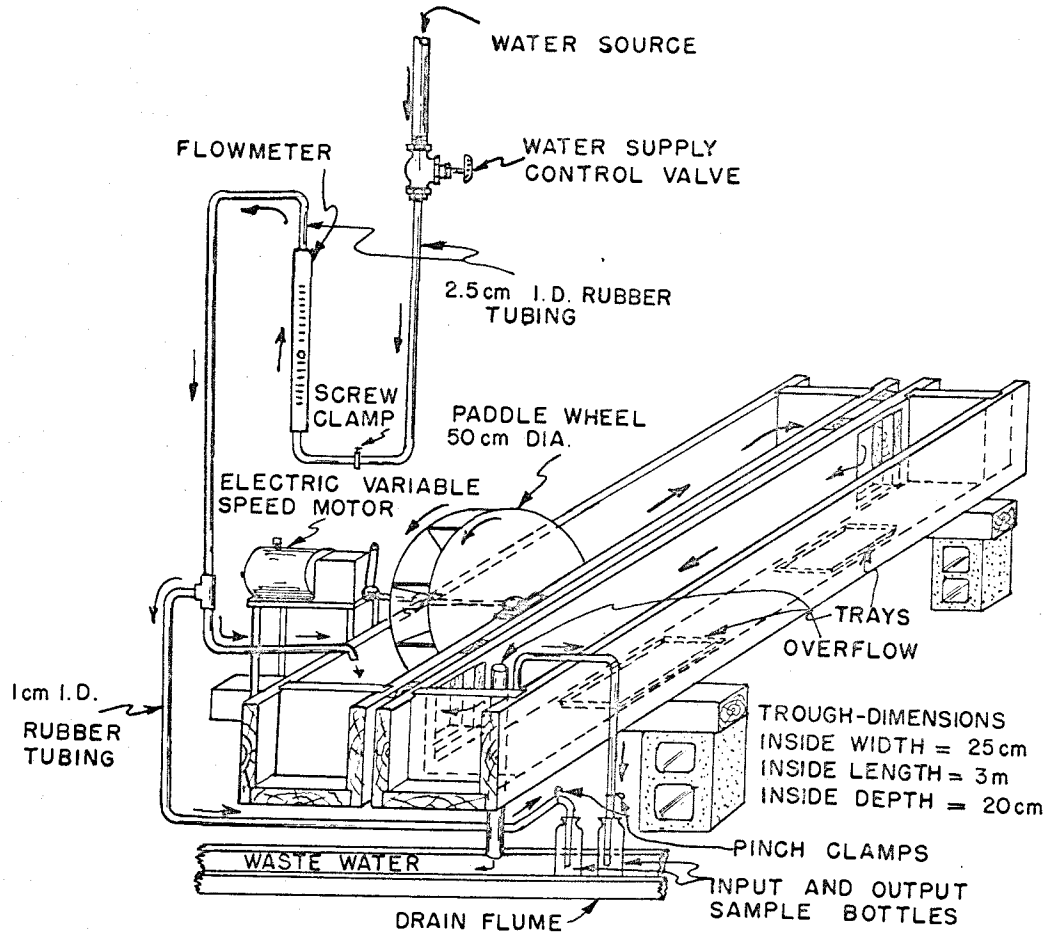

Figure 1. Diagram of one of the six laboratory streams.

water made it possible to take samples for determining dissolved oxygen concentration. Influent water could be passed through a sparging column in which nitrogen gas was used to reduce the concentration of dissolved oxygen to a desired level.

The exchange rate of water was normally maintained at two liters per minute. It had been determined through preliminary studies that, at this exchange rate, a dense growth of algae of the types common in small streams in this region would develop. The current velocity was maintained at 24 centimeters per second. This was the maximum water velocity that could be maintained without developing excessive surface agitation.

Chemical characteristics of the stream water utilized in the laboratory are summarized in Table 1. Water samples were collected from the influent lines four times a year during 1961 and 1962 and once during the winter and spring of 1963. The data show that the water quality at a particular season was about the same for the three years. In general, there is a gradual increase in the total dissolved solids, specific conductance, pH, and alkalinity during the spring and summer months and a decrease during fall and winter. At an exchange rate of two liters per minute, each stream (capacity approximately 200 liters) had 90 percent renewal of the circulating water approximately every two hours.

Illumination for each stream was provided by 16 48-inch, warm white, fluorescent tubes mounted in fixtures that could be raised or lowered to control the light intensity. Intensities up to approximately 800 foot candles could be obtained at the surface of the stream.

Table 1. Water quality summary for laboratory streams, 1961, 1962, and 1963*

Characteristic of constituent	Winter			Spring		
	3/17/61	3/6/62	2/6/63	5/23/61	5/21/62	5/14/63
Specific conductance (micromhos at 25° C.)	105	98	108	165	178	132
pH	7.8	7.2	7.4	7.9	7.7	7.7
Color	25	10		5	10	5
Dissolved solids mg/l	84	88	99	117	125	101
Hardness mg/l as $CaCO_3$	43	40	45	70	76	56
Silica (SiO_2) mg/l	23	22	24	33	35	27
Iron (Fe) mg/l	0.25	0.53	0.47	0.11	0.21	0.32
Calcium (Ca) mg/l	11	10	11	18	19	14
Magnesium (Mg) mg/l	3.7	3.7	4.3	6.1	6.8	5.1
Sodium (Na) mg/l	4.7	4.4	5.2	7.3	7.5	5.6
Potassium (K) mg/l	0.3	0.3	0.4	0.3	0.5	0.6
Bicarbonate (HCO_3) mg/l	60	52	60	97	104	77
Carbonate (CO_3) mg/l	0	0	0	0	0	0
Sulfate (SO_4) mg/l	0.4	1.6	2.0	0.4	0.2	0.2
Chloride (Cl) mg/l	4.2	4.8	4.5	4.5	5.0	4.0
Fluoride (F) mg/l	0.1	0.1	0.1	0.1	0.1	0.1
Nitrate (NO_3) mg/l	0.2	0.4	0.5	0.2	0	0.3
Phosphate (PO_4) mg/l	0.05	0.04	0.05	0.06	0.10	0.05

* These analyses were made under the supervision of L. B. Laird, District Chemist, U. S. Geological Survey, Portland, Oregon

(continued on next page)

Table 1. (Continued)

Characteristic or constituent	Summer		Fall	
	8/3/61	8/6/62	11/23/61	10/31/62
Specific conductance (micromhos at 25° C.)	206	212	129	201
pH	8.0	7.9	7.4	7.8
Color	10	10	30	10
Dissolved solids mg/l	154	149	101	141
Hardness mg/l as $CaCO_3$	91	92	52	86
Silica (SiO_2) as mg/l	40	40	27	38
Iron (Fe) mg/l	0.32	0.37	0.2	0.15
Calcium (Ca) mg/l	23	24	12	23
Magnesium (Mg) mg/l	8.2	7.8	5.4	7.0
Sodium (Na) mg/l	9.1	9.2	6.3	9.2
Potassium (K) mg/l	0.6	0.9	0.6	0.8
Bicarbonate (HCO_3) mg/l	125	127	66	120
Carbonate (CO_3) mg/l	0	0	0	0
Sulfate (SO_4) mg/l	0.6	1.6	2.4	0.4
Chloride (Cl) mg/l	4.5	5.2	7.0	5.0
Fluoride (F) mg/l	0.1	0.1	0.1	0
Nitrate (NO_3) mg/l	0.3	0.2	0.9	0.1
Phosphate (PO_4) mg/l	0.13	0.12	0.24	0.10

* These analyses were made under the supervision of L. B. Laird, District Chemist, U. S. Geological Survey, Portland, Oregon

Measurement of the illumination intensity was made with a Weston Model 756 Sunlight Illumination Meter. The lights were controlled by a time clock set to provide a photoperiod appropriate to the season.

Photosynthesis-Respiration Chamber

The photosynthesis-respiration (P-R) chamber (Figure 2), was a rectangular black, porcelain-coated, steel tank, measuring 60 centimeters long, 50 centimeters wide and 17 centimeters deep. The chamber was fitted with tubulations to allow for the circulation and exchange of water and was provided with a marine plywood water jacket for temperature control. The top of the chamber was sealed with a 6 millimeter lucite plate held in place over a rubber gasket by a series of C-clamps. The water in the chamber was circulated and mixed by two small centrifugal pumps. The influent ports were equipped with stainless steel baffles to distribute the flow from the pumps. Filtered exchange water passed from a constant head jar successively through a sparging column in which the dissolved oxygen concentration was controlled by bubbling nitrogen gas, through a smaller column in which carbon dioxide or other nutrients could be introduced, and finally through a flow meter and influent sample bottles, before entering the P-R chamber. A sample bottle was also placed in the effluent line of the chamber.

To provide illumination of greater intensity than that obtained in the laboratory streams, it was necessary to use a 1500-watt incandescent lamp, suspended on a pulley over the chamber. Reasonably

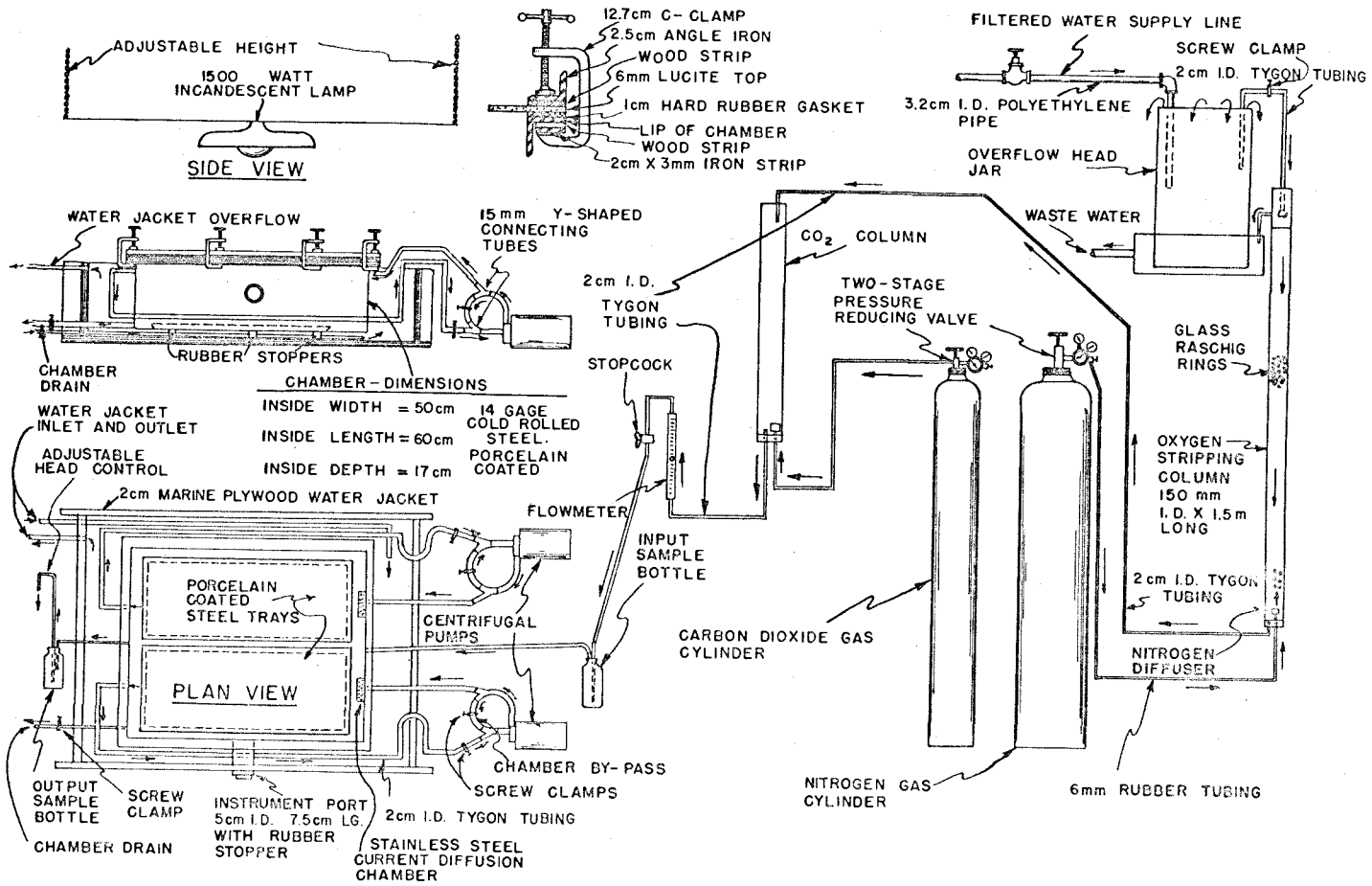

Figure 2. Diagram of the photosynthesis-respiration chamber.

even diffusion of the light into the chamber was assured by a sheet of flashed opal glass laid over the lucite cover. Light intensities as high as 2200 foot candles were obtained at the bottom of the chamber at the lowest position of the lamp. Lower intensities were obtained by raising the lamp and by placing one or more layers of dark colored nylon screen between the opal glass and the lucite cover. Light measurements were made with a hermetically sealed, selenium barrier type photocell (International Rectified DP-3) which had been calibrated by comparison with the Weston meter. All measurements were made under water, with the photocell at the bottom of the P-R chamber.

Heat transfer from the lamp to the contents of the chamber was minimized by a film of water flowing across the cover. The temperature rise in the chamber was seldom as much as 1° C.

A number of black, porcelain-coated, steel trays, measuring 50 centimeters by 20 centimeters and containing rubble and gravel bottom materials, were placed in each laboratory stream. When fully colonized, each tray served as a sample of the established community that could be removed from the stream for study in the P-R chamber.

Sampling Plant Communities in the Laboratory Streams

The communities which developed on the substrate of each stream were seeded naturally by cells entering the streams through the water supply. Composition of the plant communities remained surprisingly constant and usually varied only with respect to the relative abundance of the different species. The filamentous diatom

Melosira varians and a pennate diatom Synedra ulna consistently dominated the communities. These two species have been listed as among the dominant diatoms of the Columbia River (Williams and Scott, 60) and are typically found in the rivers and streams of Western Oregon. Oedogonium spp. were sometimes very abundant during the summer months, particularly in troughs receiving 500 foot candles or more of light. Genera of blue-green algae were always present and were frequently found growing attached to the sides of the troughs near the air-water interface. The blue-green alga Phormidium retzii formed gelatinous tufts, approximately two to three centimeters in length, that commonly attached to the larger rocks in troughs subjected to light levels of approximately 200 foot candles.

Portions of the communities were harvested to obtain estimates of biomass, organic matter, and pigment concentrations per unit area. In order to obtain a sample from a stream, the paddle wheel was first stopped to produce a standing water situation. Two water-tight wooden panels were wedged between the sides of the trough and pushed gently down between the rocks. With a distance of 20 centimeters between the panels, a section of the stream having a surface area of 500 cm^2 was enclosed. This area represented approximately 1/25 of the surface area of the colonized portion of each stream. Each rock was scoured free of organisms and removed from the sampling area. All of the water and suspended material was then siphoned from the section into a container. This suspension was thoroughly mixed in a blender, and aliquots were removed for measurements of biomass, organic matter,

pigment concentrations, and species composition. Measurement of the biomass was expressed as the dry weight of material removed from the rubble; organic content was determined by ignition of the dry material and estimates of pigment concentration by the spectrophotometric method described by Richards with Thompson (37). A Parr semi-micro oxygen bomb calorimeter No. 1411 was used in making estimates of the caloric content of the dried biomass. The techniques described in Parr Instrument Company manuals 128 (31), 130 (33), and in supplement No. 1 (32) of manual No. 128 were followed. For some of the studies, material exported from the system was collected with a #20 silk bolting cloth net placed so as to strain the water leaving the stream.

Measurement of Primary Production in the Laboratory Streams

Estimates of primary production and community respiration were based on measurements of the amounts of oxygen released by photosynthesis and the amounts utilized by respiration. Dissolved oxygen concentrations were measured using the unmodified Winkler method (American Public Health Association, 1, p. 252-255). Measurements of change of oxygen concentration in the laboratory streams had to be corrected for oxygen diffusion between the water surfaces and the air before these measurements could be used to estimate photosynthesis and respiration.

When estimates of photosynthesis, respiration, and diffusion rates in the laboratory streams were being obtained, the paddle

wheels were stopped to eliminate excessive agitation of the water surface. During these times, circulation and mixing were provided by two small centrifugal pumps in each stream.

Estimation of the net amount of oxygen evolved (uncorrected for diffusion) involved measurement of oxygen concentrations in influent and effluent water at intervals of 60 minutes during a period of three hours. Since water in a stream was well circulated and mixed by the pumps, it was assumed that the dissolved oxygen concentration of the water leaving the stream was equal to that of the water in the stream at all times. Comparison of the concentration of dissolved oxygen in water samples collected from several areas of a stream as well as from the effluent of the stream verified this assumption. The mean dissolved oxygen concentration of the water either entering or leaving a stream during a given time interval was assumed to be equal to the mean of the concentrations obtained at the beginning and end of the interval. From this information, and with knowledge of the exchange rate and volume of water in a stream, net (uncorrected) oxygen evolution in a stream for a time interval was computed from the following expression:

$$\text{net } O_2 \text{ change} = Ft\left[\frac{E_o + E_1}{2} - \frac{I_o + I_1}{2}\right] + V\,(E_1 - E_o)$$

where

F = exchange rate in liters/hour

t = time in hours

E_o = dissolved oxygen concentration in milligrams/liter of the effluent water at the beginning of the time interval.

E_1 = dissolved oxygen concentration in milligrams/liter of the effluent water at the end of the time interval.

I_o = dissolved oxygen concentration in milligrams/liter of the influent water at the beginning of the time interval.

I_1 = dissolved oxygen concentration in milligrams/liter of the influent water at the end of the time interval.

V = volume of water in the stream in liters.

In order to obtain the uncorrected measurements of community respiration, a stream was darkened with a black polyethylene sheet and the procedures outlined above were repeated. The rate of gross production for a period of time was estimated by summing the measurements of net oxygen evolved during illumination and oxygen consumed during an equivalent dark period, after both the former and latter values were corrected for diffusion of oxygen at the water surface.

The values for oxygen evolved, or oxygen consumed, for each time interval were corrected for diffusion at the water surface by determination of the mean percentage of saturation for the interval and obtaining the corresponding diffusion rate from a simple straight-line relationship. The relation between percentage of saturation and diffusion rate was established by determining the reaeration rate in a laboratory stream having no biological community. The oxygen concentration of water flowing into this stream was reduced to 3 mg/l or less by bubbling nitrogen gas through the water in a sparging column. The rate of reaeration, or diffusion rate, and the mean percentage of saturation were determined for short time intervals by

measuring the oxygen concentration of the influent and effluent water, the exchange rate, and volume of water in the stream and by using these data in the equation given above. The diffusion rate was then plotted against the mean percentage of saturation for each time interval, and a straight line was fitted to the points by the method of least squares. Diffusion rates for oxygen at different percentages of oxygen saturation were measured on four different dates (Table 2). The data obtained on July 13 and July 14, 1961, have been combined since the temperatures were similar on those dates. On July 13-14, 1961, and June 22, 1962, the water was circulated in the stream by two pumps in the same manner as during actual measurement of primary production and community respiration in a colonized stream. The datapoints for July 13-14, 1961, and June 22, 1962, when fitted with a straight line, have regression coefficients of -14.18 and -12.50. Diffusion rates determined on July 18, 1962, have also been included to show the effect of circulation by paddle wheel at 12 cm/sec on diffusion. The diffusion rates were higher and the slope of the regression line was considerably greater (-23.75) than with pump circulation. Figure 3 shows the diffusion curves plotted from these data. By using pump circulation during measurement of primary production and community respiration, it was possible to reduce the diffusion correction and still maintain adequate mixing in the system.

Table 2. Oxygen diffusion rates at different percentages of saturation determined in a laboratory stream lacking a community.

July 13-14, 1961*		June 22, 1962**		July 18, 1962***	
Diffusion mg $O_2/m^2/hr$	Percent saturation	Diffusion mg $O_2/m^2/hr$	Percent saturation	Diffusion mg $O_2/m^2/hr$	Percent saturation
786	41.4	741	33.5	1191	47.4
594	46.3	667	43.7	817	61.4
584	56.6	579	53.0	705	69.0
482	62.0	478	59.8	553	74.4
325	72.0	380	68.0	436	76.9
281	70.7	133	82.9	284	86.0
254	74.5	38	92.9	114	92.2
106	85.1				
60	91.7				
Regression Coefficient - 14.18		-12.50		-23.75	

* Circulated by two pumps; Water temperature 14.7 - 18.2° C.

** Circulated by two pumps; Water temperature 13.7 - 15.6° C.

*** Circulated at 12 cm/sec by paddle wheel; Water temperature 13.4 - 14.5° C.

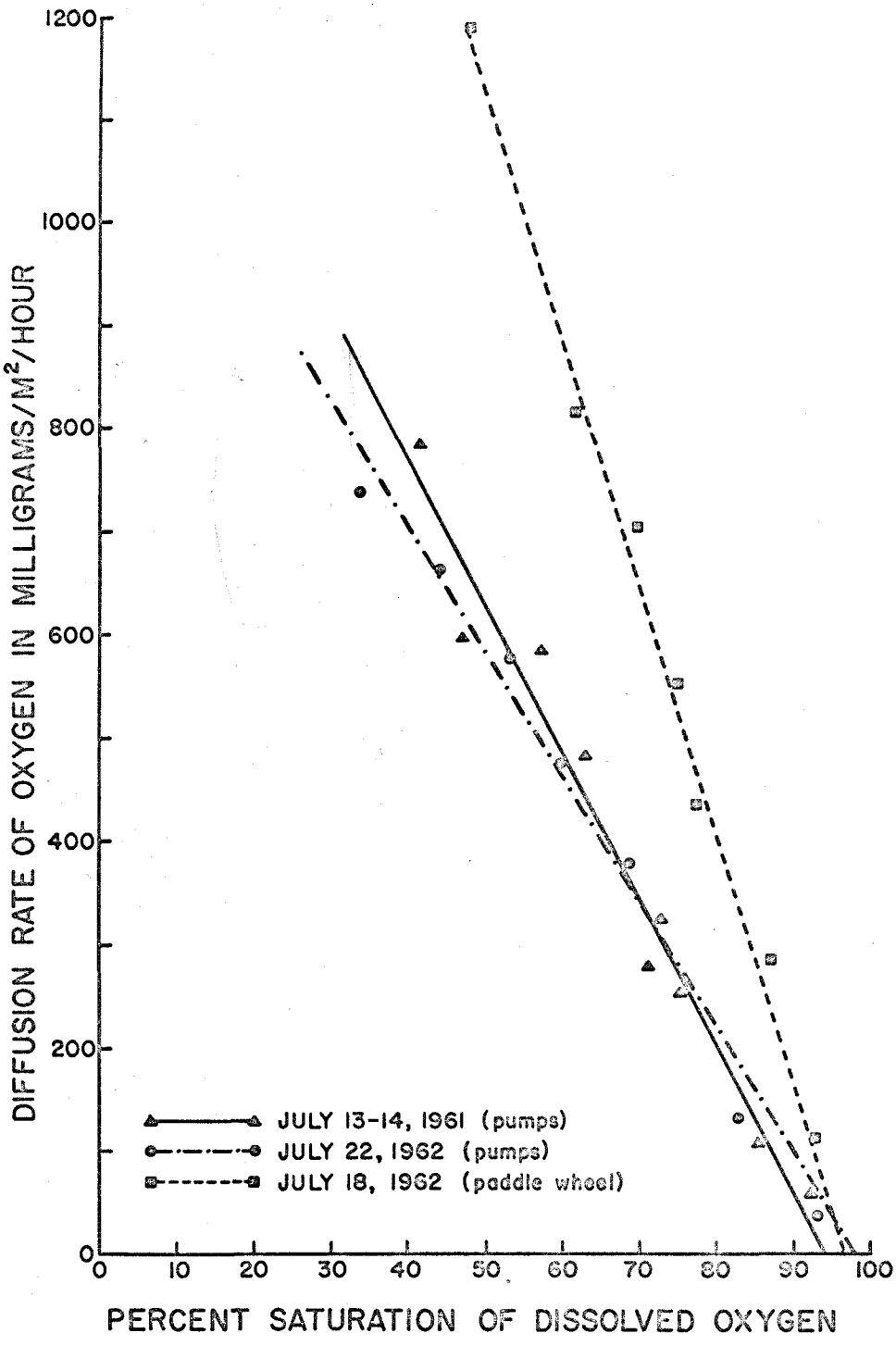

Figure 3. Relationships between percentage of saturation of dissolved oxygen and surface diffusion rate of oxygen determined in a laboratory stream having no biological community.

Measurement of Primary Production in the Photosynthesis-Respiration Chamber

Studies of the productive capacity of communities from the laboratory streams under specified conditions were made by placing trays containing portions of these communities growing attached to the stream bottom materials into the photosynthesis-respiration chamber. At the beginning of each experiment, two trays together with their contained materials were transferred from a stream to the chamber. The chamber was filled and sealed by the lucite cover in a manner that excluded all the air from the system. This procedure produced a system which was free from the influences of atmospheric diffusion. The exchange rate of the influent water was then adjusted to the desired value, usually 300 to 400 milliliters per minute. The concentration of dissolved oxygen in the influent water was reduced to approximately 5 mg/l by means of a counter flow of nitrogen bubbles in the sparging column. Reduction of oxygen concentration of the influent water prevented the water in the chamber from becoming supersaturated with oxygen, which would have tended to cause errors due to bubble formation beneath the lucite top.

The chamber having been filled with water, the air bubbles removed and the exchange rate adjusted, the conditions in the chamber were allowed to reach an equilibrium in the dark, during an eight to twelve hour period corresponding to the normal dark period of the photoperiodic cycle under which the community had developed in the streams. The lamp was turned on at the beginning of an

experiment, and after an hour of illumination, the concentrations of dissolved oxygen in the influent and effluent water were determined. Thereafter determinations were made at specified intervals. As the water in the chamber was constantly circulated by two centrifugal pumps, it was assumed that the dissolved oxygen concentration of the water leaving the chamber was identical to that of the water in the chamber at all times. The mean concentration of dissolved oxygen in the water, either entering or leaving the system during a time interval, was assumed to be equal to the average of the concentrations obtained at the beginning and the end of the interval. With these oxygen data, and the exchange rate and the volume of water in the chamber, the net rate of oxygen change could be calculated by using the equation given for the laboratory streams. In this case, however, the value for the volume of water in the chamber is substituted in the equation for the "V" value (volume of water in a stream).

Measurements of community respiration were made in exactly the same manner as were measurements of photosynthesis, except that the chamber was darkened by a black polyethylene sheet during the measurement period. The rate of gross photosynthesis was estimated by adding the net oxygen evolved during the period of illumination to the amount of oxygen consumed by respiration during an equivalent period of darkness. When the P-R chamber was employed, it was not necessary to correct the measurements of change in oxygen concentration for diffusion, as the water in the chamber did not come in contact with the surrounding air.

RESULTS

The results of laboratory studies of periphyton production, community metabolism, and community structure as related to some chemical and physical characteristics of lotic environments are presented under three principal topics: the effect of illumination intensity on primary production; the effect of concentration of molecular carbon dioxide on primary production; and seasonal variations of periphyton production, community metabolism, and community structure in the laboratory streams. The studies of the effects of illumination intensity and the concentration of molecular carbon dioxide on primary production were short term experiments and involved the use of the P-R chamber as well as the laboratory streams. The study of seasonal variations of the quantitative and qualitative characteristics of periphyton communities developed in the laboratory extended for one year and utilized two laboratory streams.

Effect of Variation in Intensity of Illumination on Primary Production

In March, 1961, the effect of illumination intensity on the rate of photosynthesis of periphyton communities developed in the laboratory streams was determined in the P-R chamber. The community utilized for this study had developed under the same conditions on the substrate of two trays ($0.2 m^2$) from two different streams. The species composition was typical of the laboratory streams throughout

the winter and spring months. The dominant plants were species of diatoms, particularly Synedra ulna, and a species of Oedogonium.

Net oxygen evolved during photosynthesis was measured for an eight hour light period at each of six different illumination intensities (80, 140, 250, 440, 720, and 2000 foot candles) on six successive days. For this particular experiment, community respiration was measured between the light periods, and these values were added to the net oxygen evolved during the related light period to estimate gross primary production (photosynthesis) at each intensity.

The relationship of gross primary production to illumination intensity is illustrated by Figure 4. Gross production by $0.2m^2$ of the community during eight hours ranged from 150 mg O_2 at 80 foot candles to 718 mg O_2 at 2000 foot candles. Community respiration during the six days varied between 7.6 and 11.2 mg O_2/hr, and the mean rate of respiration was 9.2 mg O_2/hr. For the purpose of comparing these values to production data of the remaining experiments, the rates have been expressed on the graph as milligrams of oxygen per square meter per hour. The upper curve (solid line) represents gross primary production plotted at the various illumination intensities, and the bottom curve (dotted line) shows net oxygen released during photosynthesis (gross primary production minus the mean rate of respiration for the six days) plotted similarly. The lower curve was included to provide a comparison of these data with data obtained in experiments that did not include estimates of community respiration. The increase in the rate of photosynthesis with

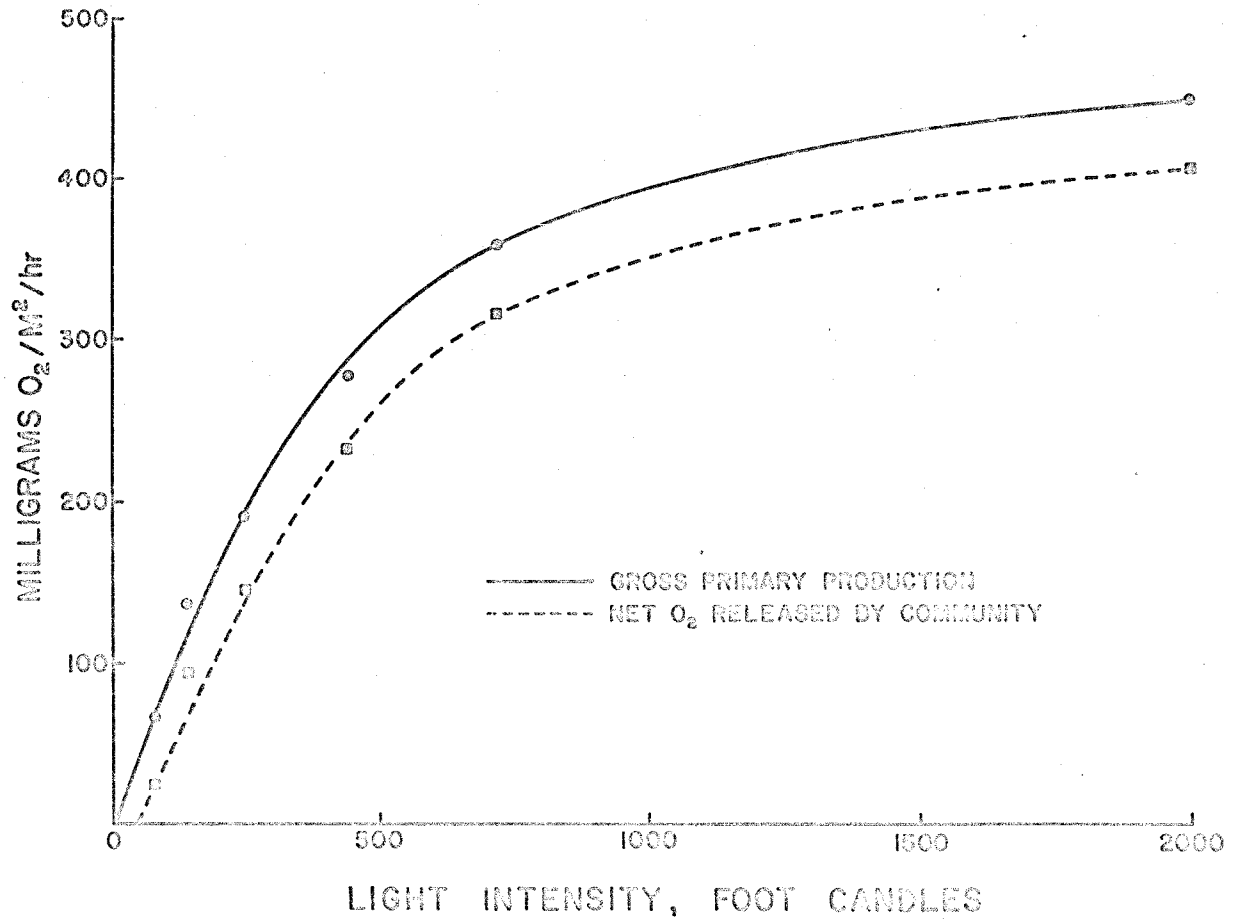

Figure 4. Relationship between illumination intensity and gross primary production determined in the photosynthesis-respiration chamber, March, 1961.

increasing light was approximately linear between 80 and 200 foot candles, and a saturation intensity was reached at approximately 2000 foot candles.

The effect of variation in illumination intensity on primary production was also investigated directly in the laboratory streams. In December, 1961, net oxygen evolution by the community in each stream was measured at one hour intervals under five different illumination intensities. Illumination intensities were determined with the Weston cell at four equally-spaced locations near the water surface of each stream. These four values were averaged to obtain an estimate of the light intensity at each stream during the time interval. The heights of the fluorescent lamps were changed every hour to give intensities ranging between 100 and 700 foot candles. Although higher intensities could not be obtained with the fluorescent tubes, the results of the P-R chamber experiment described above had already indicated that intensities between 100 and 700 foot candles had the most pronounced effect on photosynthetic rates.

In Figure 5, net oxygen evolution per square meter per hour has been related to light intensity in foot candles. Although the points represent data from six different streams, they are surprisingly well grouped, and the relationship between illumination and rate of photosynthesis was very similar to that in the March experiment using the P-R chamber. The visually fitted curve has the same general shape as the left half of the curves presented in Figure 4.

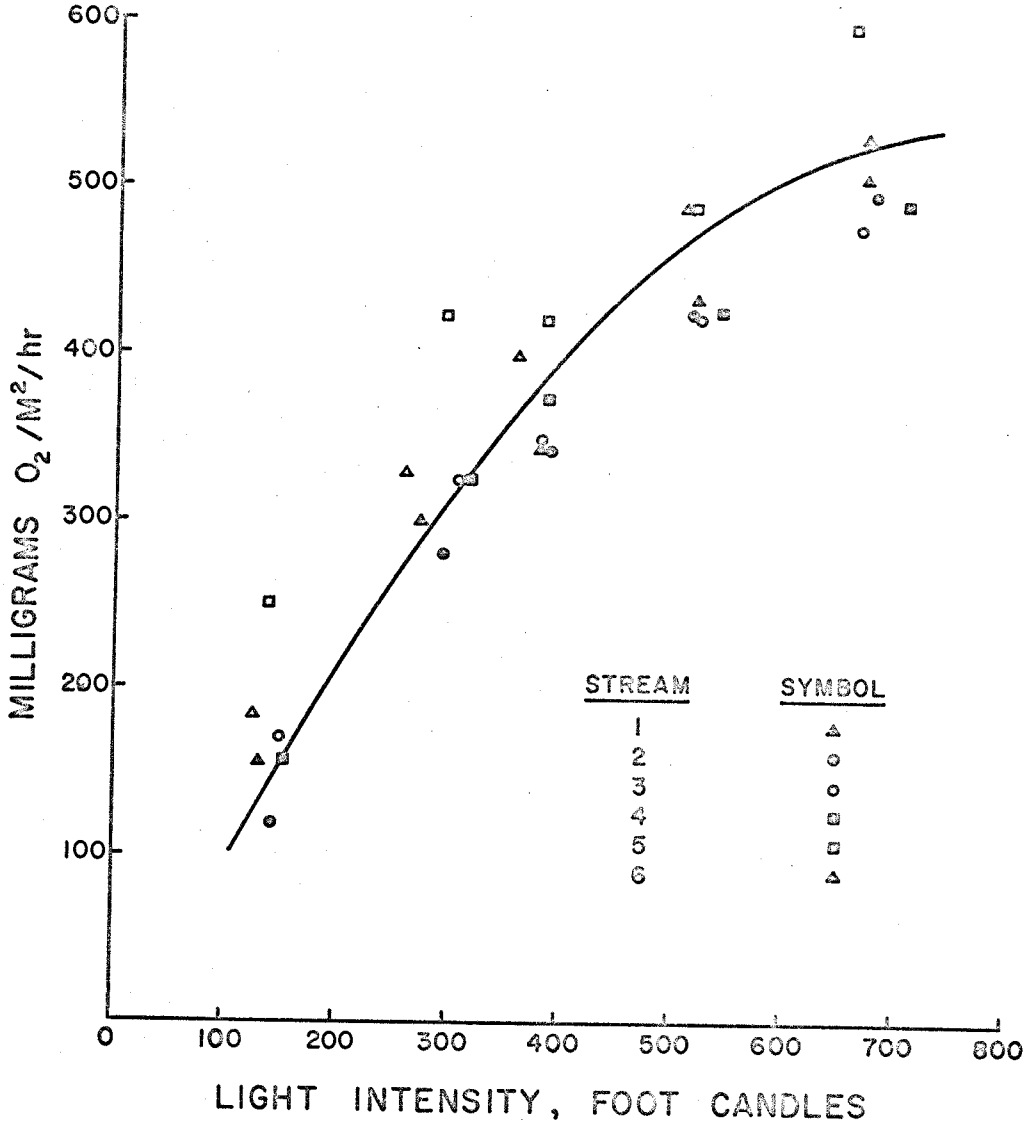

Figure 5. Relationship between illumination intensity and primary production of communities in six laboratory streams, December, 1961.

One of the most important factors determining the relationship between light and primary production is prolonged adaptation of the community to high or low intensities of light. To investigate this adaptatation factor, communities were allowed to develop in the laboratory streams at two different illumination intensities (225 and 550 foot candles) during the spring of 1962. Diurnal dark and light periods appropriate to the season were used. The communities that developed at 225 foot candles will henceforth be referred to as "shade-adapted" communities and those at 550 foot candles as "light-adapted" communities.

On July 5, 1962, two trays representing a light-adapted community were removed from a stream and placed into the P-R chamber. The autotrophic portion of this community was composed of 46 percent diatoms, 42 percent bluegreen algae, and 12 percent green algae. Net oxygen evolution was measured for 30 minute intervals at different illumination intensities up to 2000 foot candles (Figure 6). On the following day, this procedure was repeated (Figure 6) with a shade-adapted community which consisted of 67 percent diatoms, 26 percent bluegreen algae, and 7 percent green algae. The shape of the curve representing the light-adapted community was very similar to the shapes of the curves shown in Figures 4 and 5 obtained for other light-adapted communities. The curve representing production by the shade-adapted community had a different shape, however. There was a steeper initial rise in photosynthetic rate up to about 200 foot candles, a distinct decrease in slope from 200 to

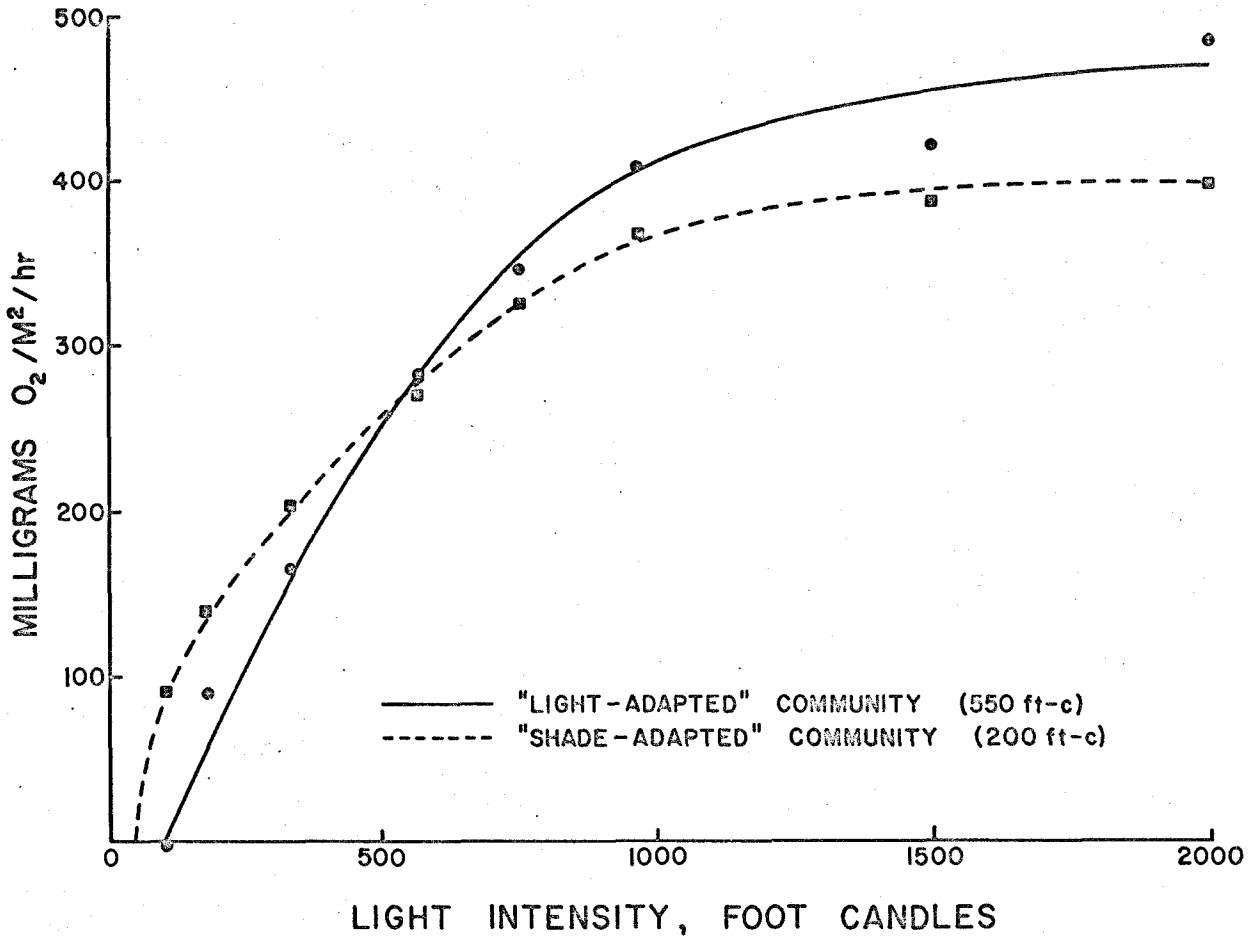

Figure 6. Relationship between illumination intensity and primary production of a "light-adapted" and "shade-adapted" community determined in the photosynthesis-respiration chamber, July, 1962.

1000 foot candles, and a leveling-off between 1000 and 2000 foot candles.

Effect of Concentration of Molecular Carbon Dioxide on Primary Production

In most of the published "carbon dioxide curves" that relate the rate of photosynthesis to the concentration of carbon dioxide, the concentration of free neutral carbon dioxide molecules has been used as the independent variable. This has also been the case in studies of aquatic plants that grew in environments where carbon dioxide frequently existed primarily in the form of carbonate and bicarbonate ions, and it was commonly assumed that, while the neutral molecular species CO_2 easily entered and left the cell, the ionic forms encountered a much greater difficulty in diffusing through the cell membrane. Although there is now much evidence that some plants can actually utilize the bicarbonate ion in photosynthesis, most investigators still agree that the intercellular concentrations of all species of carbonic acid, including HCO_3^- and $CO_3^=$, are probably determined mainly by the extracellular concentration of molecular CO_2 and are largely independent of the concentration of the ionic forms.

In general, the water which supplied the laboratory streams was characterized by relatively high concentrations of bicarbonate ions, low concentrations of free carbon dioxide molecules, and pH values near 8.0. This indicated that a low concentration of an

available form of carbon dioxide could possibly have been limiting primary production in the laboratory streams.

Two types of experiments were designed to test the effect of different concentrations of free, molecular carbon dioxide on primary production of communities developed in the laboratory streams. Since light was determined to have almost a linear relationship to photosynthetic rate up to about 200 foot candles, it appeared necessary to conduct the carbon dioxide experiments at different light intensities. In the first series of experiments, performed during June, 1961, two trays with periphyton were removed from two streams and placed in the P-R chamber. The incandescent lamp was adjusted to provide 65 foot candles of illumination, and the rate of photosynthesis was determined for eight hours on each of three successive days, each day at a different level of free carbon dioxide. The trays containing the experimental community were then returned to the laboratory streams for several days. This procedure was repeated at 670 and 2030 foot candles. The free carbon dioxide concentration was controlled by bubbling carbon dioxide gas into the water as it passed downward through a glass column. Determinations of the concentration of free carbon dioxide were made using the relationship between the concentration of free carbon dioxide, pH, temperature, bicarbonate alkalinity, and concentration of total solids (American Public Health Association, 1, p. 54-58). During August and September, 1962, a second series of carbon dioxide experiments were conducted with both light- and shade-adapted communities.

Two trays were removed from the streams and placed in the P-R chamber and oxygen evolution was measured for 30 minute intervals at eight different illumination intensities up to 200 foot candles. This procedure was followed on four successive days while introducing a different concentration of carbon dioxide each day.

The results of the first series of experiments (June, 1961) are presented in Table 3. The carbon dioxide concentrations listed in the table represent the mean free carbon dioxide concentrations of the water entering the chamber during the eight hour light periods. Since respiration rates were also determined, estimates of gross production are also included. The photosynthetic rates at 670 and 2030 foot candles have been corrected for significant changes in the biomass which occurred during the light periods. These corrections were made by determining the percentage increase or decrease of the photosynthetic rate of the first hour of a light period as compared with the last hour of the previous light period. The percentage increase or decrease was then used to adjust the initial rate at each carbon dioxide concentration.

At an illumination intensity of 65 foot candles, the addition of carbon dioxide to the water had very little effect on gross production. As the illumination intensity was increased to 670 and 2030 foot candles, however, the effect of added carbon dioxide became much more noticeable. Although this first series of experiments did not provide sufficient data to allow plotting meaningful curves relating primary production to light and free carbon dioxide

Table 3. The relationship between primary production and concentration of free carbon dioxide at 65, 670, and 2030 foot candles, June, 1961.

Date	Light (foot candles)	Mean free CO_2 (mg/l)	Net O_2 evolution ($mg/m^2/hr$)	Respiration ($mg/m^2/hr$)	Gross Production ($mg/m^2/hr$)
6/5/61	65	1.4	-1	25	24
6/7/61	65	13.8	12	25	37
6/9/61	65	5.4	11	25	36
6/13/61	670	1.2	160	30	190
6/14/61	670	7.1	185	30	215
6/15/61	670	19.1	200	30	230
6/19/61	2030	1.4	423	57	480
6/20/61	2030	14.3	496	59	555
6/21/61	2030	4.2	452	58	510

concentration, it did provide evidence that at high light intensities the concentration of free carbon dioxide had a significant effect on primary production of the laboratory communities.

The results of the second series of experiments (August and September, 1962) are presented in Figures 7 and 8. In Table 4 the mean pH, total alkalinity, temperature, and free carbon dioxide concentration of the water exchanging in the P-R chamber during the experiments have been tabulated. In August the experiment was conducted with a light-adapted community (Figure 7) and in September with a shade-adapted community (Figure 8). The procedure used in these experiments proved much more satisfactory than that followed during the experiments of June, 1961. The short time intervals (30 minutes) at each illumination intensity prevented significant changes in biomass and allowed measurements at eight intensities in one day. Furthermore, during these experiments determinations of free carbon dioxide were made on water samples collected from the effluent lines rather than the influent lines. This provided an estimate of the mean free carbon dioxide concentration in the water actually surrounding the plants instead of the mean concentration in the water entering the P-R chamber.

In Figure 7 (light-adapted community), the spread of the points plotted at a particular illumination intensity definitely increased at 950 foot candles. These data indicated that the photosynthetic rate of the light adapted community was enhanced by the addition of free carbon dioxide and that this enhancement began to take

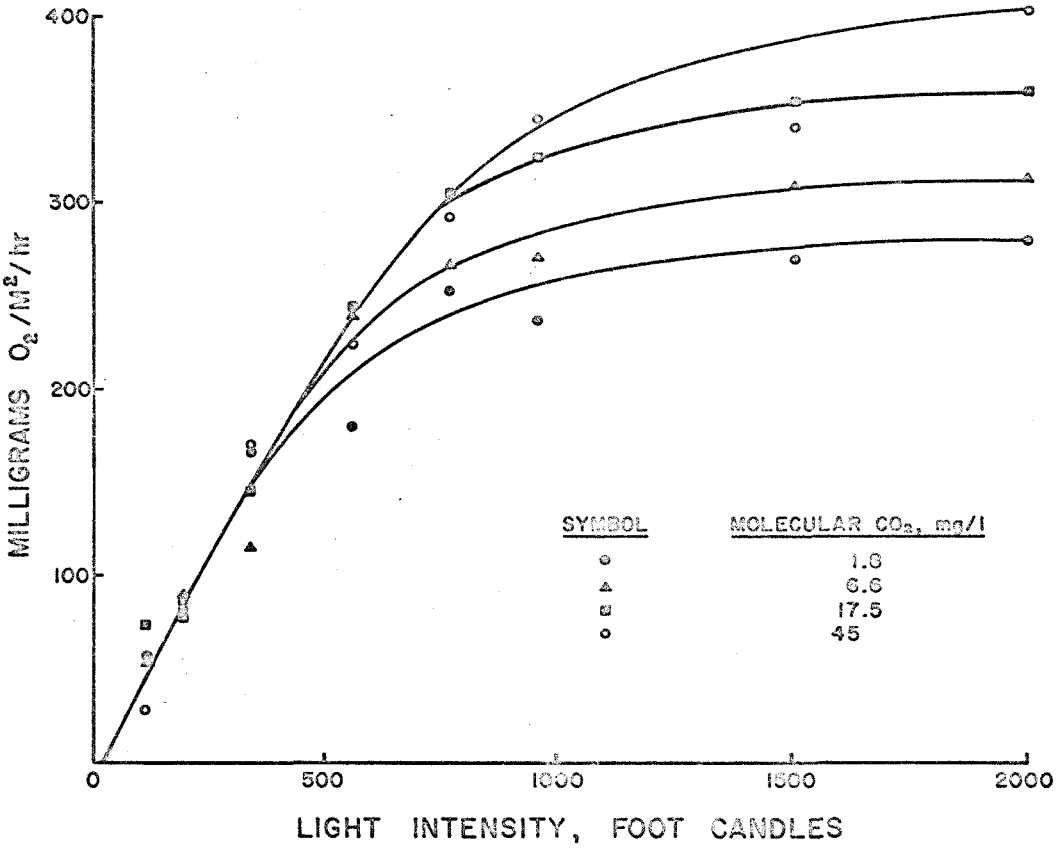

Figure 7. Relationship between the concentration of molecular carbon dioxide and primary production at different intensities of illumination for a "light-adapted" periphyton community determined in the photosynthesis-respiration chamber, August, 1962.

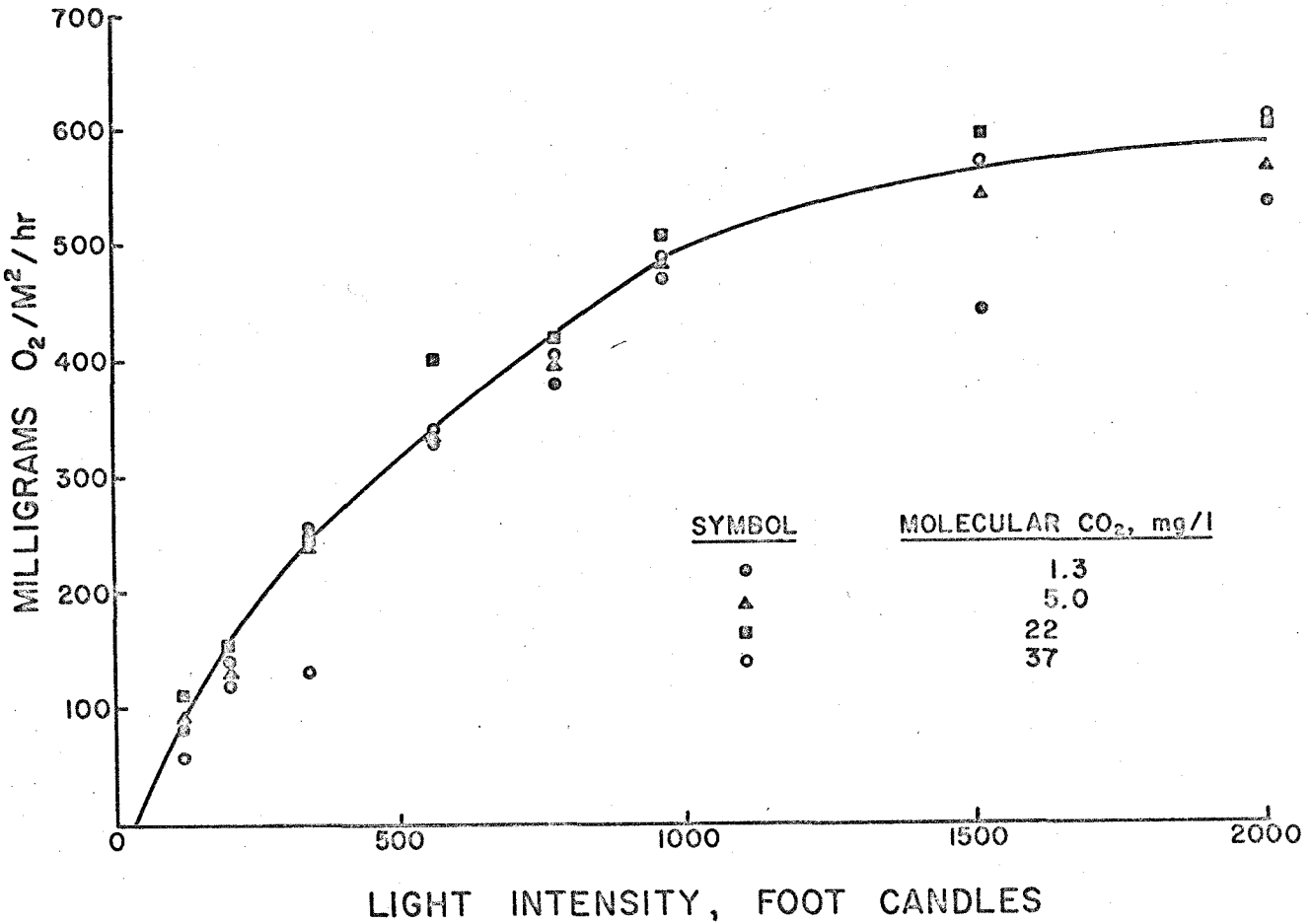

Figure 8. Relationship between the concentration of molecular carbon dioxide and primary production at different intensities of illumination for a "shade-adapted" periphyton community determined in the photosynthesis-respiration chamber, September, 1962.

Table 4. The mean pH, total alkalinity, temperature, and free carbon dioxide concentration of the exchanging water in the P-R chamber during the carbon dioxide experiments conducted August and September, 1962.

Community type	Date	pH	Total alkalinity (mg/l $CaCO_3$)	Temperature	Free CO_2 (mg/l)
Light-adapted	8/14/62	8.09	104	16.9	1.8
	8/15/62	7.53	106	17.2	6.6
	8/16/62	7.10	107	17.9	17.5
	8/17/62	6.69	105	16.6	45
Shade-adapted	9/10/62	8.21	104	16.9	1.3
	9/11/62	7.62	96	15.5	5.0
	9/12/62	7.00	101	14.9	22
	9/13/62	6.76	100	16.3	37

effect between 100 and 500 foot candles. The data plotted in Figure 8 (shade-adapted community), however, showed that the addition of free carbon dioxide did not have a significant effect on photosynthesis at any of the studied light intensities, as the spread of the points plotted at 106 foot candles was approximately the same as that of the points plotted at the higher intensities. The unusually low points at 330 and 1500 foot candles were attributed to a shading effect caused by silty cooling water which constantly flowed over the top of the chamber. On several occasions during the experiment, silt collected between the flashed opal glass and the lucite top of the chamber and had to be flushed from the top.

Seasonal Variations of Periphyton Production and Community Metabolism in Laboratory Streams

In June, 1962, two laboratory streams (Streams 1 and 6) were drained, and the rocks and sides of the troughs were cleaned. The fluorescent lights over Stream 1 were adjusted to provide the substrate with approximately 550 foot candles of illumination; the lamps over Stream 6 were raised until the stream received approximately 225 foot candles. The streams were then filled and the paddle wheels were started. As the communities developed in each of the streams, a long-term study was initiated to determine the seasonal variations of periphyton production and community metabolism under "light" and "shade" conditions. The principal objectives of this long-term study were: 1) to compare production rates of the light- and shade-adapted communities; 2) to determine fundamental relationships

between primary production, community respiration, biomass, organic matter, chlorophyll, and export with respect to seasonal variations in light and temperature; 3) to study community structure and successional patterns of the laboratory communities on a seasonal basis under "light" and "shade" conditions; and 4) to compare periphyton production and community metabolism of the laboratory communities with similar processes in natural communities.

Seasonal environmental conditions

The chemical characteristics of the water that supplied the laboratory streams have already been presented in Table 1. At the beginning of the study, the nitrate and phosphate concentrations were 0.0 and 0.1 mg/l respectively. The nitrate concentration increased during the summer and fall of 1962, reaching a maximum of 0.9 mg/l in the sample collected on October 31; during the winter and spring of 1963, the concentration of nitrate was approximately 0.5 mg/l. Phosphate concentration increased to a maximum of 0.24 mg/l during October, 1962, and subsequently decreased to 0.05 mg/l in the winter and spring of 1963. The concentration of total solids reached a maximum of 149 mg/l in the sample obtained in August, 1962, and was approximately 100 mg/l during the following fall, winter, and spring months.

Daily fluctuations in the water temperatures of the streams were measured by an Auto-lite Model 1000 thermograph. The weekly maximum, minimum, and mean temperatures have been plotted in Figure 9. These

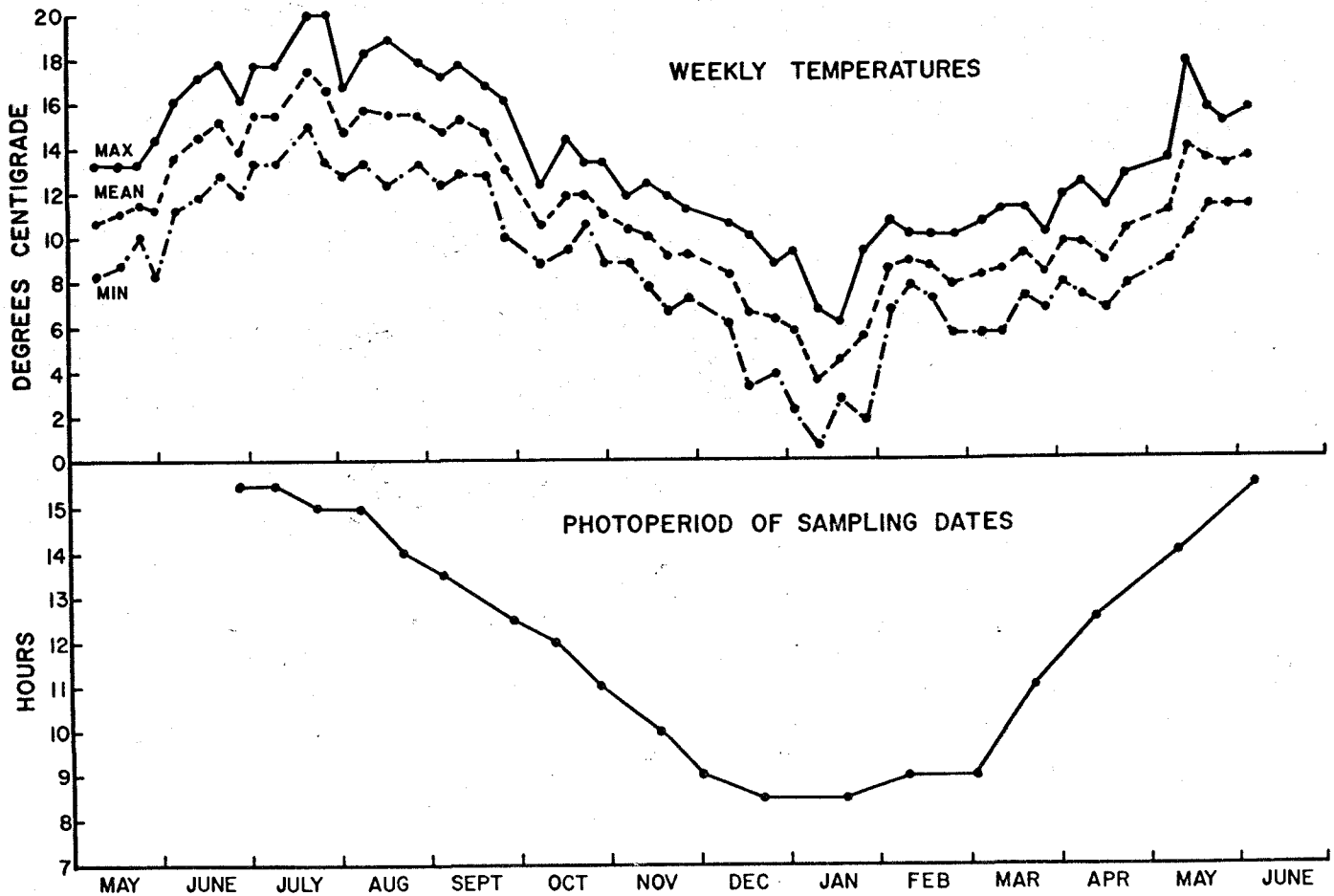

Figure 9. Weekly fluctuations in the water temperatures of the laboratory streams and lengths of the light periods on the dates when primary production was measured, May, 1962, through June, 1963.

data applied to both streams, as the source of the influent exchange water was the same for all streams and the water temperatures never varied over 0.2° C. from stream to stream. The maximum and minimum temperatures recorded during the study were 20.0° C. in July, 1962 and 0.6° C. in January, 1963.

The length of the light period was changed approximately every two weeks and corresponded to the normal day length of the particular season. The lengths of the light periods on the dates when primary production was measured have been plotted in Figure 9. The photoperiod should have been increased to 10 hours in late February before the sampling date on March 2, 1963. Unfortunately, however, failure to change the timer resulted in a 9 hour photoperiod.

As the fluorescent tubes became older, their output was somewhat reduced. Table 5 shows the mean illumination intensities reaching the streams at four dates during the investigation. Over the period of this portion of the study there was a gradual reduction of the light intensity of approximately 80 foot candles at Stream 1 and 25 foot candles at Stream 6.

Table 5. Mean illumination intensities in foot candles reaching Streams 1 and 6, June, 1962, through May, 1963.

Stream	6/18/62	7/30/62	10/4/62	2/27/63
1	544	515	504	465
6	225	211	209	203

Primary production and community respiration

In Figure 10, primary production and community respiration of Stream 1 (light-adapted) and Stream 6 (shade-adapted) have been plotted for the year extending from June, 1962, to June, 1963. At the top of Figure 10, primary production was expressed as an hourly rate (milligrams of oxygen per square meter per hour). The estimated hourly rates were then multiplied by the length of the light period (Figure 9) and these values, expressed as grams of oxygen per square meter per day, were plotted below the hourly rates. Community respiration was expressed as grams of oxygen per square meter per day.

The community developed at the higher light intensity had a primary production rate consistently higher than that of the community subjected to the lower light intensity (Figure 10 and Appendix I). In Stream 1 the maximum hourly rate of 434 $mg/m^2/hr$ was reached on August 22, 1962; in Stream 6, the maximum of 303 $mg/m^2/hr$ was attained about two months later on October 27, 1962. Minimum hourly rates were obtained during February (Stream 1) and March (Stream 6) after a period of turbid conditions and high export from the system; minimum rates were 278 $mg/m^2/hr$ (Stream 1) and 189 $mg/m^2/hr$ (Stream 6). Primary production expressed on a daily basis reached a maximum of 6.4 $g/m^2/day$ in Stream 1 and 4.4 $g/m^2/day$ in Stream 6, both on July 10, 1962. Minimum daily rates in both streams occurred during the shorter light periods of the winter months.

Community respiration reached a summer maximum of 4.1 $g/m^2/day$ in Stream 1 on July 25, 1962 (Figure 10 and Appendix I).

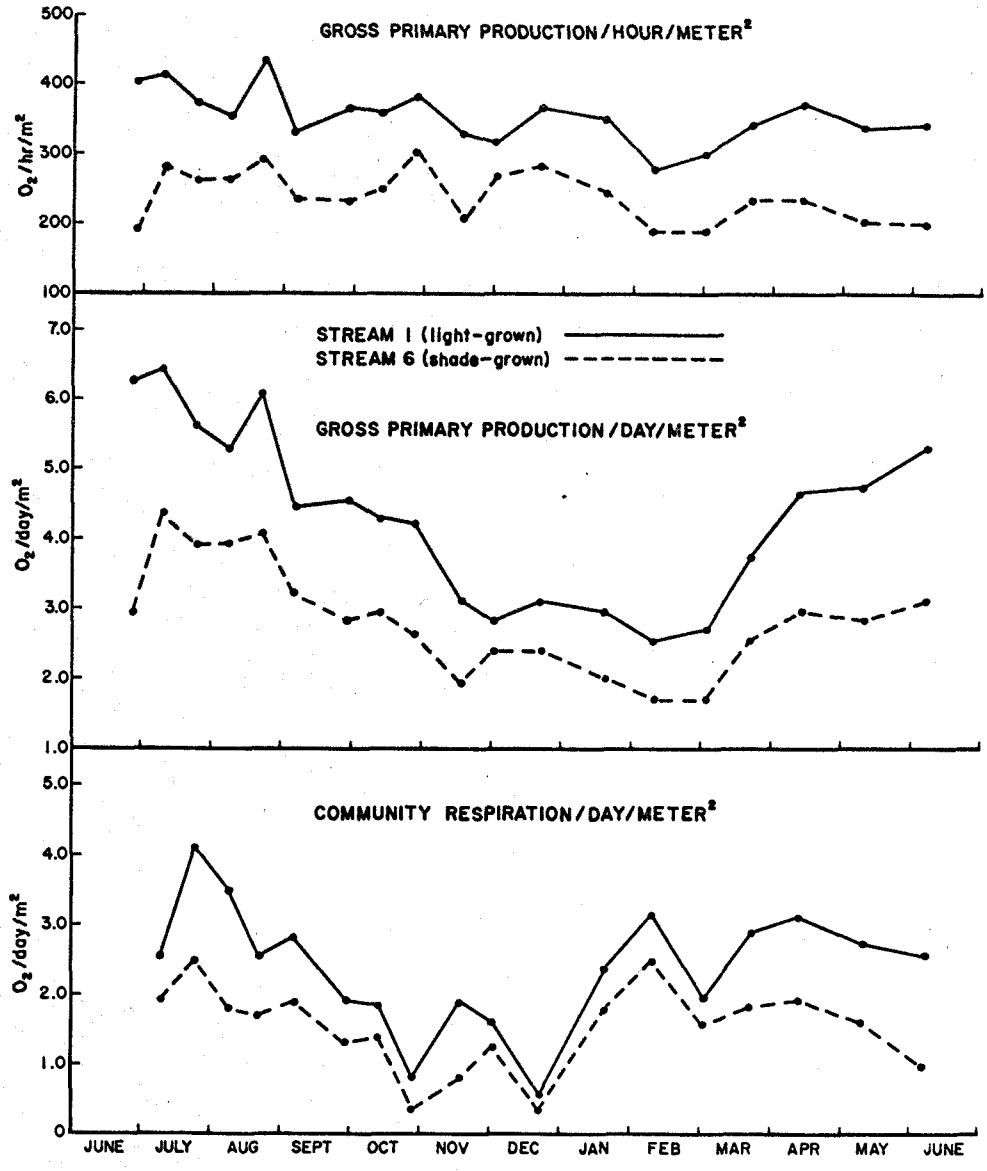

Figure 10. Gross primary production and community respiration rates determined for Stream 1 (light-grown) and Stream 6 (shade-grown), June, 1962, through June, 1963.

Subsequently the rates decreased during fall and early winter and then began to increase again in late January, reaching another maximum (3.1 $g/m^2/day$) on February 9, 1963. In Stream 6, rates of respiration followed the same general trend. A maximum of 2.5 $g/m^2/day$ was reached on July 25, 1962 and again on February 9, 1963. The extremely low rates of respiration obtained for both streams on October 27, 1962, and December 22, 1962, were inconsistant with the other values and were difficult to explain on the basis of temperature, as the lowest temperatures were not reached until January. It was concluded that these values were probably due to experimental error resulting from the loss of strength of the thiosulfate solution with age. Since the hourly changes in oxygen concentration due to community respiration were relatively small, the measurements of dissolved oxygen concentration for the estimation of diffusion rates were critical and had to be very accurate. If the normality of the thiosulfate solution used in the oxygen titrations was too low during any of the measurements, the oxygen values obtained were then too high and diffusion rates were therefore underestimated. Underestimated diffusion rates resulted in underestimated rates of respiration. After the second low value was obtained, the thiosulfate solution was restandardized each day before measurements were taken.

Biomass and organic matter

The study of biomass accumulation in the streams was initiated immediately after the streams were cleaned and refilled on June 12,

1962. To study the early development of biomass, weighed glass microscope slides were suspended in each stream by spring clothes-pins mounted on a piece of wood which was wedged between the sides of the troughs. The slides were oriented with their sides parallel to the stream flow. Periodically, a slide was removed from each stream, dried at 70° C., and reweighed to determine the dry weight of biomass which had developed on the slide. In Figure 11, these biomass estimates have been plotted against the number of hours that the slides were exposed to light in the streams.

The early development of biomass was much more rapid in Stream 1 (light-adapted) than in Stream 6 (shade-adapted). By the time all slides had been removed from the streams after 180 hours of light exposure, one slide from Stream 1 had accumulated as much as 140 mg of material. The highest dry weight of biomass found on a slide from Stream 6 at this time was 5.4 mg.

Estimates of biomass per square meter of substrate have been plotted at the top of Figure 12 (also see Appendix I). On June 28, 1962, approximately two weeks after the study was begun, the biomass was only 120 g/m^2 in Stream 1 and 89 g/m^2 in Stream 6. The quantity of biomass fluctuated considerably in both streams during the investigation, reaching a maximum of 593 g/m^2 in Stream 1 (December 22, 1962) and 565 g/m^2 in Stream 6 (April 12, 1963). Normally, the biomass of the light-adapted community (Stream 1) was greater than that of the shade-adapted community (Stream 6). Beginning in December, however, there was a general buildup of biomass in Stream 6

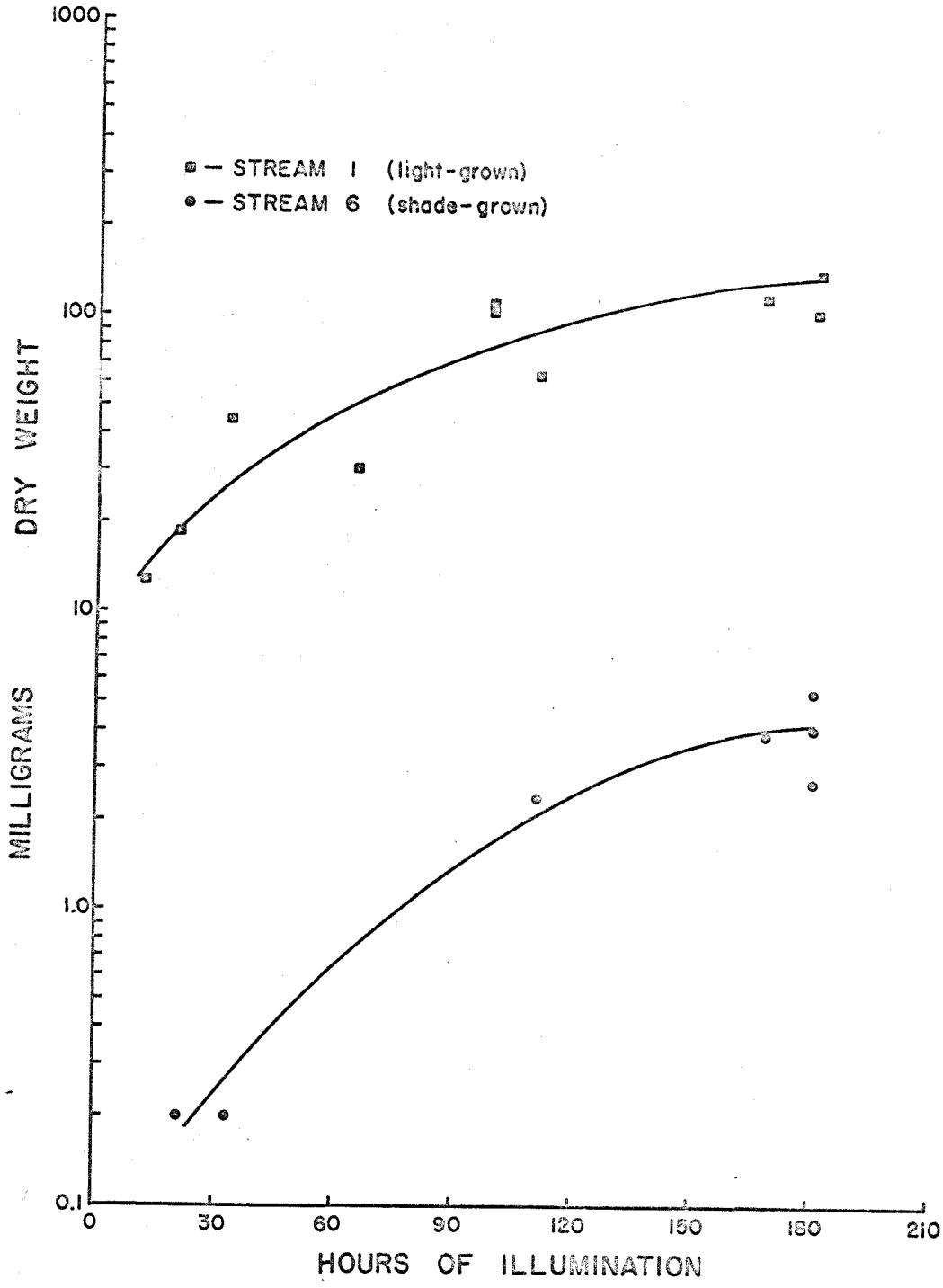

Figure 11. Rate of development of biomass on glass slides in Streams 1 and 6, June, 1962.

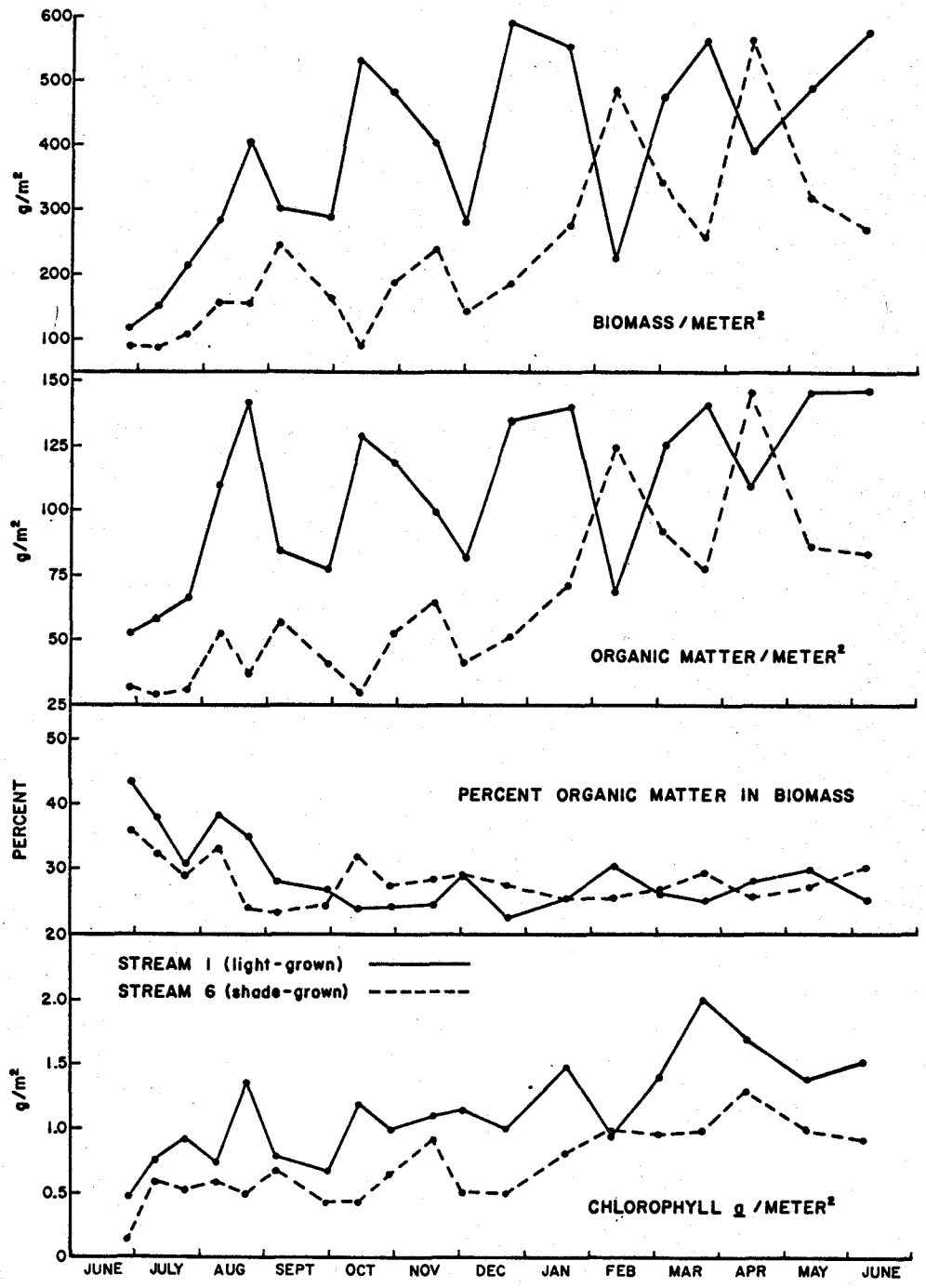

Figure 12. Estimates of biomass, organic matter, percentage of organic matter in the biomass, and chlorophyll a for Stream 1 (light-grown) and Stream 6 (shade-grown), June, 1962, through June, 1963.

which corresponded to a gradual increase in the quantity of Phormidium retzii, and on February 9 and April 12, 1963, the biomass in Stream 6 actually exceeded that in Stream 1.

The percentage of organic matter contained in the biomass was highest in both streams early in the study and gradually decreased through September; subsequently it varied between 23 and 32 percent (Figure 12 and Table 6).

The plot of organic matter per square meter for each stream (Figure 12) further emphasized the gradual buildup of Phormidium retzii in Stream 6 during the winter and spring of 1963. The lowest estimates of the organic matter in Streams 1 and 6 were obtained during the first month of the investigation and were 52 g/m^2 (June 28, 1962) and 29 g/m^2 (July 12, 1962), respectively. In Stream 1, organic matter reached distinct peaks in August (141 g/m^2), October (129 g/m^2), January (141 g/m^2), March (142 g/m^2), and May (147 g/m^2). In Stream 6, organic matter fluctuated at a relatively low level until December and then began to increase, reaching prominent peaks in February (125 g/m^2) and April (147 g/m^2).

The calories per gram of biomass and percentage of organic matter contained in the biomass have been tabulated in Table 6. Calories per gram of organic matter have also been estimated by dividing the calories per gram of biomass by the percent organic matter. The means of these values for each stream were remarkably similar. The mean number of calories per gram of biomass was 1191 in Stream 1 and 1106 in Stream 6. The biomass of Stream 1 had a mean organic

Table 6. Calories per gram of biomass, percentage of organic matter in the biomass, and calculated calories per gram of organic matter, Streams 1 and 6, July, 1962, through June, 1963.

Date	Stream 1 (light-grown)			Stream 6 (shade-grown)		
	Calories per gram biomass	Percent organic matter	Calories per gram organic matter	Calories per gram biomass	Percent organic matter	Calories per gram organic matter
7/25/62	1790	30.8	5812	1322	28.7	4606
8/8/62	1541	38.4	4013	1116	33.2	3361
8/22/62	1592	35.1	4536	1123	23.9	4699
9/5/62	1628	28.2	5771	1208	23.2	5207
11/17/62	922	24.8	3718	-	-	-
12/1/62	1223	29.4	4167	1119	28.8	3885
12/22/62	675	22.7	2974	1088	27.7	3928
1/19/63	963	25.5	3776	976	25.8	3783
2/9/63	1200	30.6	3922	968	25.7	3767
3/2/63	943	26.5	3558	1023	27.0	3789
3/22/63	872	25.2	3460	1260	29.7	4242
4/12/63	1168	28.2	4142	989	26.0	3804
5/10/63	1257	30.1	4176	1083	27.2	3982
6/6/63	903	25.7	3514	-	-	-
Mean	1191	28.7	4110	1106	27.2	4088

matter content of 28.7 percent and that of Stream 6 a mean of 27.2 percent. The mean, calculated number of calories per gram of organic matter was 4110 for Stream 1 and 4088 for Stream 6.

Chlorophyll a and carotenoids

Chlorophyll a per square meter of stream area (Figure 12 and Appendix I) gradually increased during the study in both Stream 1 (light-adapted) and Stream 6 (shade-adapted). In Stream 1, chlorophyll a increased from 0.48 g/m^2 on June 28, 1962, to a maximum of 2.01 g/m^2 on March 22, 1963. Chlorophyll a in Stream 6 increased from 0.14 g/m^2 on June 28, 1962, to a maximum of 1.30 g/m^2 on April 12, 1963. With the exception of the samples removed on February 9, 1963, the chlorophyll a content of the samples from Stream 1 was consistantly greater than that of the samples from Stream 6.

The ratios of total carotenoids expressed as Specified Pigment Units (MSPU) to milligrams of chlorophyll a are shown in Table 7. The carotenoids:chlorophyll a ratios were similar and remained almost constant in both Streams throughout the investigation. In Stream 1, the ratio varied between 0.277 and 0.419, and had a mean of 0.308. The mean ratio in Stream 6 was 0.299 and range was from 0.260 to 0.420.

Export

Collections of the biomass exported from each stream were made weekly for 24 hour periods, and these estimates of weekly export rates were plotted in Figure 13. It became apparent near the end

Table 7. Ratio of total carotenoids expressed as specified pigment units (MSPU) to milligrams of chlorophyll a, Streams 1 and 6, June, 1962, through June, 1963.

Date	Carotenoids/Chlorophyll a	
	Stream 1 (light-grown)	Stream 6 (shade-grown)
6/28/62	0.301	0.300
7/10/62	0.306	0.310
7/25/62	0.336	0.290
8/8/62	0.304	0.295
8/22/62	0.285	0.293
9/5/62	0.299	0.298
9/29/62	0.303	0.302
10/13/62	0.315	0.296
10/27/62	0.299	0.296
11/17/62	0.320	0.293
12/1/62	0.306	0.307
12/22/62	0.419	0.338
1/19/63	0.310	0.300
2/9/63	0.299	0.284
3/2/63	0.277	0.420
3/22/63	0.297	0.260
4/12/63	0.283	0.248
5/10/63	0.290	0.269
6/6/63	0.306	0.280
Mean	0.308	0.299

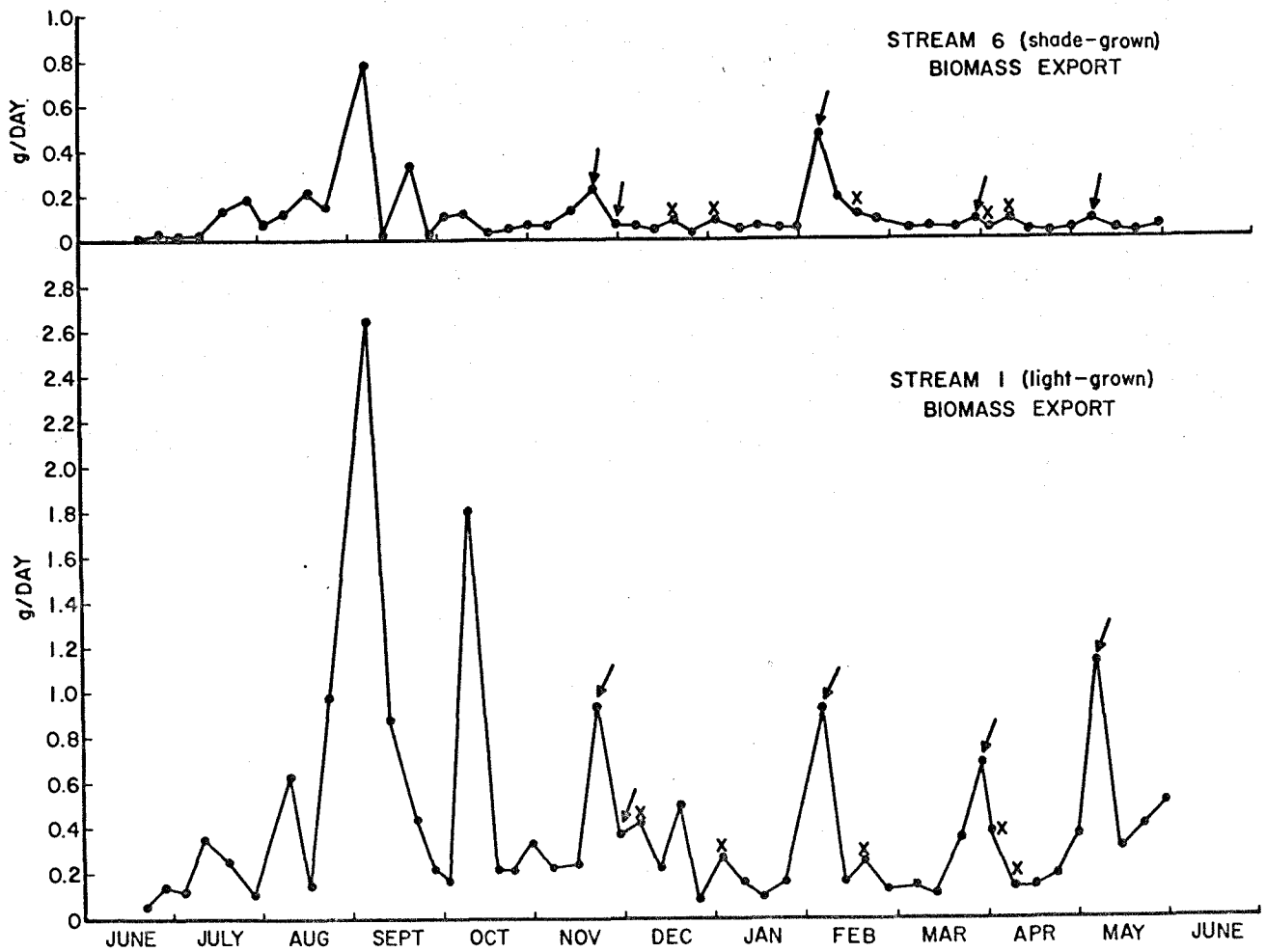

Figure 13. Rates of export of biomass from Stream 6 (shade-grown) and Stream 1 (light-grown), June, 1962, through June, 1963; arrows indicate "very turbid" conditions and "X"'s "slightly turbid" conditions.

of the study that the rate of export of material from the streams was greatly enhanced by turbid water conditions. Unfortunately, however, prior to this time, regular determinations of turbidity or "silt load" had not been made, and only daily records which subjectively indicated water conditions as "clear," "slightly turbid," or "turbid" were available for comparison. In Figure 13, notations have been included indicating these subjective estimations of turbidity. The small arrow (↓) over a point indicates that the water was considered to be very turbid on that particular date when export was measured; the "X" notation indicates "slightly turbid" conditions.

The highest rate of export for both streams was recorded during the first week in September after corresponding increases in the biomasses in July and August (Figures 12 and 13). At this time export was 2.651 g/24 hours in Stream 1 (light-adapted) and 0.782 g/24 hours in Stream 6 (shade-adapted). Subsequently, relatively high rates of export occurred in Stream 1 in mid-October (1.801 g/24 hours), late November (0.949 g/24 hours), early February (0.919 g/24 hours), late March (0.686 g/24 hours), and early May (1.124 g/24 hours) and in Stream 6 in late September (0.329 g/24 hours), late November (0.207 g/24 hours)), and early February (0.460 g/24 hours). These peaks were also associated with similar fluctuations in the biomasses of the streams.

With the increase in precipitation during late fall and winter, the communities were frequently in contact with a turbid medium, and the "silt load" carried by the influent creek water

apparently had a scouring effect on the substrate. Extremely turbid water conditions were encountered in late November, early February, late March, and early May. These periods also corresponded to periods of high export, particularly in Stream 1. As the community composition in Stream 1 often included genera of filamentous green algae (such as Oedogonium and Ulothrix) which formed long, loose, oscillating strands from the rocks, and as Stream 1 developed a large biomass rapidly with the higher light level, this stream was more vulnerable than Stream 6 to the effects of turbidity.

Community structure

Table 8 gives a list of the most abundant genera found in Streams 1 and 6 during the study. The structure of the communities which developed in the streams was similar in several respects. Both streams consistently maintained an abundant diatom flora which consisted primarily of Synedra ulna, Melosira varians, and species of Cymbella, Epithemia, and Navicula, although, visually, the diatom cells in Stream 6 appeared to have a darker pigmentation than those in Stream 1. Species of Oedogonium also developed in both streams but were particularly abundant in Stream 1 during the warmer months. Phormidium tenue and a species of Anabaena were abundant in both streams at times and grew attached to the sides of the troughs as well as on the rocks. Beginning in November, 1961, Phormidium retzii gradually became a significant part of the community in Stream 6, and by the end of the study in June, 1963, it was the dominant form in the stream.

Table 8. List of dominant genera of plants in Streams 1 and 6, June, 1962, through June, 1963.

Stream 1 (light-grown)	Stream 6 (shade-grown)
Diatoms:	Diatoms:
Cymbella	*Achnanthes*
Epithemia	*Cymbella*
Melosira	*Melosira*
Navicula	*Navicula*
Synedra	*Synedra*
Green Algae:	Green Algae:
Oedogonium	*Closterium*
Ulothrix	*Oedogonium*
Bluegreen Algae:	Bluegreen Algae:
Anabaena	*Anabaena*
Calothrix	*Phormidium*
Phormidium	

In Figure 14, the species composition of the plant communities has been divided into three principal groups: diatoms, Phormidium retzii, and "other" forms. These data were obtained by making counts of organisms when viewed on slides prepared from aliquots of biomass samples. Ten fields of each slide were counted at 430X magnification, and the relative abundance of each genus, expressed as percent of the total number organisms, was calculated from the counts. Although this technique was rather crude and subject to sampling errors due to the filamentous nature of some of the material and the "patchy" distribution of some of the species, particularly Phormidium retzii, it did show important general trends in the community structure which helped in the interpretation of production and biomass data.

In Stream 1, diatoms made up 84 percent or more of the community during the cooler months from early September, 1962, through mid-February, 1963; at other times, cells of green and bluegreen algae were present in significant numbers. The diatoms dominated in Stream 6 until early December at which time Phormidium retzii began to crowd out other species, reaching a maximum of about 75 percent of the total number of cells in March and June.

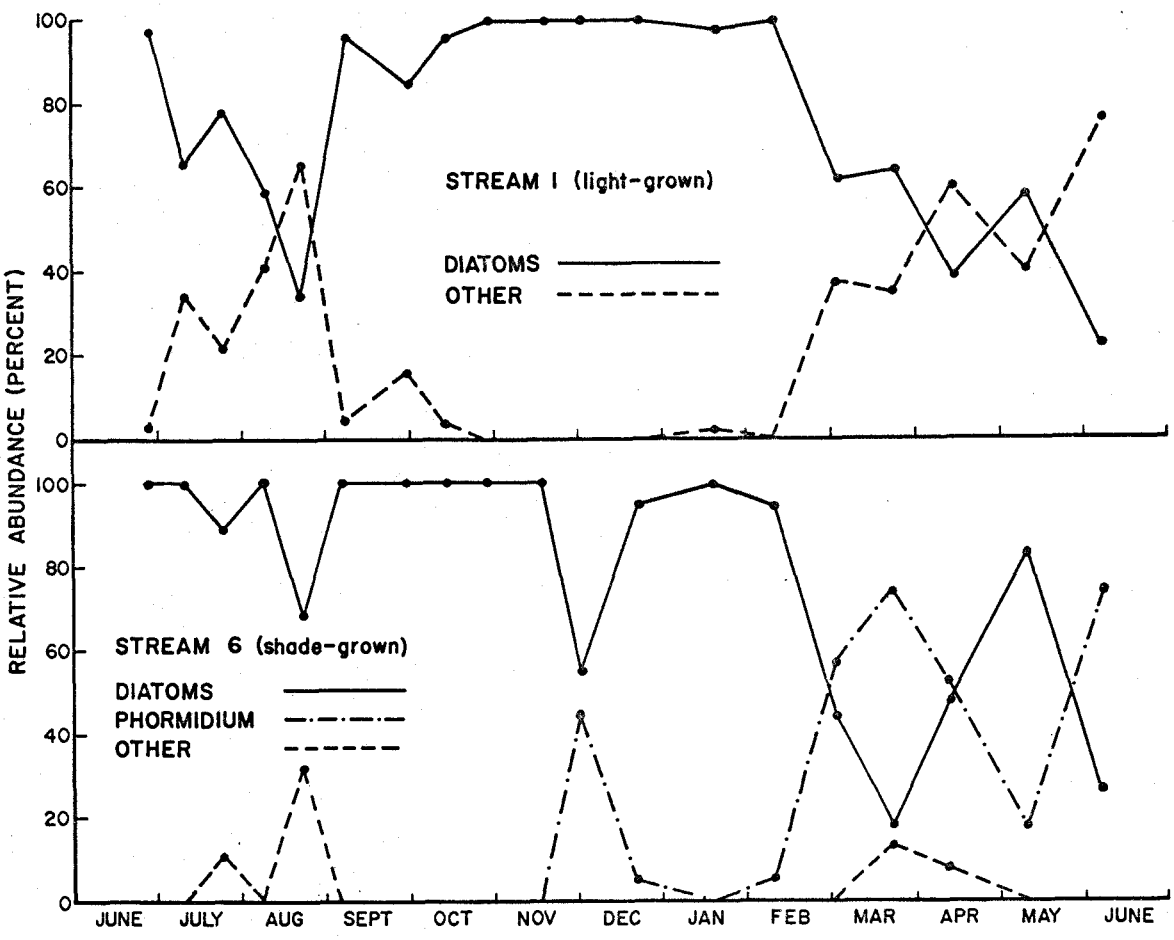

Figure 14. Structure of the plant communities in Stream 1 (light-grown) and Stream 6 (shade-grown), June, 1962, through June, 1963.

DISCUSSION

Results of the effects of variation in illumination intensity and in carbon dioxide concentration on primary production of the periphyton communities grown in laboratory streams have been given as curves expressing the rate of oxygen evolution (photosynthesis) as a function of light intensity, or $P = f(I)$, and in certain cases, with the concentration of molecular carbon dioxide as a parameter. A detailed review of the kinetics of photosynthesis, which included a discussion of the dependence of photosynthetic rate on such external factors as light intensity, carbon dioxide concentration, and temperature, was presented by Rabinowitch (36, p. 829-1189). Some of the more important aspects of this review along with some theoretical as well as ecological considerations presented by other workers will be discussed below in connection with the results of the laboratory studies presented in the previous section.

Sachs (42) based his early discussion of the dependence of photosynthesis on external factors (such as light, carbon dioxide, and temperature) on the concept of the three "cardinal points." This concept held that biological processes began only after a certain minimum value of a relevant external variable, reached the highest rate at a certain optimum value of the variable, and subsequently declined, ceasing altogether after a maximum tolerable value had been exceeded. Later, Blackman (2, p. 289) introduced his theory of "limiting factors" which stated that, "when a process is conditioned

to its rapidity by a number of separate factors, the rate of the process is limited by the pace of the 'slowest' factor." Blackman and Matthaei (4) and Blackman and Smith (3) suggested that, as photosynthesis required no minimum light intensity and showed a broad "saturation plateau" rather than a sharp optimum, curves relating light intensity to photosynthetic rate were explained better by the theory of limiting factors than by the concept of the three cardinal points. They also believed that there was no optimum intensity of light for assimilation and that no decline in photosynthetic rate occurred at high light intensities, unless there was actual injury to the kinetic mechanism of photosynthesis. According to Blackman's theory, then, a curve relating light intensity to photosynthesis theoretically consisted of a linear ascending part, terminated by a sharp break and followed by a horizontal plateau.

Rabinowitch (36, p. 965) found it impossible to accept Blackman's conclusion that the linearly ascending part of the curve goes over abruptly into the horizontal part and believed that all precise observations confirmed the opinion that light saturation is reached asymptotically. His explanation for the gradual transition from the linearly ascending part to the horizontal part of the curve was based on the inhomogeneity of light absorption which is inevitable in multicellular systems. He further pointed out that even within a single chloroplast the rate of light absorption decreased by a significant factor from the light-exposed to the shaded side. In ecological systems, such as the laboratory streams, the strongly

heterogenous nature of light absorption by mixed populations would then, according to Rabinowitch's contentions, have an even greater tendency to cause a gradual transition between the linear and horizontal parts of curves relating light intensity to primary production.

Curves relating photosynthetic rate to light intensity can be characterized by the initial slope and linear range, the compensation point, and the saturating light intensity. Rabinowitch (36, p. 981) believes that, theoretically, the linear range can not be exactly defined, as all curves of this nature are probably hyperbolae and can only approach straight lines asymptotically. In any case, the almost linear segment of the curves corresponds to "a state in which the primary photochemical process is so slow that the catalysts which participate in the nonphotochemical steps can supply the substrates needed for, and transform the intermediates formed by, the primary process, without depletion of the former or accumulation of the latter" (Rabinowitch, 36, p. 1012). The compensation point is defined as the light intensity at which the oxygen evolved during photosynthesis is exactly balanced by the oxygen consumed during respiration, i. e., the net gas exchange is zero. In ecological work, it must be stated whether the term "compensation point" as used refers to the gas exchange during a photosynthetically active period alone, or whether, the compensation point is figured on the basis of a normal 24 hour day which includes both light and dark periods. In the work presented in this thesis, the symbol $C.P._L$

is used to designate the former value and $C.P._{24}$ the latter value. The saturating light intensity is that intensity at which a further increase in the light flux no longer produces a concurrent increase in the rate of photosynthesis. It has been shown to vary widely from species to species and is dependent on optical density, carbon dioxide supply, temperature, and such internal factors as age and adaptation.

According to Rabinowitch (36, p. 981), at room temperature and with an adequate supply of carbon dioxide, the linear range usually extends up to 1-2 klux of white light (ca. 100-200 foot candles). This general conclusion also appears to hold for the light-adapted periphyton communities grown in the laboratory streams (Figures 4, 5, 6, and 7). On the other hand, the linear range of the curves plotted for the shade-adapted communities does not appear to extend beyond 100 foot candles (Figures 6 and 8). It is realized, however, that these conclusions are only generalizations based on visually fitted curves.

Values for the compensation points, $C.P._L$ and $C.P._{24}$, have been estimated from the data plotted in Figure 4. The mean community respiration during the experiment was 46 mg $O_2/m^2/hr$. Using the solid-line curve in Figure 4, this rate of oxygen consumption therefore corresponded to a $C.P._L$ of about 50 foot candles (538 lux). Assuming a 24 hour day consisting of a 12 hour light period and 12 hours of darkness, the $C.P._{24}$ would be in the neighborhood of 100 foot candles.

The compensation point depends primarily on the photosynthetic capacity of the plants and the rate of respiration, if the carbon dioxide supply is not too low. Communities consisting of a mixture of heterotrophic animals and bacteria as well as plant species at different ages and in various stages of photosynthetic activity and decomposition can be expected to have a higher compensation point than that determined for a young, fully active, unispecific plant population. In Table 9, the $C.P._L$ estimated for the laboratory community is compared to $C.P._L$ values for different species of green and other algae obtained by other workers and tabulated by Rabinowitch (36, p. 983). The table shows that the $C.P._L$ of the periphyton community is slightly higher than that of any of the listed species of algae.

Rabinowitch (36, p. 986 and 1013) has pointed out that the saturating light intensity is usually never reached suddenly. This effect is particularly pronounced in a periphyton community where light absorption is strongly heterogeneous due to shading effects resulting from the dense aggregation of material on the substrate.

In all the curves relating light to primary production that were determined for the laboratory periphyton communities, the saturating light intensity was reached gradually (Figures 4, 6, 7, and 8). In curves plotted for the light-adapted communities, the saturating intensity was in the vicinity of 2000 foot candles. A shade-adapted community (Figure 6) appeared to reach light saturation at only a slightly lower intensity (ca. 1700 foot candles). Ryther (38) found that the saturating light intensity for marine

Table 9. Compensation point, $C.P._L$, of a laboratory stream community and of different species of green and colored algae*.

Classification	Plant species	$C.P._L$, Lux	Temp. °C.
Green Algae:	Spirogyra sp.	174	
	Cladophora sp.	253	
	Enteromorpha compressa	457	16
	Ulva lactuca	357	16
	Cladophora rupestris	322	16
	Chlorella pyrenoidosa	400	25
Colored Algae:	Fucus serratus	408	16
	Laminaria saccharina	345	16
	Plocamium coccineum	299	16
	Phyllophora brodiaei	312	16
	Delesseria sanguinea	270	16
Laboratory Community	Mixed, consisting of species of diatoms and Oedogonium sp.	538	10.2 (Mean)

* Compensation points of the green algae and colored algae obtained by other workers as tabulated by Rabinowitch (1951, p. 983).

phytoplankton, grown in culture at 350, 1000, and 1500 foot candles and under natural sunlight, ranged from approximately 500 to 2500 foot candles depending on whether the organisms were species of diatoms, dinoflagellates, or Chlorophyta. Curves published by Wassink and Kersten (55) indicated that the diatom, Nitzschia sp., grown in Richter solution and 5 percent CO_2, reached light saturation at about 6 ergs/cm^2.sec. This value is approximately equivalent to 1500 foot candles of photosynthetically active sunlight.

It is commonly believed that adaptation to strong or weak light involves an adjustment of the concentration of some rate-limiting catalyst, i.e., the enzyme responsible for the saturation of photosynthesis (Rabinowitch, 36, p. 993 and Steemann Nielsen and Hanson, 49). In general, shade-adapted plants contain more chlorophyll and accessory pigments than light-adapted species or individuals, and their curves relating light intensity to photosynthetic rate usually exhibit a steep initial slope and a relatively low saturating intensity (van der Paauw, 30; Steemann Nielsen and Hansen, 49; and Rabinowitch, 36, p. 986). The shade-adapted periphyton communities which developed in the laboratory streams also showed these same general characteristics, with the exception that the saturating intensity was not as low as might be expected. The relatively high light intensity that was required for the saturation of the shade-adapted communities was not surprising, however, considering the number of species involved and the extremely heterogeneous nature of light absorption by communities of this kind.

Besides the difference in initial slopes, the most striking difference between curves plotted for shade-adapted communities and those for light-adapted communities was in the nature and extent of the inflection from the linear segment toward the horizontal. This inflection in the curves for shade-adapted communities was longer, more gradual, and more irregular than that showed by the curves for light-adapted communities (Figure 6).

Smith (45) proposed the empirical equation

$$KI = P(Pm^2 - P^2)^{-\frac{1}{2}} \qquad (1)$$

to relate photosynthetic rate (P) and light intensity (I) when K was a constant that located the curve on the scale of light intensity and P_m was the asymptotic maximum rate. He believed that equations of this type were useful as a criterion for the validity of any theoretical description of photosynthesis. Similar curves, but differing in slope and inflection, resulted from changing the exponents in the equation. Talling (51) also found that Smith's equation fit data obtained for species of freshwater plankton diatoms. He expressed photosynthetic rates as relative values, however, and changed equation (1) slightly to

$$KI = p(1 - p^2)^{-\frac{1}{2}} \qquad (2)$$

where p is equal to P/Pm. If the function $p(1 - p^2)^{-\frac{1}{2}}$ was plotted against light intensity, a straight line relationship indicated that equation (2) was applicable to the data. Such plots were made in Figure 15 using data obtained in March, 1961, and July, 1962, and previously presented in Figures 4 and 6. The curve obtained in March

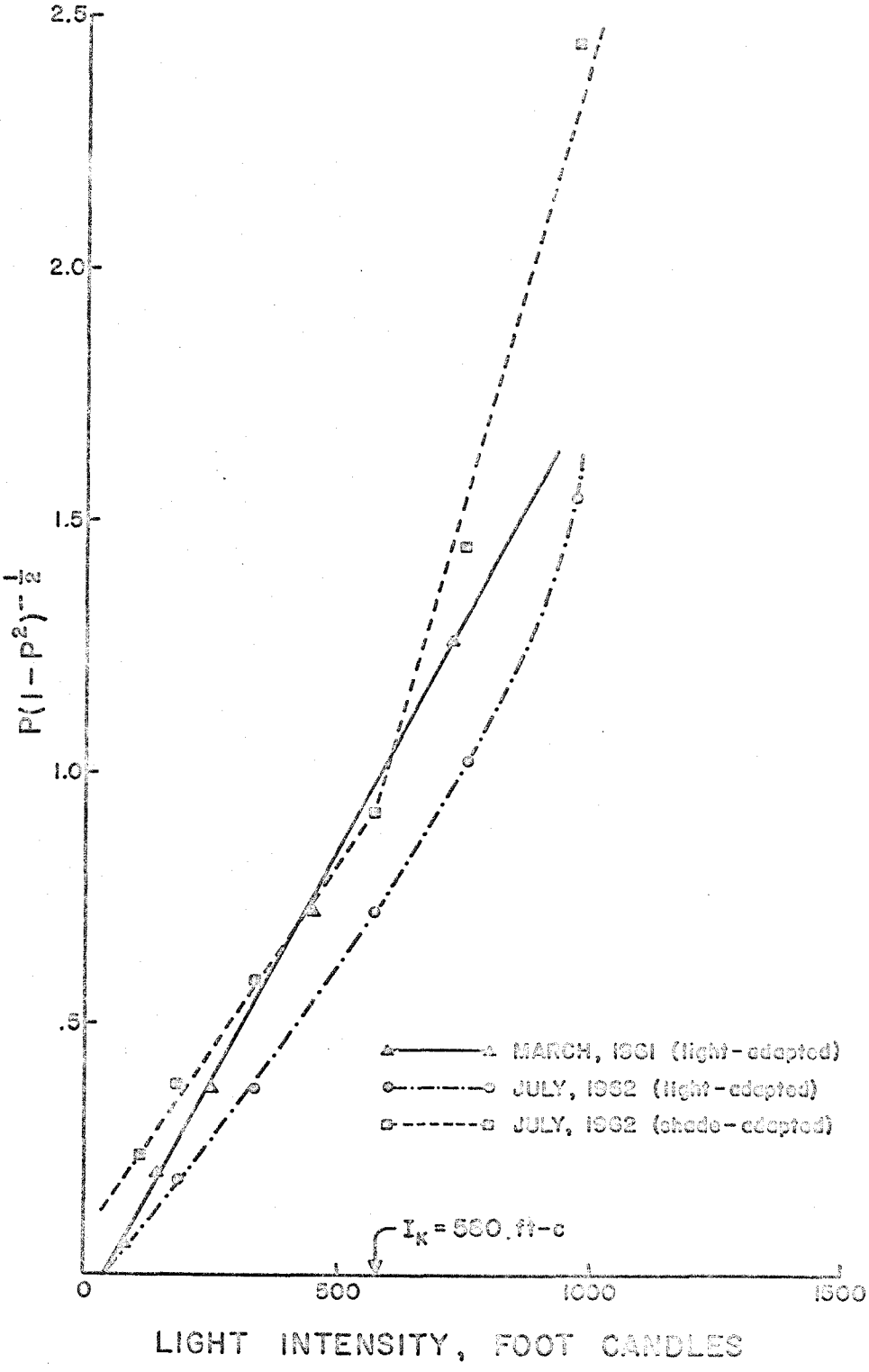

Figure 15. Relationships between values for the function $p(1 - p^2)^{-\frac{1}{2}}$ and illumination intensity plotted for "light- and "shade-adapted" communities.

1961, for a light-adapted community fit equation (2) very well, and a straight line was fitted to the values for the function $p(1-p^2)^{-\frac{1}{2}}$ by the method of least squares (Figure 15). Values for the function were also computed and plotted for the July, 1962, curves. The plot obtained for the light-adapted community showed a slight curvature, indicating that the data did not fit equation (2) as well as the March, 1961, curve. This line was made almost straight, however, by raising the exponent of p to the fourth power, i.e., by changing p^2 to p^4 in the denominator. Equation (2) did not, even approximately, fit the curve for the shade-adapted community, as the plot of $p(1 - p^2)^{-\frac{1}{2}}$ yielded two approximately linear segments with very different slopes. It was concluded, then, that curves relating primary production to light intensity obtained for the light-adapted periphyton communities could be characterized by equations of this type, while curves determined for the shade-adapted communities could not be expressed mathematically in this manner.

Theoretical discussions of curves relating the rate of photosynthesis to the concentration of carbon dioxide at different light intensities have been presented by Blackman (2), Bose (6, p. 265), Lundegardh (16), Singh and Lal (43), and Harder (11). Rabinowitch (36, p. 1014) has observed that most curve sets, $P = f(F_1)$ with F_2 as parameter, with P as the photosynthetic rate, F_1, the light intensity, and F_2, the concentration of molecular carbon dioxide, are of the type in which F_2 determines the maximum rate of a partial process that does not depend on the independent variable, F_1. This

process therefore imposes a horizontal ceiling on the curve $P = f(F_1)$, but does not affect its initial slope. Kinetic curves published by Wassink and Kersten (55) where F_2 equals the carbon dioxide concentration and those presented by Noddack and Kopp (20) and Talling (51) with F_2 as the temperature are examples of this type of relationship. It appears, also, that the carbon dioxide curves obtained during August and September, 1962, for the laboratory periphyton communities show these general characteristics (Figures 7 and 8).

Rabinowitch (35, p. 188-209; 36, p. 886-910) has presented a detailed review of work concerning the absorption of carbon dioxide by plant cells and has concluded that leaves contain two main carbon dioxide absorbing factors: solid carbonates, and a water soluble buffer. The cell water of a terrestrial plant, if it were pure, would contain in contact with the free atmosphere at 25^{o} C., about 9×10^{-6} mole per liter of carbon dioxide. If the cell water were unbuffered, about 15 percent of the dissolved carbon dioxide would be in the form of bicarbonate ions, and under these conditions, the sap would be acid. With almost all plants investigated, however, the absorption of carbon dioxide was in excess of this normal solubility, and this excess absorption was attributed to a conversion of carbon dioxide into bicarbonate by alkalizing agents, the most important of which were solid alkaline earth carbonates and dissolved primary phosphate. Although most of this experimental work has been performed with land plants, it is reasonable to expect the same general chemical systems to function also in aquatic plants, particularly the

aquatic vascular plants.

The role of bicarbonate ions in photosynthesis is still not well understood. It has been assumed by many investigators that cell membranes are quite permeable to carbon dioxide molecules, while at the same time, almost impermeable to bicarbonate ions. Early work using Warburg's buffers which contained tens of thousands of HCO_3^- and $CO_3^=$ ions for each CO_2 molecule indicated that the curves showing the yield of photosynthesis in relation to the concentration of the species CO_2 in these mixtures had approximately the same shape as those obtained in experiments with land plants supplied with free CO_2 molecules only. Similarly, Osterhout and Dorcas (25) found that the rate of penetration of carbonic acid into the interior of the unicellular alga, Valonia, was proportional to the external concentration of carbon dioxide and unaffected by the addition of a large quantity of carbonate and bicarbonate ions. More recent studies (Steemann Nielsen, 48; Osterlind, 26, 27, 28, and 29; and Hood and Park, 12), however, have accumulated evidence indicating that bicarbonate ions actually penetrate into the cell from outside in some species and play a direct part in photosynthesis.

Blackman and Smith (3) found a continued increase in the rate of photosynthesis with increasing carbon dioxide concentration until the latter reached a value as high as 400×10^{-5} mole per liter. Less extreme values ranging from $20 - 30 \times 10^{-5}$ mole per liter CO_2 were found by Harder (11) and Smith (46, 47) in vascular

aquatic plants and Emerson and Green (8) in Gigartina. Even more careful investigations, notably that of Hoover and co-workers (13) on vascular plants and Emerson and Green (9) on Chlorella, found the rise of photosynthesis with increasing carbon dioxide concentration ceased as early as between 0.5 - 5 x 10^{-5} mole per liter CO_2. The lower results were obtained by experiments with land plants in rapidly circulating gas, and with algae in well-stirred acid or alkaline solutions. The accepted explanation is the higher values were due to insufficient circulation and consequent depletion of carbon dioxide in the medium surrounding the plants. Rabinowitch (36, p. 908) concluded that whenever the rate of photosynthesis was enhanced by increasing the external concentration of carbon dioxide much above 10 x 10^{-5} M, the reason was slow outside supply to the photosythesizing cells, and consequent exhaustion of the reduction substrate.

In the light-adapted periphyton community (Figure 7), primary production was continuously enhanced by increasing the supply of molecular carbon dioxide to a concentration as high as 45 milligrams per liter (100 x 10^{-5} M). From the prior discussion of saturation concentrations, it appeared that any enhancement beyond 6.6 milligrams per liter (15 x 10^{-5} M) would indicate an exhaustion of carbon dioxide in the immediate vicinity of the plant cells. As this exhaustion apparently persisted even while the water in the 50 liter P-R chamber was circulated rapidly by two pumps, it is suggested that the periphyton communities were particularly susceptible

to carbon dioxide exhaustion effects. This was not surprising, however, considering the sessile nature of the organisms making up these communities. The non-photosynthesizing part of the community (heterotrophic organisms amd dead and decomposing autotrophs), which were also packed on the substrate in close contact with the autotrophic forms, undoubtedly reduced the amount of surface area of the photosynthetically active part of the community that was in contact with surrounding nutrient medium. In addition, the autotrophic forms, in mass, probably limited their own exposed surface area. It was therefore concluded that, for complex ecological systems at least, the effect of the concentration of carbon dioxide, and perhaps that of other nutrients also, on the rate of photosynthesis was primarily influenced by such factors as circulation and mixing that controlled the external diffusion gradients in the immediate vicinity of the cells.

Talling (51) defined an expression I_k to indicate the onset of light saturation of photosynthesis. The I_k value is equivalent to the light intensity at which extrapolations of the initial linear region and light-saturated region of the photosynthesis-light intensity curve intersect. It can be estimated either graphically by extrapolations, or mathematically, if the data conform to the equation

$$KI = p(1 - p^2)^{-\frac{1}{2}} \qquad (2)$$

If conformation exists, I_k is equal to K^{-1} and can be read off as the light intensity at which the function $p(1 - p^2)^{-\frac{1}{2}}$ equals one.

The I_k values are useful in providing a numerical evaluation of the effect of a parameter F_2, such as carbon dioxide concentration or temperature, on the relationship between light intensity and photosynthetic rate.

Table 10. I_k values at different concentrations of free carbon dioxide determined for light- and shade-adapted communities, August and September, 1962.

Community	Date	Temperature (°C.)	Free CO_2 (mg/l)	I_k (foot candles)
Light-adapted	8/14/62	16.9	1.8	590
	8/15/62	17.2	6.6	660
	8/16/62	17.9	17.5	760
	8/17/62	16.6	45	845
Shade-adapted	9/10/62	16.9	1.3	530
	9/11/62	15.5	5.0	560
	9/12/62	14.9	22	590
	9/13/62	16.3	37	600

Table 10 gives graphically determined I_k values from the curves plotted in Figures 7 and 8. The effect of providing the light-adapted community with additional free carbon dioxide was shown by the increase in the I_k value from 590 to 845 foot candles, which corresponded to an increase of free carbon dioxide from 1.8 to 45 mg/l. In the shade-adapted community, the addition of carbon dioxide had very little effect on the shape of the photosynthesis-light intensity curve, and the I_k value only increased correspondingly from 530 to 600 foot candles. It was interesting to compare the I_k value determined for the light-adapted community when carbon

dioxide was not added (see lowest curve in Figure 7 and first line in Table 10) with a mathematically determined I_k value for a similar light-adapted community (Figure 4). It was mentioned above that the March, 1961, data plotted in Figure 4 conformed to equation (2) and that the I_k value for such curves was equal to the light intensity at which $p(1 - p^2)^{-\frac{1}{2}}$ was equal to one. In Figure 15, then, the I_k value for the March, 1961, data was 580 foot candles. This value was in close agreement with the graphically extrapolated value of 590 foot candles (August, 1962, data) shown in Table 10. Thus for a light-adapted periphyton community under normal laboratory conditions, the onset of light saturation (I_k) was approximately 580 to 590 foot candles.

The results of the investigation of the seasonal variations of periphyton production and community metabolism under "light" and "shade" conditions made possible the comparison of the laboratory communities with stream communities in nature. These data also provided the opportunity to carefully examine, in the laboratory, some of the relationships between primary production, community respiration, biomass, organic matter, chlorophyll, and export with respect to seasonal variations in photoperiod and temperature. Further, it was possible to study interesting contrasts in the successional pattern and community structure of the light- and shade-grown laboratory communities.

Odum (21) reviewed literature that presented estimates of gross primary production of organic matter in various types of ecosystems. He found that values for eutrophic lakes were usually about

1 g/m^2/day; oceanic waters had gross production magnitudes of 0.17-1.6 g/m^2 day; terrestrial agriculture under the best circumstances sustained net production of 10 - 20 g/m^2/day; and mass Chlorella cultures under optimum conditions yielded a net production of 2 - 19 g/m^2/day. Odum (21 and 22) also tabulated the productivity of a number of flowing water communities on the basis of oxygen metabolism data and concluded that primary production in flowing waters was very high as compared to other types of ecosystems. Gross production varied from 0.24 g/m^2/day in the White River in Indiana to 59 g/m^2/day in Homosassa Springs in Florida. Gross primary production of the laboratory periphyton communities was 1.7 - 4.1 g O_2/m^2/day for the shade-grown community and 2.5 - 6.4 g O_2/m^2/day for the light-grown community. These values were roughly compared with the above magnitudes of gross production by assuming a photosynthetic quotient of one (O_2 evolved/CO_2 assimilated = 1) and converting the oxygen data to organic matter on the basis of 0.94 g organic matter / g O_2. The ranges then became 1.6 - 3.9 g organic matter/m^2/day and 2.4 - 6.0 g organic matter/m^2/day, respectively. It appeared that, in general, gross production in the laboratory streams was slightly greater than that normally reported for eutrophic lakes and oceanic waters and more characteristic of the least-productive flowing water systems.

The results of numerous measurements of primary production in different kinds of environments have prompted investigations concerning the effects of current velocity on productivity in lotic

systems. Odum (21) suggested that the current renewed the depleted requirements for life and removed accumulating byproducts of metabolism. Whitford (58) believed that the action of the current rapidly removed material near the cell surface and produced a steep diffusion gradient, thereby increasing exchange of materials between organism and environment. He felt that the current must exceed 15 centimeters per second and displace the relatively quiet water within $\frac{1}{4}$ mm of the plant surface to produce the effect. Whitford and Schumacher (59) performed experiments with the filamentous green alga, Oedogonium kurzii, and found that phosphorus uptake was over 10 times greater and respiration over 70 percent greater in a current of 18 centimeters per second than in still water. The "current effect" as discussed by these workers was therefore the same kind of effect as that brought about in the laboratory by rapid circulation and mixing of cultures. This was discussed above in connection with the carbon dioxide experiments.

The ratio of the daily rate of photosynthesis to the daily rate of community respiration expressed in the same units (P/R ratio) has frequently been used to characterize aquatic communities and to classify them into autotrophic and heterotrophic types (Odum, 21). If production exceeded respiration (P/R greater than 1.0), the community, as a whole, was autotrophic, and there was a net accumulation of biomass, which was either stored locally or exported from the system. If, on the other hand, the P/R ratio was less than 1.0, the community was heterotrophic, and there was a net

loss of biomass from the system that had to eventually be replenishd by imports from the outside, if the community was to survive.

The P/R ratios for the shade- and light-grown periphyton communities have been plotted at the bottom of Figure 16 (also see Appendix I). The extremely high ratios recorded on October 27 and December 22, 1962, were inconsistant with the other values and were possibly due to the error in determination of community respiration that was discussed earlier. Excluding these abnormally high values, the P/R ratios varied between 0.79 and 2.54 in Stream 1 (light-adapted) and 0.69 and 3.24 in Stream 6 (shade-adapted). The P/R ratio dropped below 1.00 in both streams on only one sampling date (February 9, 1963). At this time, the water in the streams was very turbid, photosynthetic rates were low, and the rates of export and community respiration were higher than usual. A prolonged period of turbid conditions in February apparently caused a reduction in light energy reaching the plant communities and stimulated an increase in the bacterial decomposition of part of the communities. Also, possibly a significant fraction of the photosynthetically active part of each community was scoured free from the rocks by the heavy silt load and exported from the system. Summarizing, then, it appeared that the laboratory periphyton communities could be characterized as autotrophic communities with P/R ratios normally ranging from about 1.3 to 2.5 Odum (21) tabulated P/R ratios determined for autotrophic flowing water communities in nature and showed that the ratio was usually between 1.0 and 3.0, but extended

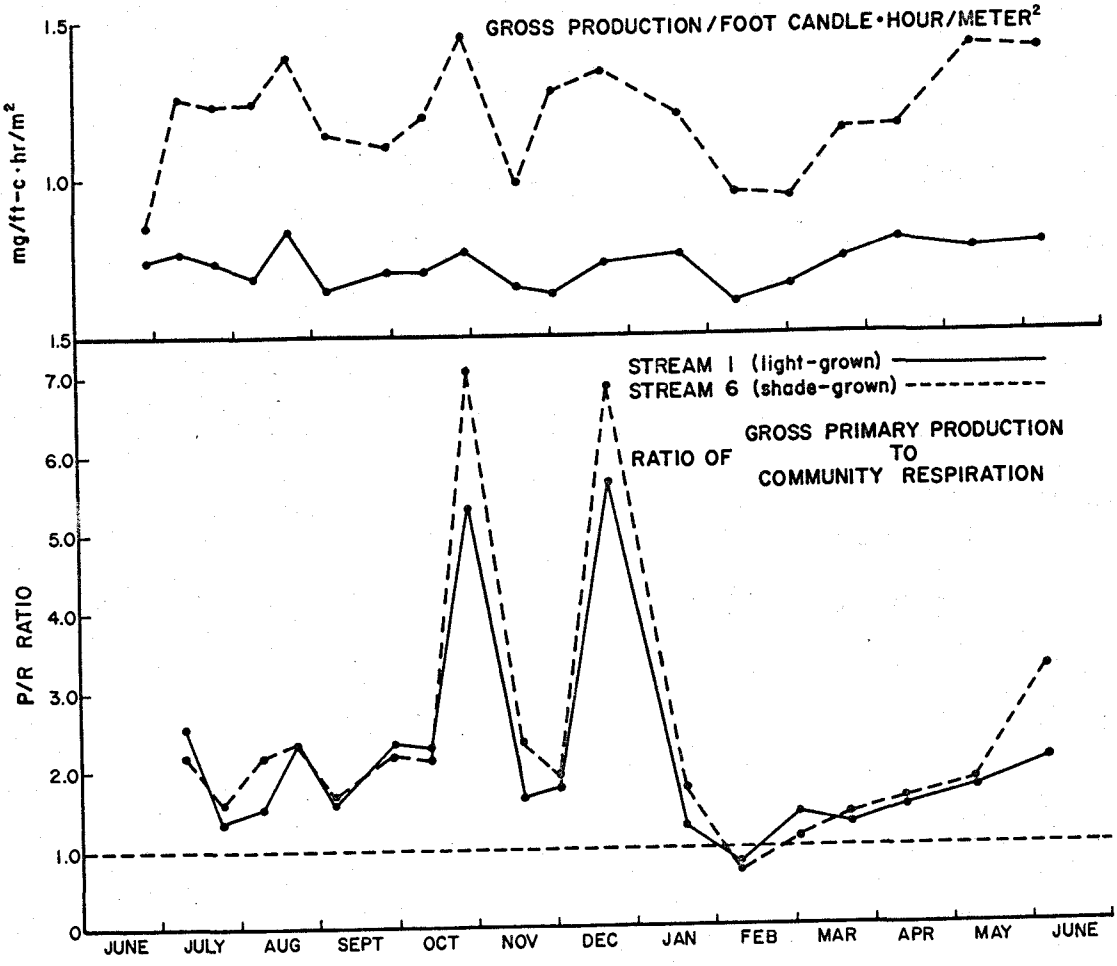

Figure 16. Gross primary production per foot candle-hour and ratios of gross primary production to community respiration (P/R ratios) calculated for Stream 1 (light-grown) and Stream 6 (shade-grown), June, 1962, through June, 1963.

as high as 7.0 in one case. Odum and Hoskin (23) found that communities developing in a laboratory stream microcosm had P/R ratios varying between 0.6 and 1.3.

It was of interest to compare the annual rates of primary production in the laboratory streams with similar rates found in various natural ecosystems. McConnell and Sigler (18) have compiled a list of annual production rates expressed as kilograms of glucose per square meter per year for a number of different natural environments. In Table 11 these values have been retabulated with values for the artificial streams. Annual rates of gross production for the laboratory streams were estimated by graphically integrating the oxygen metabolism data shown earlier in the middle section of Figure 10. The data permitted an integration between the limits of June 28, 1962, and June 6, 1963 (343 days). Although this interval was not quite a full year, it was close enough for comparative purposes. The integrations yielded values of 1.344 kg O_2/m^2 for Stream 1 (light-grown) and 0.908 kg O_2/m^2 for Stream 6 (shade-grown). These oxygen values were then expressed as glucose by assuming a photosynthetic quotient of one and multipling by 0.94. Table 11 shows that annual gross primary production in the laboratory streams was well within the range of values found for environments in nature.

Some workers, notably Odum (22), have found it useful to construct an energy balance sheet that shows the gains and losses of energy to an ecosystem during a period of time. Such a balance

Table 11. Comparative rates of gross primary production expressed on an annual basis.

Water	Glucose produced $kg/m^2/year$
Canyon section of Logan River	1.2
Third impoundment Logan River	4.6
Canyon Road (below first impoundment Logan River)	5.0
Mendon Bridge, last riffle before valley base level	3.1
Eniwetok Atoll	8.8
Weber Lake	0.6
11 Florida Springs	0.2 - 21.5
Stream 1, light-adapted	1.3*
Stream 6, shade-adapted	0.9*

* Calculated for 343 days instead of a full year of 365 days.

sheet serves to check the estimation of the production and losses in the system and provides an overall view of the productive capacity of the environment. In any community gross primary production is either eventually lost by export and community respiratory activities or accumulates as biomass in the system. Thus, assuming no import of organic material into the system:

$$\triangle B = P - R - E$$

where $\triangle B$ is the change in biomass, P the production rate, R the community respiration rate, and E the export rate for a particular period of time.

Table 12 is an energy balance sheet for Streams 1 and 6 computed for a time interval extending from July 10, 1962, to May 28, 1963. Gross primary production and community respiration were estimated by the integration of the oxygen metabolism data plotted in Figure 10. The oxygen data were then converted to kilocalories by the same conversion factor used by Odum and Hoskin (23, p. 131), i.e., by figuring 3.5 kcal/g O_2. Grams of biomass exported or accumulated were converted to kilocalories using the estimates of the mean number of calories per gram of biomass found during the study (Table 6).

It was evident from Table 12 that rather large discrepancies existed when accounting for the fate of the gross primary production in each stream in terms of community respiration, accumulation of biomass, and export of biomass collected in a #20 mesh plankton net. This discrepancy was 17 percent in Stream 1 and 28 percent in

Table 12. Energy balance sheet for Streams 1 and 6, July 10, 1962, through May 28, 1963.

Stream 1 (light-grown):	Additions (kilocalories/m^2)		Accumulation and losses (kilocalories/m^2)
Gross primary production	4274		
Community respiration			2832
Export of biomass			178
Accumulation of biomass			506
	4274		3516
Discrepancy		758	

Stream 6 (shade-grown):	Additions (kilocalories/m^2)		Accumulation and losses (kilocalories/m^2)
Gross primary production	3003		
Community respiration			1866
Export of biomass			37
Accumulation of biomass			254
	3003		2157
Discrepancy		846	

Stream 6. The most obvious source of the large discrepancies appeared to be in the estimation of export, as the production and respiration values agreed well with similar estimates in the photosynthesis-respiration chamber and the P/R ratios were typical of other autotrophic periphyton communities. Nelson and Scott (19) found that, at low to moderate flows, the dissolved and colloidal organic load of water collected from the Middle Oconee River was two to ten times greater than the particulate organic matter, while at high flows, the particulate organic matter was at times double the dissolved and colloidal fraction. The concentration of the dissolved and colloidal organic matter was usually from 10 to 20 milligrams per liter and failed to show any seasonal variations.

To evaluate the contribution of dissolved and small particulate organic matter to the export in the laboratory streams, water samples were removed from Stream 1, strained through a #20 mesh plankton net, and analyzed for organic matter content using the method described by Slater (44). Unfortunately, these analyses were made as an after-thought, five months after the termination of the seasonal study, and consequently were only an indication of the order of magnitude of the export of dissolved and small particulate organic substances. The estimates were also considered minimal, as the water was not turbid and the biomass was relatively small as a result of grazing activities by aquatic snails. The organic matter content after straining through the plankton net was estimated at 4.8 mg/l. After the exchange water was turned off for 24 hours and the organic matter allowed to accumulate in the system, the

concentration had increased to 5.2 mg/l. If the increase of 0.4 mg/l was multiplied by the stream volume of 200 liters and divided by the total area of community substrate in the stream (1.25 m^2), it was found that approximately 65 milligrams of dissolved and small particulate organic matter were leached from one square meter of the community in 24 hours. Sixty-five milligrams per day is equivalent to about 100 kilocalories per year. Thus, these determinations suggested that the contribution of dissolved and small particulate organic matter to the export was significant, and as these were probably minimum estimates, this unmeasured fraction could have accounted for at least part of the discrepancies noted in the energy balance sheet.

To obtain an estimate of the efficiency with which the laboratory periphyton communities fixed light energy as organic matter, measurements of the incident light energy were made in Streams 1 and 6 at 50 different locations near the community using a circular, eight junction Eppley thermopile (Serial No. 4565) with bismuth silver elements. The instrument was calibrated to develop a mean e.m.f. of 0.114 microvolts/microwatt/cm^2. A one millimeter pyrex window was used to filter out most of the energy unavailable for photosynthesis. It was possible to make only one series of measurements for each stream, as the instrument was only available for several days. Although the output of the fluorescent tubes became slightly reduced during the study (Table 5), the energy measurements were made on October 4, 1962, approximately midway through the

investigation, and probably approximated the mean energy output by the tubes during the 12 month period. The actual efficiency computations involved the integration of the daily rates of gross primary production (Figure 10) for a time interval beginning June 28, 1962, and ending June 6, 1963. The oxygen data were then converted to energy units by multiplying by 3.5 kcal/g O_2 as described earlier. The total number of light hours during the time interval was estimated from Figure 9, and this value was multiplied by the mean of the thermopile readings for each stream to obtain the total available energy output by the fluorescent tubes. The efficiency calculations are outlined below:

Stream 1 (light-grown)

Primary production, 343 days	=	1,344.2 g O_2/m^2
3.5 kcal/g O_2 X 1344.2 g O_2/m^2	=	4,704.7 kcal/m^2
Total light hours	=	4,117.3
Mean thermopile reading	=	0.89 cal/hr/cm^2
Total available energy output from tubes, 343 days	=	36,643.97 kcal/m^2
Efficiency	=	$\frac{4,704.7 \text{ kcal/m}^2}{36,643.97 \text{ kcal/m}^2}$
	=	12.84%

Stream 6 (shade-grown)

Primary production, 343 days	=	907.7 g O_2/m^2
3.5 kcal/g O_2 X 907.7 g/m^2	=	3,176.95 kcal/m^2
Total light hours	=	4,117.3
Mean thermopile reading	=	0.34 cal/hr/cm^2
Total available energy output from tubes, 343 days	=	13,998.82 kcal/m^2
Efficiency	=	$\frac{3,176.95 \text{ kcal/m}^2}{13,998.82 \text{ kcal/m2}}$
	=	22.69%

The efficiencies of fixation of usable light energy for various communities are compared to those of the laboratory periphyton communities in Table 13. The efficiencies of the laboratory communities in Streams 1 and 6 were considerably higher than efficiencies estimated for three natural ecosystems (Silver Springs, a Georgia salt marsh, and Root Spring), and appeared to resemble more closely those reported by Wassink, Kok, and van Oorschot (56, p. 57) for small cultures of Chlorella. The "shade-grown" community in Stream 6 was more efficient than the "light-grown" community in Stream 1. These results agreed with the findings of Wassink, Kok, and van Oorschot (56, p. 55-62) who observed that lower light intensities gave rise to higher efficiency and that excessive illumination appeared an important factor in producing low efficiency under natural conditions. Also Rabinowitch (36, p. 979) has pointed out that the initial slope of a light-photosynthesis curve (i.e., the initial linear range commonly associated with low light

Table 13. Efficiencies of fixation of usable light energy (gross production/usable light) by various communities as compared to those of the laboratory periphyton communities.

Community	Percent	Source
Laboratory microcosm	3	Odum and Hoskin (23)
Silver Springs	5.3	Odum (22)
Georgia salt marsh	6.1	Teal (53)
Root Spring	0.2	Teal (52)
Marine phytoplankton, visible sunlight below saturation intensity	17.5	Ryther (40)
Chlorella, small cultures (5000 - 8000 lux)	12 - 15	Wassink, Kok, and van Oorschot (56)
Chlorella, small cultures (1500 - 3000 lux)	20 - 24	
Stream 1 (ca. 6000 lux)	12.8	
Stream 6 (ca. 2000 lux)	22.7	

intensities) determines the maximum quantum yield, or efficiency. In other words, as soon as the light level is increased to an intensity at which the rate of photosynthesis is no longer directly proportional to the light intensity, or $\frac{dP}{dI} \neq$ constant, the efficiency of energy utilization by the plants begins to decrease.

It is often useful to express efficiency of light utilization on a foot candle-hour basis. The ratio of gross primary production to foot candle-hours for several communities subjected to the same type of light source provides quick comparisons of efficiencies, especially if energy measurements are not immediately available. A plot of such ratios for the periphyton communities are shown in Figure 16. Here, again, the higher efficiency of the shade-grown community is well demonstrated.

When the periphyton communities first began to develop on the clean substrate in Streams 1 and 6 in the summer, 1962, photosynthetic rates were high relative to the weight of organic matter present; but as the communities became older and organic detritus began to accumulate on the rocks, the ratio of the hourly rate of primary production to the weight of organic matter decreased (Figure 17, top). Since organic matter accumulated relatively slowly in Stream 6 at the lower light intensity, the ratios remained high for a longer period and were more erratic than those estimated for Stream 1. The gradual buildup of Phormidium retzii in Stream 6, however, brought about a slow accumulation of organic matter in the stream and a reduction and stabilization of the production-organic

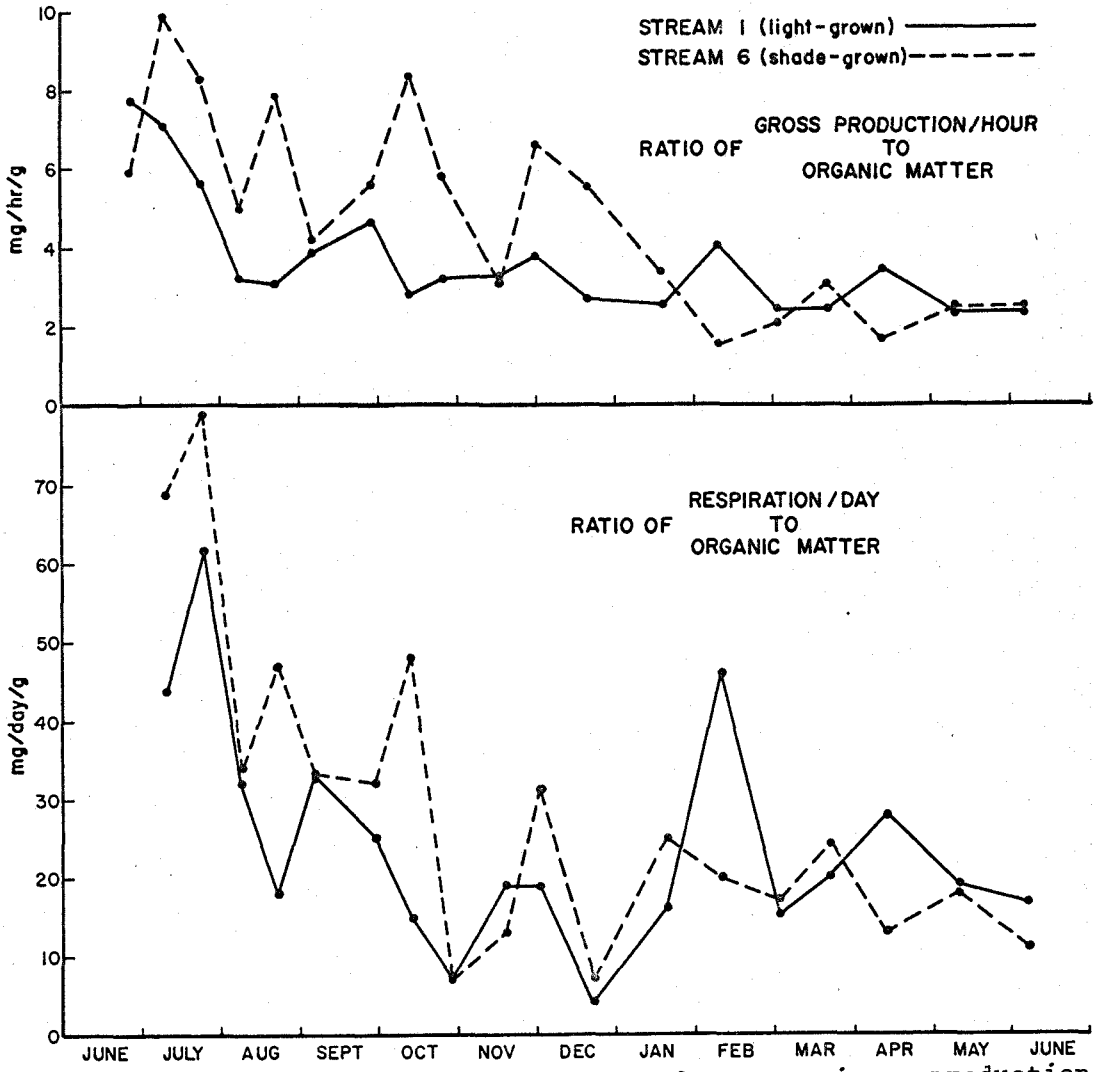

Figure 17. Ratios of the hourly rate of gross primary production and the daily rate of community respiration to organic matter, Stream 1 (light-grown) and Stream 6 (shade-grown), June, 1962, through June, 1963.

matter ratios by late January, 1963 (Figures 12, 14, and 17). The younger, more vigorously growing communities present in early summer, 1962, also exhibited higher ratios of daily rate of community respiration to weight of organic matter, although these ratios were more strongly affected by seasonal fluctuations in temperature than the production-organic matter ratios (Figure 17, bottom, Figures 9 and 10). Both ratios were also affected by turbidity and export (Figure 13).

Odum, McConnell, and Abbott (24) listed comparative chlorophyll data obtained for plankton communities, algal cultures, littoral and emergent plant communities, shallow aquatic communities, and terrestrial communities. The chlorophyll a content of these diverse communities during seasons with maximum light intensity ranged from about 0.1 g/m^2 to 3.0 g/m^2. The chlorophyll a content of the laboratory periphyton communities was well within this range, varying between 0.48 and 2.01 g/m^2 in Stream 1 (light-grown) and 0.14 and 1.30 g/m^2 in Stream 6 (shade-grown). In general, however, the concentration of chlorophyll in the laboratory communities was usually slightly higher than concentrations normally reported for the majority of shallow, flowing water environments.

Strickland (50, p. 50) has discussed the use of a plant pigment for the quantitative evaluation of the concentration of a phytoplankton crop. The most severe criticisms to the estimation of standing crop from pigment analyses were based mainly on the grounds of the variability of the chlorophyll content of the phytoplankters

and the erroneous results brought about by the presence of detrital chlorophyll. Grzenda and Brehmer (10) have attempted to estimate stream periphyton production on artificial plexiglass substrata by establishing a relationship between "phytopigment" density and weight of organic material. Their method required the removal of the periphyton before the growth was dense enough to slough off the surface of the plate. Thus, this technique was actually a measure of the rate of colonization by young cells rather than an estimate of either standing crop of periphyton in the stream or true stream periphyton production under equilibrium conditions where the younger, faster-growing, plant cells were also in contact with older cells, non-living organic detritus, as well as heterotrophic organisms.

The ratios of milligrams of chlorophyll a to grams of organic matter for Streams 1 and 6 are plotted at the top of Figure 18. The chlorophyll a content of the laboratory periphyton communities ranged from approximately 0.4 to 2 percent of the dry weight of organic material. Rabinowitch (35, p. 410-411) has tabulated values obtained by various workers for the concentration of chlorophylls in species of green, brown, red, and blue-green algae. For green algae, the chlorophyll content (sum of chlorophyll a and b) was from 0.16 to 4.9 percent of dry weight (ash included); for the bluegreen alga, Gloeocapsa montana, the percentages for cells grown in strong and weak light were 0.3 and 0.7, respectively. These percentages no doubt would have been somewhat higher if the material had been ashed in a muffle furnace and the results put on an organic matter

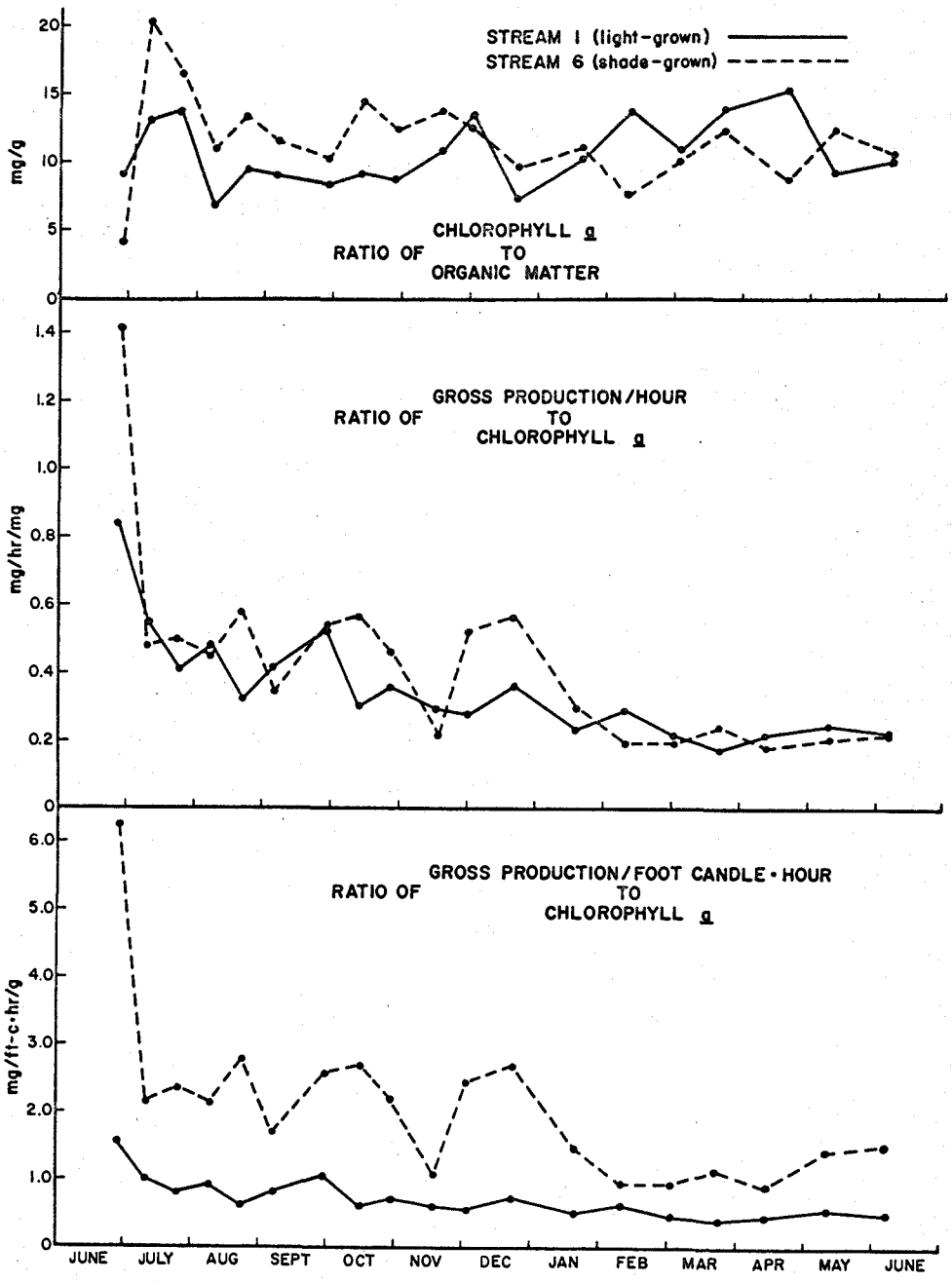

Figure 18. Ratios of chlorophyll a to organic matter and ratios of gross primary production to chlorophyll a, Stream 1 (light-grown) and Stream 6 (shade-grown), June, 1962, through June, 1963.

basis. In any case, however, the percentages were relatively higher for plant cells grown at low light intensities. This generalization also held for the laboratory periphyton communities until December when Phormidium retzii began to account for a significant increase of organic matter in Stream 6 (shade-grown). After November, the buildup of organic matter and the change from a predominantly diatom flora to a flora dominated by bluegreen algae in Stream 6 (Figures 12 and 14) plus the gradual increase of chlorophyll content of the community in Stream 1 (Figure 12) apparently explained a decrease in the chlorophyll-organic matter ratios for Stream 6 and an increase in the ratios for Stream 1. Perhaps the slow increase of chlorophyll a per square meter exhibited by both streams during the study (Figure 12) was due to a slow accumulation of detrital or non-photosynthetically active chlorophyll. According to Bogorad (5, p. 401), mineral nutrition, light intensity, and cell age can all be major factors in influencing the concentration of chlorophyll in an individual organism. Summarizing, it appears that, at least in the laboratory communities studied here, the chlorophyll-organic matter ratio is not constant enough to be useful in the estimation of biomass or standing crop of periphyton from chlorophyll data.

As chlorophyll a has been considered an essential catalyst for photosynthesis, many investigators have attempted to express the gross rate of photosynthesis at a given light intensity as a function of the chlorophyll a content of the community. Strickland

(50, p. 90-93) has tabulated gross photosynthesis-chlorophyll a ratios obtained by a number of workers and found that the range was usually between 1 and 10 milligrams of carbon per hour for each milligram of chlorophyll when the illumination was around 0.1 langley per minute of photosynthetically active radiation. Ryther and Yentsch (41) suggested 3.7 mg C/hr per milligram of chlorophyll a as a good mean value. The use of a simple equation to estimate gross primary production from chlorophyll data, although an attractive concept, has many limitations, and in many cases a variation as great as 2- or 3-fold is likely to occur (Strickland, 50, p. 90-93).

The use of chlorophyll data to estimate primary production in small, rapidly flowing, streams has particular appeal, as it is often very difficult to obtain meaningful oxygen and carbon dioxide metabolism data in turbulent environments. Waters (57), Grzenda and Brehmer (10), and McConnell and Sigler (18) have tried to estimate the productivity of stream periphyton by analyses of pigment data, but have failed to demonstrate that a constant enough relationship existed between primary production and pigment concentration to make these estimates reliable. The laboratory streams offered an excellent opportunity to experimentally examine the validity of such estimates. The gross primary production-chlorophyll a ratios obtained for the laboratory communities were plotted in Figure 18 (middle). These ratios varied from about 0.2 to 1.4 milligrams of oxygen per hour per milligram of chlorophyll a. The plots were

smoothed out somewhat by expressing primary production on a foot candle-hour basis, which indicated that a constant light intensity favored the constancy of the ratio (Figure 18, bottom). After mid-October the ratios obtained for Stream 1 only varied from 0.4 to 0.7 milligrams oxygen per foot candle-hour per gram of chlorophyll a; while on the other hand, the ratios for Stream 6 were erratic until mid-February, after which time the community became more stable as Phormidium retzii became a dominant constituent. Ratios expressed on a foot candle-hour basis were higher for Stream 6 due to the greater efficiency of light utilization by the shade-grown community (Figures 16 and 18). Conditions which appeared to favor a constant production-chlorophyll a ratio were therefore: a constant illumination intensity and a stable community with respect to species composition and age composition of the plant cells.

The difference in the successional patterns of the light- and shade-grown periphyton communities helped explain many of the differences observed with respect to biomass, organic matter, chlorophyll a and the relationships between these quantities and primary production and community respiration. In Stream 1 (light-grown), the community was established and was reasonably stable by the end of August, 1962. Subsequent changes in the community structure could then be followed and predicted on a seasonal basis, with species of green algae supplementing an ever-present diatom flora during the warmer months (Figure 14, top). In contrast, however, community succession in Stream 6 (shade-grown) was a much slower process,

and a stabilization or "climax" was not reached until near the end of the study, when Phormidium retzii and P. tenue almost covered the entire available substrate (Figure 14, bottom). Although the species of Phormidium grew very slowly, they were apparently able to compete very well with the diatom flora for attachment substrate when the community was subjected to reduced light intensities, and once established, were able to effectively crowd out the other periphyton species. The relatively instable state of the biomass and concentrations of organic matter and chlorophyll in Stream 6 as well as the erratic ratios of these factors to production and respiration were discussed earlier.

SUMMARY AND CONCLUSIONS

1. Laboratory streams and a photosynthesis-respiration chamber were employed to study periphyton production and community metabolism in lotic environments.
2. Curves relating illumination intensity to primary production for the "light-adapted" periphyton communities, in general, were characterized by a linear range extending to between 100 and 200 foot candles, a $C.P._L$ of about 50 foot candles, and a saturating intensity in the vicinity of 2000 foot candles.
3. Curves relating illumination intensity to primary production for the "shade-adapted" periphyton communities exhibited a steep initial slope, a short linear range not extending beyond 100 foot candles, a long and gradual inflection from the linear segment toward the horizontal, and a saturating intensity only slightly less than that observed with respect to the "light-adapted" communities.
4. Curves relating primary production to light intensity obtained for the light-adapted periphyton communities could be characterized by mathematical equations such as those described by Smith (45) and Talling (51), while curves determined for the shade-adapted communities could not be expressed mathematically in this manner.
5. In the light-adapted periphyton community, primary production was continuously enhanced by increasing the supply of molecular

carbon dioxide to a concentration as high as 45 mg/l; no such significant enhancement was found in the shade-adapted community.

6. Gross primary production of the laboratory periphyton communities was 1.7 - 4.1 g O_2/m^2/day for the shade-grown community and 2.5 - 6.4 g O_2/m^2/day for the light-grown community. In general, gross production in the laboratory streams was slightly greater than that normally reported for eutrophic lakes and oceanic waters and more characteristic of the least-productive flowing water systems.
7. The laboratory periphyton communities could be characterized as autotrophic communities with P/R ratios normally ranging from about 1.3 to 2.5.
8. Gross production for 343 days was estimated at 1.344 kg O_2/m^2 for the light-grown community and 0.908 kg O_2/m^2 for the shade-grown community. These values were well within the range of values determined for environments in nature for similar periods of time.
9. Export of periphyton from the streams was greatly enhanced by turbid water conditions. The contribution of dissolved and small particulate organic matter to the export is significant and must be considered in attempting to balance the additions and losses of energy to the system.
10. The efficiency of fixation of usable light energy as organic matter was 12.8 percent for the light-grown community and

22.7 percent for the shade-grown community. The efficiencies of the laboratory communities were considerably higher than efficiencies estimated for most natural ecosystems and appeared to resemble more closely those for small cultures of Chlorella.

11. The chlorophyll a content of the light-grown periphyton community varied between 0.48 and 2.01 g/m^2 and that of the shade-grown community between 0.14 and 1.30 g/m^2. Although the chlorophyll a content of the laboratory communities was well within the range of values reported for a number of different types of communities in nature, the content of chlorophyll in the laboratory communities was usually slightly higher than that normally found in the majority of shallow, flowing water environments.

12. The chlorophyll a content of the laboratory periphyton communities ranged from approximately 0.4 to 2 percent of the ash-free dry weight of the material.

13. The gross primary production-chlorophyll a ratios found for the laboratory communities varied from 0.2 to 1.4 milligrams of oxygen per hour per milligram of chlorophyll a. The ratios obtained for the light-grown periphyton community became relatively constant during the fifth month of the study; the ratios for the shade-grown community were erratic until the ninth month of the study.

14. In the stream subjected to the higher light intensity, the community was well established and reasonably stable by the end of the third month of the investigation, with species of green algae supplementing an ever-present diatom flora during the warmer months. Community succession in the shade-grown community was a much slower process, and a stabilization was not reached until near the end of the study, when the species of blue-green algae Phormidium retzii and P. tenue almost covered the entire available substrate.

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APPENDIX

Appendix I. Gross primary production, community respiration, biomass, organic matter, and chlorophyll a values and P/R ratios for periphyton communities in Streams 1 and 6, June 1962 through June 1963.

Characteristic	June 28 1962	July 10 1962	July 25 1962	Aug. 8 1962	Aug. 22 1962
Stream 1:					
Gross Production/hr/m^2(mg O_2)	404	415	375	354	434
Gross Production/day/m^2(g O_2)	6.262	6.433	5.625	5.310	6.082
Respiration/day/m^2(g O_2)	-	2.544	4.104	3.504	2.568
P/R Ratio	-	2.54	1.37	1.52	2.37
Biomass/m^2(g)	120	152	217	286	403
Organic Matter/m^2(g)	52.3	58.1	66.7	110.1	141.3
Chlorophyll a/m^2(g)	0.480	0.760	0.920	0.740	1.356
Stream 6:					
Gross Production/hr/m^2(mg O_2)	192	281	260	262	292
Gross Production/day/m^2(g O_2)	2.976	4.356	3.900	3.930	4.099
Respiration/day/m^2(g O_2)	-	1.968	2.496	1.800	1.728
P/R Ratio	-	2.20	1.57	2.18	2.37
Biomass/m^2(g)	89	88	109	159	155
Organic Matter/m^2(g)	32.1	28.5	31.4	52.7	37.0
Chlorophyll a/m^2(g)	0.136	0.580	0.520	0.580	0.498

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Appendix I. (continued)

Characteristic	Sept. 5 1962	Sept. 29 1962	Oct. 13 1962	Oct. 27 1962	Nov. 17 1962
Stream 1:					
Gross Production/hr/m^2(mg O_2)	330	363	358	382	328
Gross Production/day/m^2(g O_2)	4.461	4.540	4.301	4.206	3.116
Respiration/day/m^2(g O_2)	2.832	1.930	1.871	0.792	1.894
P/R Ratio	1.58	2.35	2.30	5.31	1.65
Biomass/m^2(g)	301	287	532	483	402
Organic Matter/m^2(g)	85.0	77.9	128.7	119.1	99.8
Chlorophyll a/m^2(g)	0.782	0.676	1.190	1.054	1.108
Stream 6:					
Gross Production/hr/m^2(mg O_2)	237	229	249	303	205
Gross Production/day/m^2(g O_2)	3.197	2.860	2.986	2.666	1.959
Respiration/day/m^2(g O_2)	1.896	1.310	1.418	0.375	0.826
P/R Ratio	1.69	2.18	2.11	7.11	2.36
Biomass/m^2(g)	246	165	92	189	243
Organic Matter/m^2(g)	57.1	40.7	29.7	52.0	65.9
Chlorophyll a/m^2(g)	0.694	0.422	0.436	0.652	0.918

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Appendix I. (continued)

Characteristic	Dec. 1 1962	Dec. 22 1962	Jan. 19 1963	Feb. 9 1963	Mar. 2 1963
Stream 1:					
Gross Production/hr/m^2(mg O_2)	317	367	350	278	303
Gross Production/day/m^2(g O_2)	2.853	3.122	2.972	2.502	2.729
Respiration/day/m^2(g O_2)	1.611	0.552	2.362	3.149	1.939
P/R Ratio	1.77	5.66	1.26	0.79	1.41
Biomass/m^2(g)	282	593	552	225	475
Organic Matter/m^2(g)	82.8	134.8	140.6	69.0	125.9
Chlorophyll a/m^2(g)	1.148	1.000	1.482	0.960	1.406
Stream 6:					
Gross Production/hr/m^2(mg O_2)	266	281	244	190	189
Gross Production/day/m^2(g O_2)	2.394	2.387	2.074	1.710	1.699
Respiration/day/m^2(g O_2)	1.245	0.347	1.766	2.496	1.543
P/R Ratio	1.92	6.88	1.77	0.69	1.10
Biomass/m^2(g)	140	183	278	487	343
Organic Matter/m^2(g)	40.4	50.8	71.9	125.1	92.8
Chlorophyll a/m^2(g)	0.514	0.498	0.810	0.974	0.956

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Appendix I. (continued)

Characteristic	Mar. 22 1963	Apr. 12 1963	May 10 1963	June 6 1963
Stream 1:				
Gross Production/hr/m^2(mg O_2)	343	374	340	344
Gross Production/day/m^2(g O_2)	3.757	4.680	4.760	5.332
Respiration/day/m^2(g O_2)	2.880	3.110	2.736	2.568
P/R Ratio	1.30	1.50	1.74	2.08
Biomass/m_2(g)	562	391	487	574
Organic Matter/m^2(g)	141.9	110.4	146.6	147.8
Chlorophyll a/m^2(g)	2.012	1.704	1.392	1.528
Stream 6:				
Gross Production/hr/m^2(mg O_2)	234	236	204	201
Gross Production/day/m^2(g O_2)	2.574	2.950	2.856	3.112
Respiration/day/m^2(g O_2)	1.824	1.920	1.584	0.960
P/R Ratio	1.41	1.54	1.80	3.24
Biomass/m^2(g)	260	565	319	273
Organic Matter/m^2(g)	77.4	147.2	86.8	83.8
Chlorophyll a/m^2(g)	0.972	1.296	0.990	0.910