METABOLISM OF ALGAL COMMUNITIES IN EXPERIMENTAL STREAMS

by

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TABLE OF CONTENTS

	Page
INTRODUCTION	1
METHODS AND MATERIALS	5
Artificial Stream Apparatus	5
Photosynthesis-Respiration Chamber	7
Methods of Estimating Production	10
Methods of Estimating Biomass and Community Composition	13
Experimental Variables and Analytical Procedures	14
Light Energy	14
Nutrient Materials	15
RESULTS	17
Periphyton Communities	17
Community Description	17
Community Succession	24
Biomass	25
Light Energy	28
Nutrient Materials	32
DISCUSSION	43
SUMMARY	54
BIBLIOGRAPHY	56
APPENDIX	59

LIST OF FIGURES

Figure		Page
1.	Artificial stream apparatus	6
2.	Photosynthesis-respiration chamber	8
3.	Comparison of the succession of periphyton communities grown under light and shade conditions	26
4.	The influence of light on gross production	31
5.	The influence of exchange rate of water on gross production in experimental streams with no artificial current. (Communities grown at 3.7 liters per minute)	33
6.	The influence of exchange rate of water on gross production in experimental streams with .33 foot per second current velocity. (Communities grown at 2 liters per minute)	36
7.	The influence of a limiting factor on gross production in the photosynthesis-respiration chamber	39
8.	The influence of kilocalories of incident light per square meter per day on per cent of efficiency of light utilization	52

LIST OF TABLES

TABLE		Page
1.	Composition of Artificial Stream Communities by Group in Per Cent by Number of Cells	18
2.	The Influence of Experimental Conditions on the Composition of Stream Communities by Major Group in Per Cent by Number . . .	21
3.	Mean in Grams per Square Meter of Dry Biomass, Nitrogen and Phosphorus and Per Cent Nitrogen and Phosphorus in Communities F, G and H.	27
4.	Respiration, Production and Light Energy per Square Meter per Hour of Test Period for Shaded Community D and Non-shaded Community E on Sunny and Cloudy Days . . .	29
5.	Proportion in Per Cent of Green Algae and Diatoms in Stream Communities	35
6.	Production, Respiration and Solar Energy in Kilocalories per Square Meter per Day, Photosynthesis-Respiration Ratios, and Per Cent Efficiencies of Solar Energy Utilization	45
7.	Average Gross Production Values as Grams per Square Meter per Day in Natural and Other Aquatic Ecosystems	49
8.	Efficiency in Per Cent of Light Utilization by Aquatic Plant Communities	51

LIST OF APPENDIX TABLES

TABLE		Page
A	Structure of Experimental Stream Communities	59
B	Counts of Organisms During Succession for Communities D and E	61
C	Total Phosphorus, Nitrogen, Crude Protein and Biomass for Experimental Streams	62
D	Water Analyses by U. S. Geological Survey of Samples from Water Supply Stream	64
E	Nitrate Determinations on Input and Output Water from Experimental Streams	66
F	Phosphate Determinations from Input and Output Water from Experimental Streams	67
G	Phosphate and Nitrate Determinations from Photosynthesis-Respiration Chamber	68
H	Gross and Net Production and Respiration Rates as Milligrams of Oxygen per Square Meter per Hour and per Day . .	69

METABOLISM OF ALGAL COMMUNITIES IN EXPERIMENTAL STREAMS

INTRODUCTION

Recent investigations in stream ecology have centered around studies of the flow of energy through communities and evaluations of the efficiencies of production and utilization at various trophic levels. In the spring of 1959, experiments designed to study the energy exchange in simplified communities in artificial streams were begun at the Pacific Cooperative Water Pollution and Fisheries Research Laboratories, Oregon State University. Six artificial streams permitted study of community energy relationships under controlled conditions. The work reported here concerns primary production or the transfer of solar energy to plants.

The trophic-dynamic approach to ecology proposed by Hutchinson and Lindeman (11, p. 44) views the food pyramid in terms of energy flow through an ecosystem rather than in terms of biomass. Lindeman (15, p. 636-673) developed the concept of "trophic levels" which allowed him to consider separately the efficiencies with which the plant level fixed solar energy and the herbivore and carnivore levels transferred this to animal tissue.

Ivlev (12, p. 98-120) pointed out that, except for the dependence of most plants on solar energy, in reality the energy relationships are so complex that no trophic level entirely dependent upon the previous level can be defined. He advised investigation of particular pathways of energy flow from the solar source through plants to a final "product" of interest to man. He suggested a scheme of analysis employing complementary ecological and physiological evaluations of energy relations by working from "product" back to the ultimate energy source. Though complex, this is perhaps the most thorough-going and reasonable approach to evaluating energy relations in ecosystems which has been proposed thus far.

An admirable demonstration of the trophic-dynamics of an ecosystem was done by Teal (33, p. 283-302) for a temperate cold spring. The convincing nature of Teal's demonstration stems in part from his careful definitions and procedures and to a considerable extent from the simplicity of the spring ecosystem. Odum (20, p. 85-97) (21, p. 55-112) has been able to show encouraging progress toward the understanding of trophic relationships in more complex ecosystems of flowing fresh waters in Florida.

The study of the trophic-dynamics of ecosystems necessitates quantitative measure of rates of energy flow

through the trophic levels. Ryther (30, p. 72-84) discussed the various methods which have been used for the measurement of primary production in flowing waters.

Estimates of energy flow for the biological processes of uptake, assimilation, respiration, and production can be used to determine certain biological efficiencies which should increase understanding of community structure and succession. These efficiencies have been summarized by Odum and Odum (17, p. 43-87).

Odum and Hoskin (22, p. 115-133) have published some studies of the community metabolism of a laboratory stream microcosm. The stream consisted of a glass-jacketed condenser through which they circulated a culture medium by means of a pump. The condenser was illuminated with photo-flood lamps and was cooled by tap water flowing through the jacket. The apparatus was equipped for temperature determinations, sampling, renewal of the medium and maintenance of a supply of oxygen and carbon dioxide. The studies primarily covered the metabolism and succession of algal communities; and, while the studies seem somewhat preliminary, the results are of value and indicate the imaginative approach to be very worthwhile.

It is hoped that study of the metabolism of simplified communities in controlled artificial streams may allow some

of the variables found in nature to be isolated for more precise examination. Perhaps the relative importance of factors limiting the production of autotrophic organisms in stream ecosystems can be better understood in this way.

The use of production estimates was chosen to show the effect upon periphyton communities of experimental variables superimposed upon otherwise closely controlled conditions. Light and nutrient levels were the principal factors studied. Differences in community composition occurred during some of the experiments, and interesting comparisons between the action of factors on different communities were possible.

METHODS AND MATERIALS

Artificial Stream Apparatus

The experimental stream apparatus (figure 1) was a modification of the artificial streams used by DeWitt et al. (6) in a study of the effects of pulp-mill wastes on some fresh-water organisms. It consisted of six pairs of parallel-set troughs, each trough being ten feet long, ten inches wide and eight inches deep. Openings at both ends between each pair allowed the water to be circulated by a variable speed paddlewheel. In some experiments, the openings at the water inflow ends were closed and the paddlewheels removed. This permitted only water movement caused by the exchange water passing through the stream. A bottle to sample the inflow water was attached by a T-tube to the supply line close to each trough. A siphon to sample the effluent water was located just ahead of the overflow standpipe.

The bottom materials consisted of forty liters of mixed rubble and gravel taken from a nearby stream. The rubble consisted of water-smoothed rocks ranging from three to six inches in diameter. The gravel averaged from one half to one and one half inches in diameter. The volume of bottom materials was carefully measured to aid

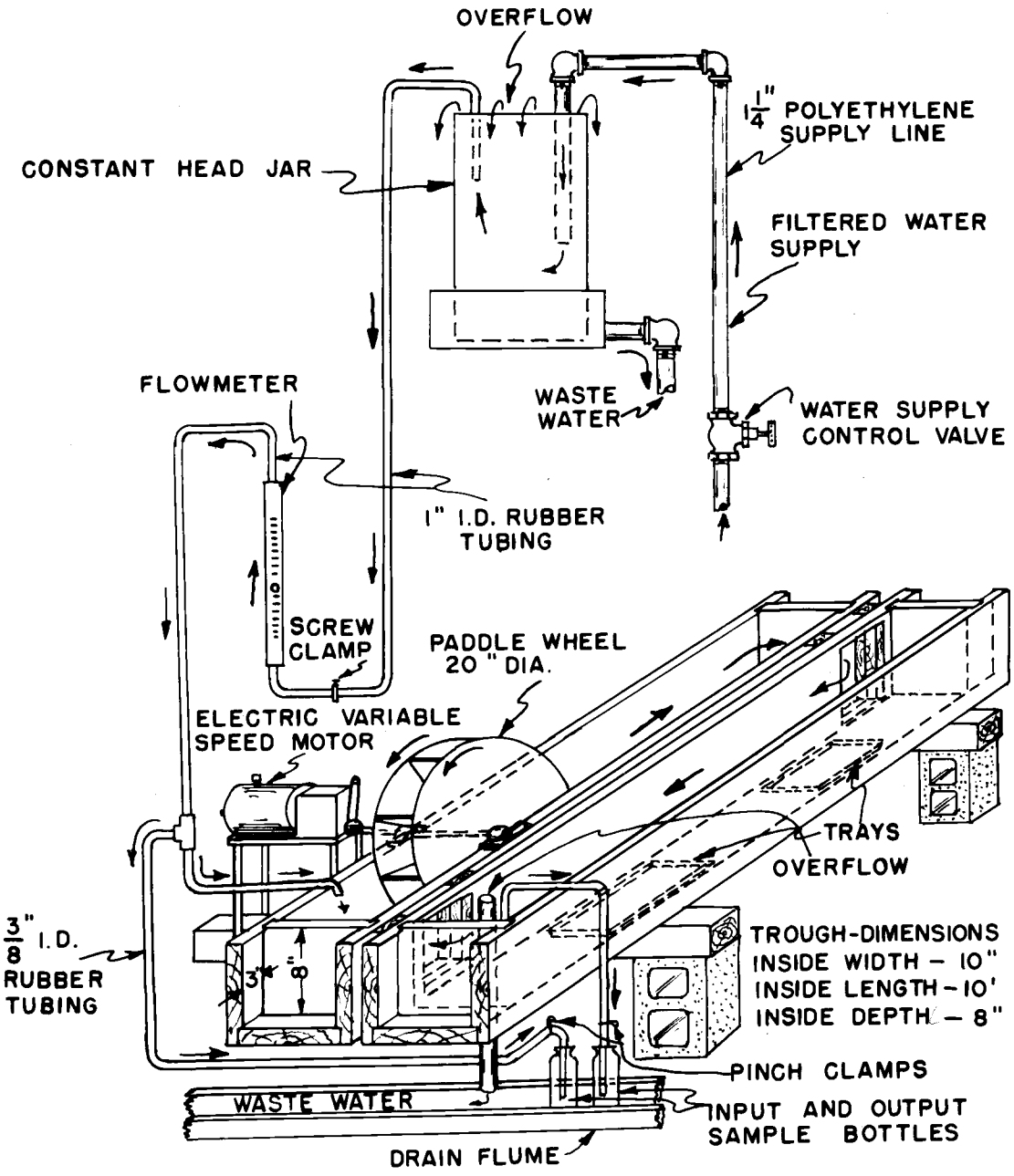

Figure 1. Artificial stream apparatus.

in calculation of the volume of water present in the stream. The water supply was obtained from a series of springs situated at the head of a small stream running past the laboratory. The water was passed through a column of filter medium and gravel to remove large suspended organic material and insect larvae. Sufficient algal cells and insect eggs passed through the filter to seed the streams. The water for some experiments was not filtered. The rate of exchange of water was regulated by valves and measured by flow-meters with a capacity up to 5.1 gallong per minute. The artificial stream apparatus was located in a concrete block building 25 feet long, 20 feet wide and 15 feet high at the peak. The north half of the roof was constructed of corrugated translucent plastic, and the south half of the roof was of corrugated metal. The south wall was covered with glass windows. The north wall had two windows, the east wall two windows, and the west wall one window.

Photosynthesis-Respiration Chamber

The photosynthesis-respiration chamber (figure 2) consisted of a black porcelain-coated steel tank set in a marine plywood waterjacket. A lucite top was sealed with a rubber gasket and held tightly by C-clamps. Water was

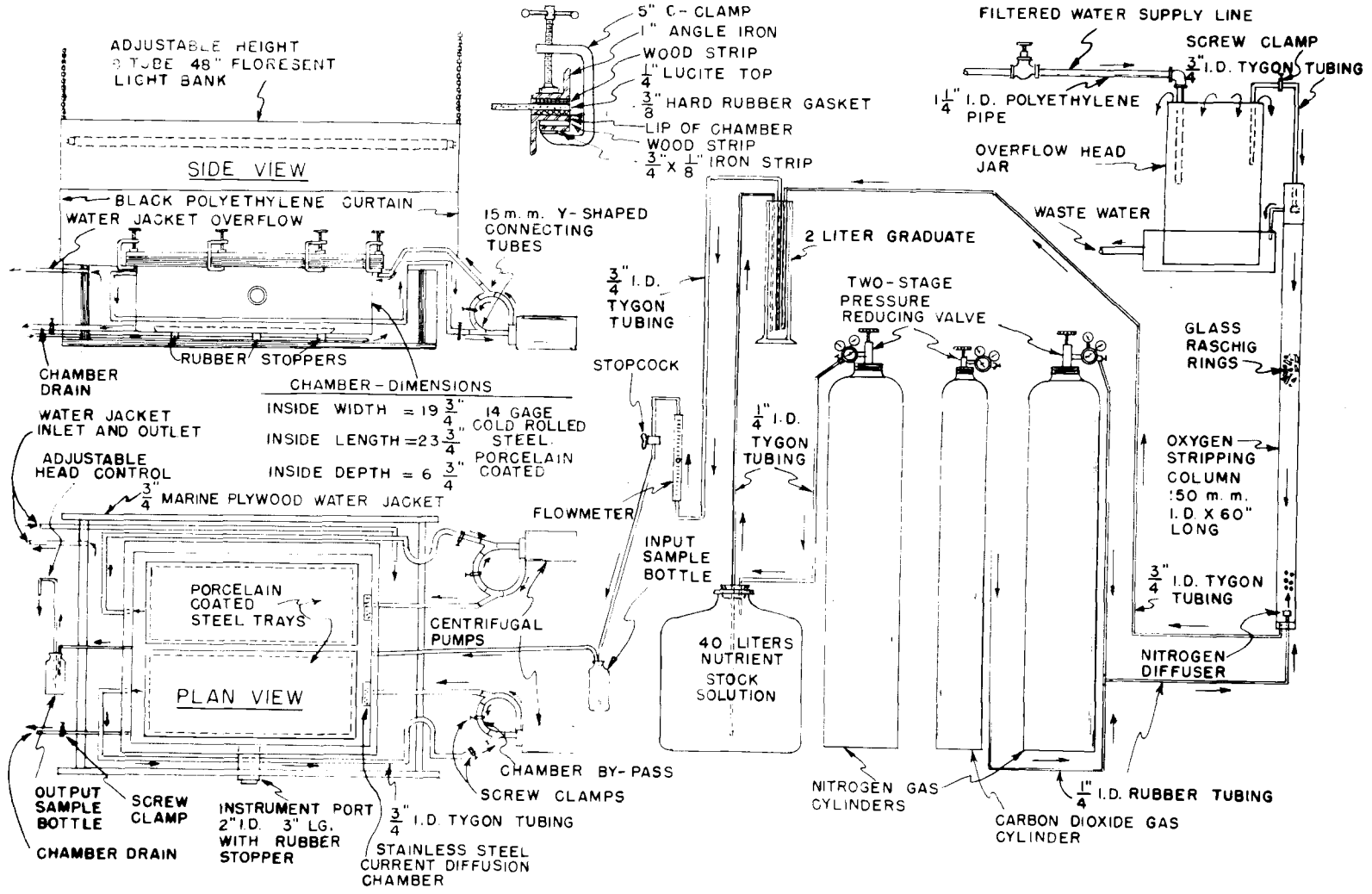

Figure 5. Photosynthesis-respiration chamber.

circulated through the chamber by two centrifugal pumps. Stainless steel baffles were located on the inflow lines from the pumps to distribute the flow of water.

A bank of eight fluorescent lights, adjustable in height, was suspended over the chamber. A black polyethylene curtain was hung from the light bank around the chamber to cut out light from the sides. Water sampling bottles were located on the inflow and outflow lines. Filtered water was supplied from a constant head jar. The water was first passed through a column where the dissolved oxygen could be lowered and the carbon dioxide could be increased. The water then passed through a two-liter graduated cylinder where a nutrient solution could be continuously added from a stock carboy by pressure of nitrogen from a gas cylinder. The water, controlled by a stopcock, was finally siphoned through a flowmeter before passing through the inflow sample bottle, the photosynthesis-respiration chamber, and the outflow sample bottle. Two black porcelain-coated steel trays measuring 19½ by 8 inches were placed in the chamber. These trays contained stream bottom materials and a biota which had developed while they were in the artificial streams.

Methods of Estimating Production

Estimates of production in the artificial streams depended on determining the differences in dissolved oxygen concentration in the water entering and leaving the streams. Determination of dissolved oxygen was made by the Alsterberg (azide) modification of the Winkler method, titrating a 100-milliliter aliquot of a 300-milliliter water sample. It was assumed that there is a constant relationship between the amount of oxygen released and the amount of carbon dioxide utilized in the synthesis of carbohydrate. The level of oxygen in the outflow was assumed to be the same as that in the streams and the chamber where the water was thoroughly mixed, except when the streams were not circulated by the paddlewheels.

Periodic determinations of dissolved oxygen were made on the inflow and outflow water. The mean of the values for dissolved oxygen in the inflow water for a given period of time was subtracted from the mean for the outflow water for this period. This gave a mean difference for the period of time. This mean difference was then multiplied by the rate of exchange water in liters per hour passing through the stream to obtain the milligrams of oxygen produced in the stream which passed out of the stream during that period. The difference between the outflow water at

the beginning and end of the period was then multiplied by the volume of water contained in the stream to determine the amount of oxygen stored in the stream for that period of time. The sum of the oxygen passed and that stored was considered to be the amount of oxygen produced above the respiration requirements of the community for that period of time.

The stream was darkened with black polyethylene sheeting for the respiration estimate. This was obtained by measuring, as described above, the amount of oxygen used from the inflow and stored water during a similar time period the previous day. The sum of the oxygen produced during a light period and the oxygen used during a comparable dark period was considered to represent the gross production for a period of time. The production in the streams was estimated for three periods during a day. These were from 9:00 a.m. to 11:00 a.m., from 11:00 a.m. to 1:30 p.m., and from 1:30 p.m. to 3:30 p.m. The sum of the estimates of gross production for the six and one half hour period was converted to mean gross production per square meter per hour. This was used to compare the effects of different sets of conditions on the communities in the streams. When the streams were not circulated, oxygen curves under dark and light conditions for inflow

and outflow water were used for production estimates in a manner similar to the method described by Odum (19, p. 102-117).

Production estimates in the photosynthesis-respiration chamber were obtained from two trays of bottom materials with biota grown in the artificial streams. The trays were placed in the photosynthesis-respiration chamber and the top securely fastened in place. The exchange rate of water was adjusted to 300 milliliters per minute. This was slightly more than the equivalent flow for the two trays on the basis of area of bottom material when they were in the artificial streams. A black polyethylene cover was placed flat against the glass for respiration estimates. The lights were used during the photosynthesis determinations. The incoming water was adjusted when necessary to deliver the desired quantities of dissolved oxygen, carbon dioxide and nutrients. The chamber was darkened and allowed to run overnight to stabilize and to provide a respiration estimate. The chamber was then illuminated to permit photosynthesis. Another period was allowed to replace, by exchange, the water in the chamber before the effect of photosynthesis was determined. Differences in oxygen and nutrient level in inflow and outflow water samples were used for these determinations. It was assumed that a

community under constant conditions would reach a state of equilibrium in which the difference in inflow and outflow was the result of the activity of the community under those fixed conditions.

Methods of Estimating Biomass and Community Composition

The terms "biomass" and "standing crop" are used to designate the dry weight of living and dead plants and animals present in the artificial streams after the macroscopic animals were removed. Estimates of standing crop in the artificial streams were made by placing two tightly fitting plywood gates in the streams twelve inches apart. The rocks were then scrubbed clean and rinsed in the water between the two gates. All of the bottom gravel was removed. The sides of the tanks were scraped clean of algae. The water between the gates was then siphoned out through a plankton net.

The macroscopic animals in the sample were removed under a dissecting microscope. The samples were then thoroughly mixed with a magnetic stirrer and an aliquant portion removed and counted for community composition. The remainder was dried and weighed. The dried material was then ground and mixed. Total phosphorous was determined by the Fiske-Subbarow method (2, p. 354). Total

nitrogen was determined by the Kjeldahl method (2, p. 12-13). The total nitrogen was converted to crude protein by multiplying by a factor of 6.25. Counts of algal cells attached to glass slides suspended in the experimental streams were made to determine percent of community composition during succession.

Experimental Variables and Analytical Procedures

The principal experimental variables tested were light energy and nutrient materials. The influences of these on the production and succession of various plant communities in the experimental streams were studied.

Light Energy. In order to study production and succession of algal communities at different light levels, two streams were left exposed to natural lighting as it existed in the laboratory building and two streams were covered with two layers of 1/16th-inch mesh nylon screen. Production estimates were taken on the streams on sunny days and cloudy days. Light measurements were made in footcandles with a Weston Illumination Meter Model 756. A conversion factor of 37.0 was used to convert mean footcandles to gram calories per square meter per hour. This conversion factor is the product of: 10.764 lux per footcandle (9, p. 2880) times 4 ergs per lux (25, p. 837)

times 2.3889×10^{-8} gram calories per square centimeter per second for each erg (9, p. 2874) times 10,000 square centimeters per square meter, times 3,600 seconds per hour. This gives 37.0 gram calories per square meter per hour per footcandle. The factor 37.0 was multiplied by the mean number of footcandles reaching the surface of the stream and divided by 1.56, the area of the artificial stream in square meters. This estimate of gram calories was used to compare the effect of different light intensities on gross production and the efficiency of utilization of solar energy by the plant community.

Nutrient Materials. In most natural streams, production may be assumed to be limited by available nutrient materials or light energy. If adequate light is available, increases in nutrient materials should result in increases in production rate up to the capacity of the existing plant community to utilize the light and nutrients. Different rates of exchange water flowing through the streams were used to present multiple amounts of the entire nutrient complement to the experimental communities. It was possible to establish by this means that nutrients were limiting under some conditions. In an attempt to identify the limiting nutrients in one series of experiments, 2 liters of exchange water were supplied continuously, and the

phosphate and nitrate concentrations were supplemented individually and then together. Determinations were made on the concentrations of phosphate and nitrate entering and leaving the streams. Phosphate determinations were made by a sodium molybdate hydrazine sulphate reduction (4, p. 873-877). Nitrate determinations were made by the phenoldisulphonic acid method (2, p. 535-536). Carbon dioxide was determined by using the temperature, pH, total solids and bicarbonate alkalinity and a nomograph (1, p. 57).

RESULTS

Periphyton Communities

The composition of the periphyton communities that developed in the artificial streams was determined in part by seeding from the water supply and in part by experimental conditions. Succession occurred during the colonization period, and the organisms that could best compete under the particular conditions present in a stream provided the basis for the different types of communities that became established.

Community Description. Eight major communities developed during the study, and these are described in Table 1. The different conditions under which the various communities developed are also given in Table 1. Where a particular community developed in more than one stream, the description is based on the mean community composition for all streams having that community. Communities A, B and C each occurred in only a single stream. Communities D and E each developed in two streams, while communities G and H each occurred in three streams. Though communities were grown under different conditions, they could be tested under the same conditions or different conditions in production studies, which usually required only two days. When

TABLE 1. Composition of Artificial Stream Communities by Group in Per Cent by Number of Cells

Grown in Fall and Winter with Non-filtered Water					
Current and light		No current and light		No current and shaded	
COMMUNITY A (1 stream)		COMMUNITY B (1 stream)		COMMUNITY C (1 stream)	
Cocconeis	62.0	Iron Bacteria	61.0	Iron Bacteria	90.0
Iron Bacteria	27.0	Achnanthes	9.5	Vorticella	2.1
Achnanthes	1.5	Pinnularia	7.3	Gomphonema	1.9
Stigeoclonium	.5	Cocconeis	5.5	Stigeoclonium	1.8
Pinnularia	.7	Tabellaria	2.4	Cocconeis	.7
Hormotila	.5	Chrococcus	2.2	Chryptomonas	.6

Grown in Spring and Summer with No Current					
Non-filtered, shaded		Non-filtered, light		Filtered water, light	
COMMUNITY D (2 streams)		COMMUNITY E (2 streams)		COMMUNITY F (6 streams)	
Iron Bacteria	36.0	Stigeoclonium	56.0	Stigeoclonium	33.3
Pinnularia	24.0	Pinnularia	11.9	Oedogonium	26.7
Navicula	9.6	Achnanthes	8.2	Chlamydamonas	24.0
Cocconeis	8.4	Cocconeis	5.3	Gomphonema	4.2
Stigeoclonium	7.3	Nitzschia	4.7	Bodo	3.0
Achnanthes	4.8	Chlamydamonas	3.3	Surirella	2.5

TABLE 1. (Continued)

Grown in Fall and Winter with Filtered Water in Light and Current

COMMUNITY G (3 streams)		COMMUNITY G' (3 streams)		COMMUNITY H (3 streams)	
Melosira	31.9	Oedogonium	46.3	Melosira	62.6
Oedogonium	28.4	Melosira	23.9	Oedogonium	13.6
Fragillaria	9.8	Cylindrospermum	13.2	Fragillaria	9.7
Cylindrospermum	8.3	Fragillaria	5.4	Cylindrospermum	5.0
Hormidium	2.9	Hormidium	2.5	Mougeotia	2.2
Rhopalodia	2.7	Closterium	1.9	Hormidium	1.5

the same community developed in more than one stream, its production could be tested under different experimental conditions.

Community A was predominantly a sessile diatom, Cocconeis, community. Community B contained a large percentage of bacteria with some diatoms present. Community C consisted almost entirely of bacteria with very few other organisms present. Community D was a combination of bacteria and diatoms. Community E had a filamentous green alga , Stigeoclonium, dominant. Community F was a combination of the green algae, Stigeoclonium, Oedogonium and Chlamydamonas. Community G was a combination of a filamentous diatom, Melosira, and Oedogonium. Community G' was a subcommunity that developed with large floating mats of Oedogonium, Melosira and Cylindrospermum. In community H, Melosira was the dominant plant organism present.

Table 2 summarizes the influence of experimental conditions on the contribution in per cent by number of the major taxonomic groups in the different communities. Each community is shown once under each main group, and the percentage contribution of that group follows. The conditions existing during the development of each community are indicated by the appropriate entries of the community designation under the experimental conditions.

TABLE 2. The Influence of Experimental Conditions on the Composition of Stream Communities by Major Group in Per Cent by Number

Group	Experimental Conditions								Percent of Comm.
	Spr. and Summer	Fall and Winter	Filt. Water	Non-filt. Water	Cur.	No Cur.	Shade	No Shade	
Green Algae	F	-	F	-	-	F	-	F	85.15
	E	-	-	E	-	E	-	E	59.40
	-	G'	G'	-	G'	-	-	G'	51.95
	-	G	G	-	G	-	-	G	36.42
	-	H	H	-	H	-	-	H	18.67
	D	-	-	D	-	D	D	-	9.86
	-	B	-	B	-	B	-	B	2.88
	-	C	-	C	-	C	C	-	1.77
	-	A	-	A	A	-	-	A	1.20
Diatoms	-	H	H	-	H	-	-	H	74.49
	-	A	-	A	A	-	-	A	65.66
	D	-	-	D	-	D	D	-	50.99
	-	G	G	-	G	-	-	G	47.73
	E	-	-	E	-	E	-	E	33.61
	-	G'	G'	-	G'	-	-	G'	31.06
	-	B	-	B	-	B	-	B	29.99
	F	-	F	-	-	F	-	F	10.53
	-	C	-	C	C	-	C	-	4.07
Blue-Green Algae	-	G'	G'	-	G'	-	-	G'	14.63
	-	G	G	-	G	-	-	G	8.73
	-	H	H	-	H	-	-	H	5.98
	E	-	-	E	-	E	-	E	3.13
	-	B	-	B	-	B	-	B	2.46
	D	-	-	D	-	D	D	-	1.59
	-	A	-	A	A	-	-	A	.80

TABLE 2. (Continued)

Group	Experimental Conditions								Percent of Comm.
	Spr. and Summer	Fall and Winter	Filt. Water	Non-filt. Water	Cur.	No Cur.	Shade	No Shade	
Blue-grn.	F	-	F	-	-	F	-	F	.25
Algae	-	C	-	C	-	C	C	-	.12
Iron	-	C	-	C	-	C	C	-	89.88
Bacteria	-	B	-	B	-	B	-	B	61.11
	D	-	-	D	-	D	D	-	35.99
	-	A	-	A	A	-	-	A	27.19
	E	-	-	E	-	E	-	E	2.99
	F	-	F	-	-	F	-	F	.21
	-	H	H	-	H	-	-	H	.17
Ciliates	-	C	-	C	-	C	C	-	2.15
	-	A	-	A	A	-	-	A	.80
	-	B	-	B	-	B	-	B	.59
	F	-	F	-	-	F	-	F	.43
	D	-	-	D	-	D	D	-	.30
	E	-	-	E	-	E	-	E	.27
	-	G	G	-	G	-	-	G	.02
Flagel-	F	-	F	-	-	F	-	F	3.24
lates	-	B	-	B	-	B	-	B	2.25
	D	-	-	D	-	D	D	-	1.23
	-	C	-	C	-	C	C	-	.68
	E	-	-	E	-	E	-	E	.54
	-	A	-	A	A	-	-	A	.07
	-	G	G	-	G	-	-	G	.02

The communities developed at higher light intensities seemed to produce more autotrophic plants than those at lower intensities. The shaded communities were usually dominated by bacteria and diatoms. In the spring the green algae were more plentiful, and in the fall the diatoms and blue-green algae were dominant. When the water was filtered the green algae were the principal organisms, while in non-filtered water the bacteria were the most abundant. The protozoans seemed to be more abundant in the fall than in the spring. The bacteria were more plentiful when the community was shaded, when water velocities were low, and when the water was not filtered. In the fall, bacteria were slightly more numerous in shaded community C than they were in non-shaded community E. The bacteria in community C in the fall and winter were twice as abundant as in community D in the spring and summer. In non-filtered water the bacteria were 14 times more numerous than in filtered water. The non-filtered water was higher in organic detritus and in iron from a leaf rack on the non-filtered water supply tank.

The green algae were six times more abundant in the spring in the streams having high light intensities than in the shaded streams. In the spring they were six times more numerous than in the fall in both shaded and non-shaded

streams. The diatoms were more plentiful in the fall and winter than in the spring and summer. The diatoms appeared to be overshadowed by the green algae in the spring and summer. The diatoms reached a higher stage of development in the non-shaded than in the shaded communities where there was little competition for space and nutrients. Both lower temperature and lower light intensities may have acted to reduce competition by green and blue-green algae.

Blue-green algae were 12 times more plentiful in community E with non-filtered water than they were in community F with filtered water. Blue-green algae tended also to reach a higher stage of development in the fall when the dissolved organic content in the water was no doubt higher.

Experimental conditions had little apparent effect on numbers of ciliates. Flagellates were slightly more abundant in communities having filtered water and little current, perhaps because zoospores from some of the green algae made an important contribution under these conditions.

Community Succession. Community succession in the streams was studied under shaded and non-shaded conditions by counting the forms present on glass microscope slides suspended in the streams. Counts were made every two days for a period of 28 days. Successional differences between

community D, grown at the high light intensity, and community E, grown at the low light intensity are shown in figure 3. In the higher light intensity, the diatoms exhibited an early, rapid increase, but were eventually dominated by the green forms such as Stigeoclonium. In the streams having the low light intensity, the diatom populations did not develop as rapidly as they did at the higher light intensity nor reach the high concentration. The diatoms continued to dominate the autotrophic population in the shaded community throughout the experimental period. The green algae appeared unable to compete successfully with the diatoms and bacteria under conditions of subdued light.

Biomass

The mean weights and ranges of weights per square meter of dry biomass, nitrogen and phosphorus for communities F, G and H are given in Table 3. The percentages of nitrogen and phosphorus are also given. The individual weights on which these means and ranges are based are given in Appendix Table C.

The mean weights and percentages of phosphorus and nitrogen for community F were higher than those of community H. Community F was predominantly green algae, and

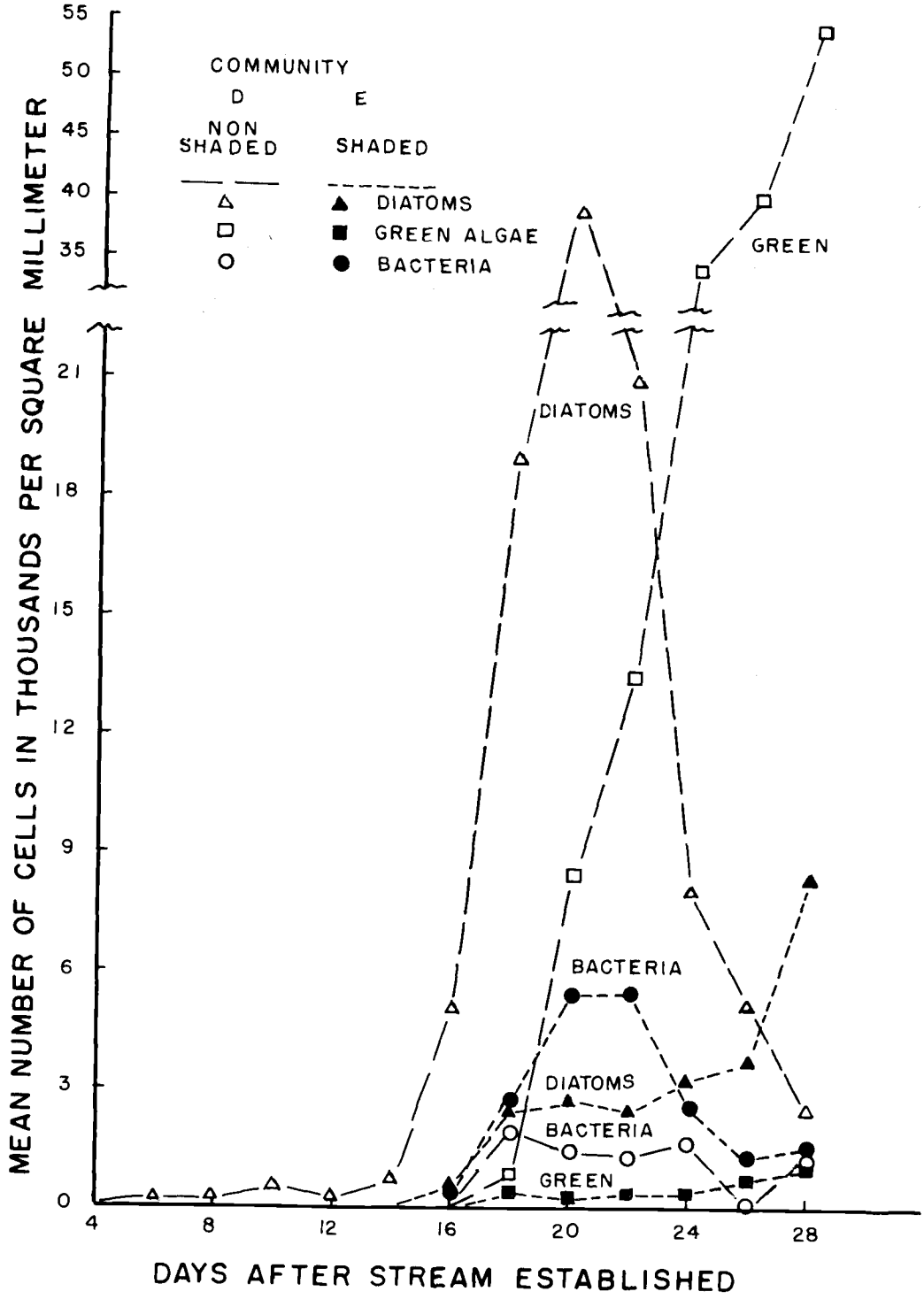

Figure 3. Succession of periphyton on glass microscope slides in communities D and E grown under shaded and non-shaded conditions.

TABLE 3. Mean in Grams per Square Meter of Dry Biomass, Nitrogen and Phosphorus and Per Cent Nitrogen and Phosphorus in Communities F, G and H

Community		Biomass (mg/m^2)	Nitrogen (mg/m^2)	Phosphorus (mg/m^2)	Nitrogen (percent)	Phosphorus (percent)
F	mean	116	.260	.0351	2.24	.307
	range	41-299	.117-.538	.0139-.0825	1.17-4.55	.265-.347
G	mean	102	.158	.0244	1.52	.237
	range	45-193	.086-.248	.0090-.0552	1.18-2.06	.120-.324
H	mean	100	.126	.0208	1.36	.218
	range	23-246	.040-.324	.0058-.0324	.95-1.72	.158-.286

community H was predominantly diatoms. Community G had slightly more diatoms than green algae. The large proportion of silica in the diatoms may have accounted for the lower percentages of phosphorus and nitrogen in community H.

Weight of biomass in the standing crop plotted against production showed no correlation. This was probably due to differences in the amount of dead material in the samples. Chlorophyll estimates might have shown a closer correlation to production.

Light Energy

Shaded community D in streams 1 and 2 (Table 4) had small populations of algae and large populations of bacteria. Community E in streams 3 and 4 was grown under a higher light intensity and had larger populations of green algae and smaller populations of bacteria. Production of oxygen in screened stream 2 D on a cloudy day was not enough to satisfy the respiration need of the community. The production of oxygen by community 3 E under natural lighting on a sunny day was more than double the production of oxygen in community 4 E on a cloudy day. Production by community E under all conditions was much greater than respiration and much greater than production by community D.

TABLE 4. Respiration, Production and Light Energy per Square Meter per Hour of Test Period for Shaded Community D and Non-shaded Community E on Sunny and Cloudy Days

Stream and Community	Day	Respiration as mg O_2	Gross Production as mg O_2	Light Energy as kcal
1 D (shaded)	sunny	21.95	36.68	142
2 D (shaded)	cloudy	27.71	6.70	98
3 E (non-shaded)	sunny	89.44	260.65	494
4 E (non-shaded)	cloudy	26.92	123.86	334

Diurnal curves of the oxygen production exhibited a midday slump for both shaded and non-shaded communities. Yentsch and Ryther (35, p. 140) observed diurnal fluctuations in the chlorophyll a content of natural phytoplankton populations with the highest concentrations occurring during the morning and afternoon, low values at midday and at night; and this may be the basis of the midday slump that occurred in the experimental streams.

Figure 4 shows the gross production in milligrams of oxygen produced per square meter per hour in the artificial streams plotted against the kilogram calories of light energy received at the surface of the water for experiments under different conditions. All of the squares and triangles represent estimates of production under conditions of 1/3 foot per second current with 2 liters per minute of exchange water and natural lighting on communities G and H. The open squares represent estimates taken during August and September 1960, and the dark squares and all of the triangles represent estimates taken during October and November 1960. The triangles represent estimates of production when nitrate was added to the streams, and the inverted triangles represent production estimates taken when phosphate was added to the streams. The circles represent production estimates taken in July 1959 under no current

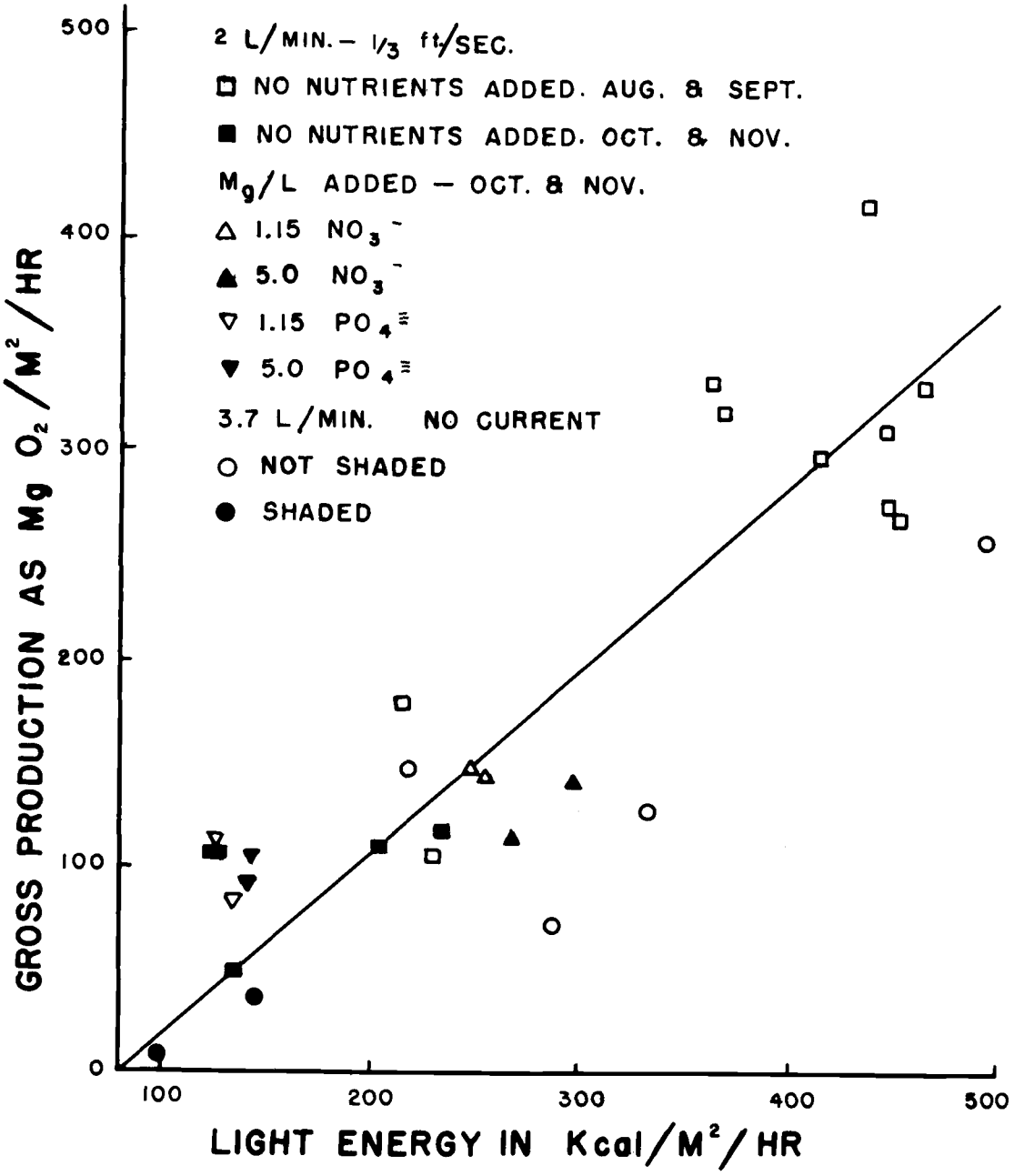

Figure 4. The influence of light on gross production.

conditions with 3.7 liters per minute of exchange water on communities D and E. The open circles were production estimates taken in natural lighting on community E, and the dark circles were production estimates taken in shaded community D.

A strong linear relation between gross production and light energy available at the water surface is demonstrated in figure 4. The deviations from the visually positioned line are, no doubt, in large part due to the several variables being tested in the different experiments. That the relation is so strong even with the many variables contributing to the variation suggests the dominant role played by light.

Nutrient Materials

Figure 5 illustrates the relationship between gross production and the rate of exchange of stream water, and thus the rate of delivery of the total nutrient complement. The production estimates were made on community F, which was grown at 3.7 liters per minute during the spring and summer of 1960. Only an imperceptible current was produced in the streams. When these production estimates were made, sunny days with high light intensities eliminated light as a limiting factor.

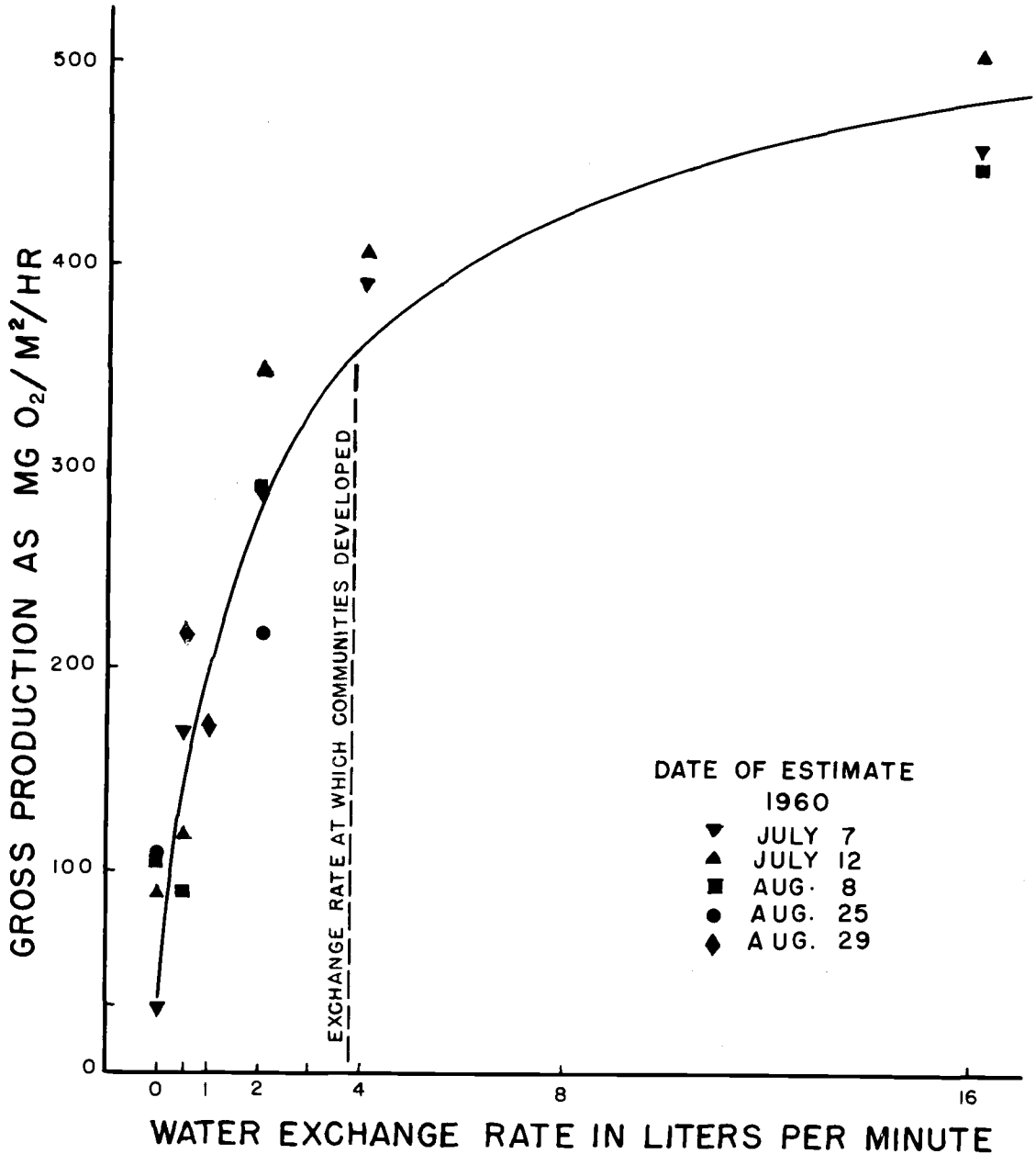

Fig. 5. The influence of exchange rate of water on gross production in experimental streams with no artificial current. (Communities grown at 4.0 liters per minute)

Gross production can be seen in figure 5 to have increased very steeply with increases in exchange rate from 0 to about 4 liters per minute. A slower increase in production rate occurred with further increases in exchange rate from 4 liters to 16 liters per minute. It is instructive to note that for these communities developed at exchange rates of 3.7 liters per minute, production rate increased very sharply with increases in exchange rates up to this development level; but the production rate did not increase as rapidly when exchange rates were increased over the developmental level. Light intensities were high during this experiment, and productive biomass appears to have limited production rate at the higher exchange rates. These communities were apparently producing at nearly their maximum possible rate under the conditions at which they were developed. Increases in nutrient supply provided only a slight advantage, which no doubt would have eventually resulted in higher productive biomasses and associated higher production rates with further increases in nutrient supply.

Figure 6 shows the relationship between gross production and the rate of exchange water for green algae community G' and diatom community H (Table 5) on a sunny day, October 31, and a cloudy day, November 3, 1960. The

TABLE 5. Proportion in Per Cent of Green Algae and Diatoms in Stream Communities

Date	Group	Community and Stream Number					
		H-1	G'-2	H-3	G'-4	G'-5	H-6
10/24/60	Diatoms	74	30	74	33	39	73
	Green algae	26	70	26	67	61	27
11/2/60	Diatoms	62	36	72	35	24	73
	Green algae	38	63	28	65	76	27

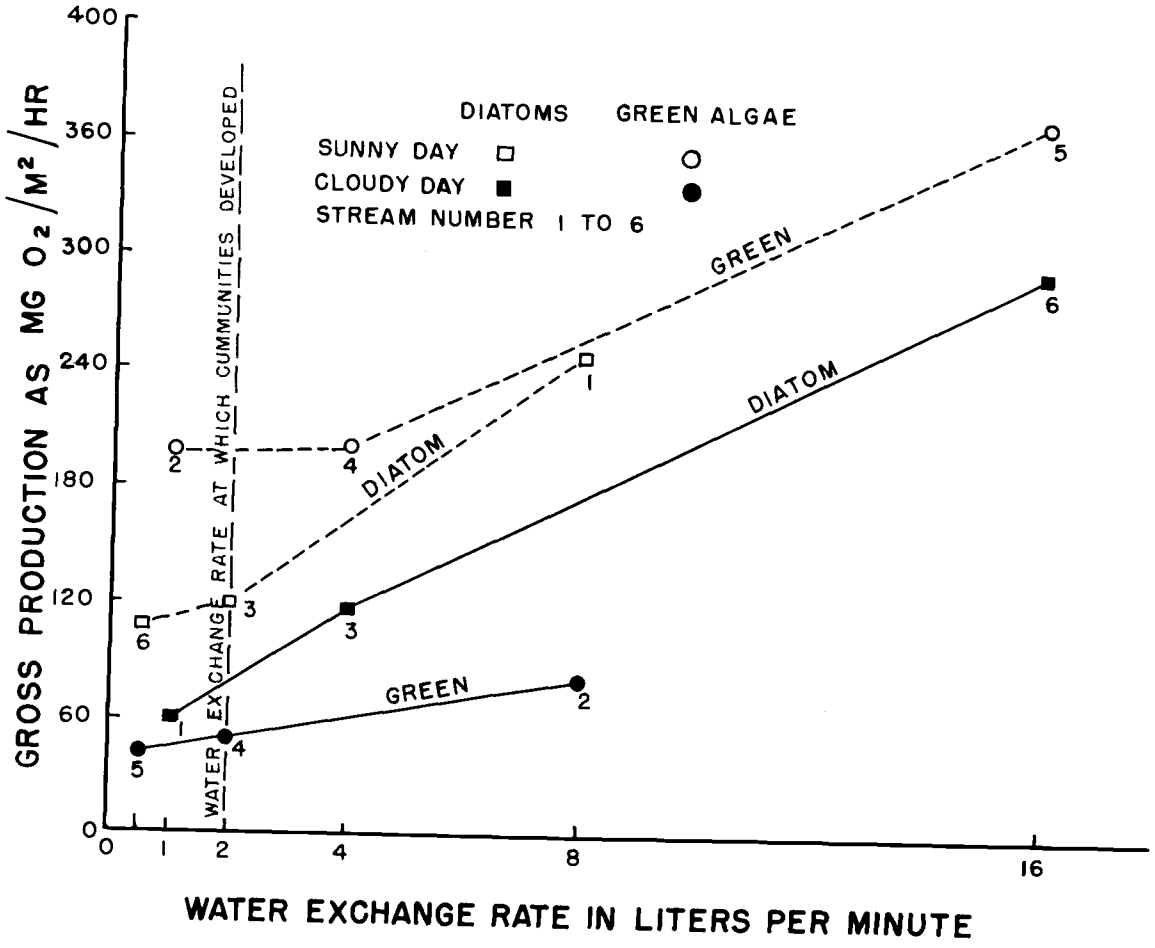

Figure 6. The influence of exchange rate of water on gross production in experimental streams with .33 feet per second current velocity. (Communities grown at 2 liters per minute)

communities were grown at an exchange rate of water of 2 liters per minute.

Production rates increased with increases in exchange rate and hence increases in the total nutrient complement. On the cloudy day, the green algae exhibited only a small increase in production rate with increasing exchange rate. The diatom community H exhibited much greater increase in production rate with increases in exchange rate on the cloudy day. The diatom community had higher production rates than the green algae community on the cloudy day at comparable exchange rates.

Production on the sunny day was higher than on the cloudy day for both communities, as might be expected. Loss of oxygen to the atmosphere was greater for streams 3, 4, 5 and 6, because of the diffusion at the paddlewheels than for streams 1 and 2, which were circulated by the jet action of small pumps. The loss was apparently greater at particular exchange rates on the sunny day than on the cloudy day. Thus the shapes and positions of the curves are somewhat in error. Nevertheless, the curves still indicate the green algae to be more productive than the diatoms on the sunny day, the reverse being true on the cloudy day. This may suggest a possible explanation for the dominance of green algae communities in the spring at

higher light intensities, and the dominance of the diatom communities in the fall at lower light intensities.

The concentrations of phosphate and nitrate in the stream water were increased experimentally to determine if either of these nutrient materials could be limiting production rates in the streams. On November 10, 1960, the exchange rate of water was set at 2 liters per minute, and the phosphate concentration in two of the streams was increased by 1.15 milligrams per liter. Two of the streams received a phosphate increase of 5 milligrams per liter, and two streams received only the phosphate concentration present in the water supply. The concentrations of nitrate were similarly increased by 1.15 milligrams per liter and 5 milligrams per liter in an experiment on November 21, 1960. There were no significant increases in production rates with increases in the concentrations of either phosphate or nitrate. Apparently some other nutrient material was limiting production at this time of the year.

To make further experiments on nutrients possible, trays were removed from the artificial streams with the plant communities intact and placed in the photosynthesis-respiration chamber. Figure 7 shows production rates obtained in the photosynthesis-respiration chamber plotted against hours of continuous exposure to light. Production

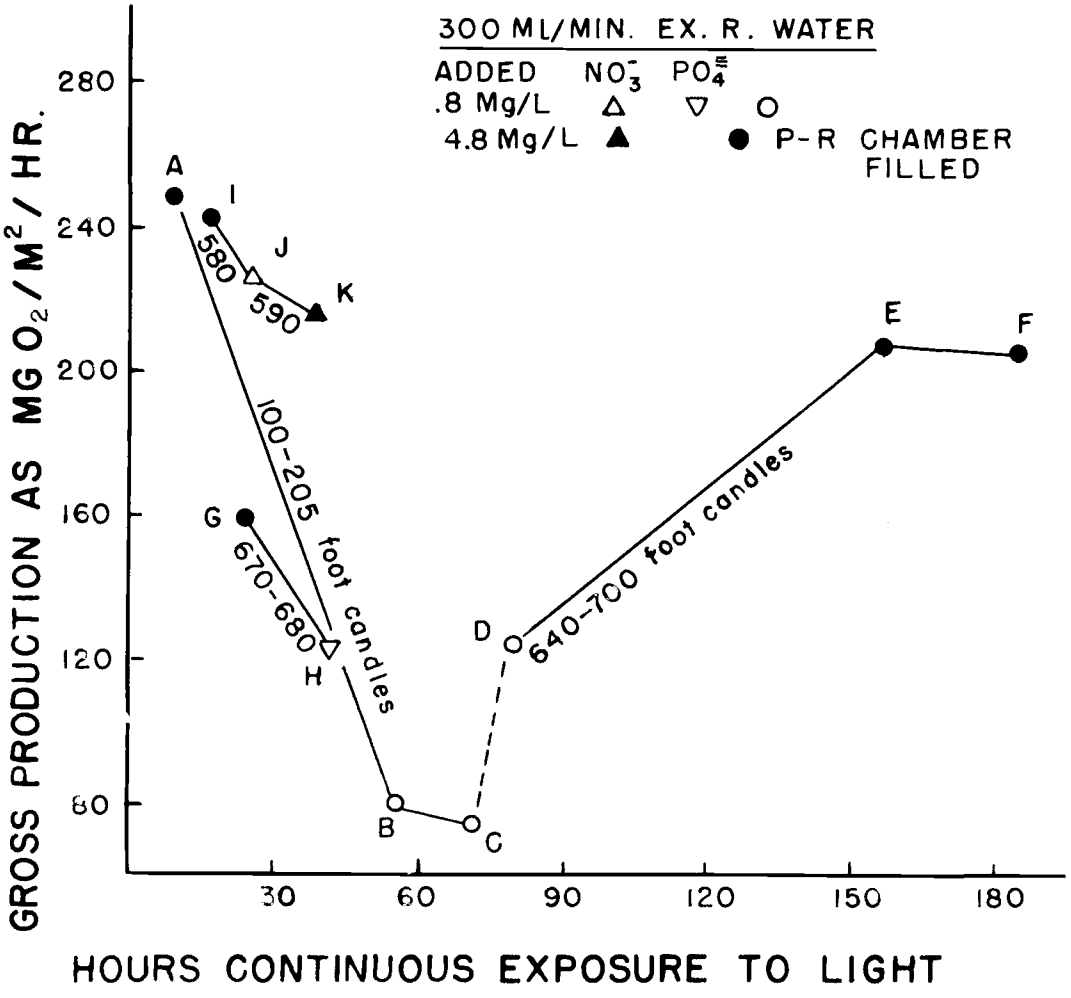

Figure 7. The influence of a limiting factor on gross production in the photosynthesis-respiration chamber.

estimates on one set of trays are connected by a line. The respiration estimates necessary to determine gross production were made with the chamber darkened prior to the period of light exposure. Filtered exchange water was supplied to the photosynthesis-respiration chamber at 300 milliliters per minute, which was proportional to the exchange in the artificial streams at the rate of 2 liters per minute. Production estimate A was made after approximately 8 hours of light exposure. Production estimates B and C were made after 55 and 70 hours of continuous light. By this time the community was presumably dependent on the 300 milliliters per minute of exchange water to supply nutrients. The rapid decrease in production rate from A to B and then to C was probably due to depletion of the supply of essential nutrients present in the original volume of water. This rate of exchange apparently did not supply nutrients in sufficient quantity to maintain the original high rate of production.

Estimate D was based on the same community and exchange flow of water at a higher light intensity. Estimates E and F were each made after the chamber had been drained and refilled with 50 liters of water. The increase in production from point D to E was probably caused by the additional nutrient supply in the water used to refill the

chamber. To verify this, the chamber was again drained and refilled before making production estimate F, which was found to remain high although some 30 hours of continuous illumination had passed.

The community on which estimates G and H were made exhibited a decline in production rate from point G to H. The photosynthesis-respiration chamber was filled prior to estimate G, and 0.8 milligrams per liter of phosphate was added to the exchange water prior to estimate H.

Estimates J and K were made on a community on another set of trays after the addition of 0.8 and 4.8 milligrams per liter of nitrate to the exchange flow. Increase in nitrate concentration did not prevent a decline in production rate.

An examination of the data on exchange rate appears to indicate that nutrients limited production when present below the level at which the communities were grown in the artificial streams and increased production when present above this level. Communities on trays placed in the photosynthesis-respiration chamber with 50 liters of water had high production rates which decreased when the rate of exchange was proportional to that in the artificial streams. Complete replacement of the water in the chamber resulted in a marked increase in production rate over that obtained

at the proportional exchange rate. The addition of nitrate and phosphate to the artificial streams and photosynthesis-respiration chamber indicated that in the fall these were not the nutrients limiting production. The nutrients were added as potassium phosphate and potassium nitrate. Carbon dioxide was also supplemented. This would eliminate potassium and carbon dioxide as limiting factors at these light levels.

DISCUSSION

To obtain the efficiencies of utilization of light energy by the stream communities and the photosynthesis-respiration ratios, it was necessary to have production estimates per square meter per day. Production is reported in the results section as the mean per square meter per hour for the six and one-half hour test period from 9:00 a.m. to 3:30 p.m. In order to estimate the production for the other two parts of the daylight, it was assumed that oxygen production and respiration balanced at sunrise and sunset. Then, the difference in the dissolved oxygen in the inflow and outflow water at 9:00 a.m. was used as the height of a triangle of which the time from sunrise to 9:00 a.m. was the base; and the area within this triangle was used as an estimate of the oxygen produced above the respiration requirements of the community prior to the first determination at 9:00 a.m. The difference in the dissolved oxygen in the inflow and outflow water at 3:30 p.m. was used as the height of another triangle, with the time from 3:30 p.m. to sunset as the base, and the area of this triangle was used for making the estimate of production from 3:30 p.m. to sunset. The sum of the estimates of oxygen produced above the respiration requirement prior to 9:00 a.m., after 3:30 p.m., and

from 9:00 a.m. to 3:30 p.m. was added to the estimate of respiration from sunrise to sunset. This provided an estimate of gross production per day. The previously computed mean respiration per hour was multiplied by 24 to obtain the daily respiration estimate.

The estimates of gross production and respiration as milligrams of oxygen per square meter per day were converted to gram calories (Table 6) by multiplying by a factor of 3.53. To arrive at this factor the assumptions had to be made that each gram atom of carbon fixed was equivalent to 113 kilocalories of potential energy (25, p. 45) and that the photosynthetic quotient was 1 (25, p. 33). Then, 1 milligram of oxygen produced would be equivalent to 3.53 gram calories of energy. If the photosynthetic quotient was actually higher than 1, as suggested by Ryther (30, p. 75), these estimates would be high; and consequently the efficiencies of utilization of light computed by using this factor will be higher than actually existed. Photosynthetic quotients close to 1 seem probable where the products of photosynthesis are carbohydrates. When the ultimate products of photosynthesis are fats or proteins, the photosynthetic quotient seems to be higher (30, p. 74) (21, p. 93).

The efficiency of utilization of solar energy by the community was obtained by dividing the energy of community

TABLE 6. Production, Respiration and Solar Energy in Kilocalories per Square Meter per Day, Photosynthesis-Respiration Ratios, and Per Cent Efficiencies of Solar Energy Utilization

Comm. Type	Ex. R. l/min.	Date 1960	Vel. ft./sec.	Gross P.	Resp.	Net P.	Light	Eff.	P/R
F	3.7	6/30	Imp.[1]	19.136	4.242	19.070	--	--	4.51
F	3.7	6/30	Imp.	21.208	5.355	20.159	--	--	3.96
F	3.7	6/30	Imp.	20.230	5.065	20.159	--	--	3.99
F	3.7	6/30	Imp.	15.126	2.316	15.096	--	--	6.53
F	3.7	6/30	Imp.	18.688	11.430	18.562	--	--	1.63
F	3.7	6/30	Imp.	17.004	3.474	16.952	--	--	4.89
F	0.0	7/8	Imp.	4.988	1.789	4.967	--	--	2.79
F	0.5	7/8	Imp.	8.218	6.753	8.151	--	--	1.22
F	2.0	7/8	Imp.	13.474	7.074	13.396	--	--	1.90
F	4.0	7/8	Imp.	18.423	5.499	18.352	--	--	3.35
F	8.0	7/8	Imp.	13.202	.586	13.195	--	--	2.25
F	16.0	7/8	Imp.	22.006	4.744	21.935	--	--	4.64
F	0.0	7/12	Imp.	4.478	1.789	4.458	--	--	2.50
F	0.5	7/12	Imp.	5.867	6.752	5.806	--	--	.87
F	2.0	7/12	Imp.	15.698	7.074	15.620	--	--	2.22
F	4.0	7/12	Imp.	18.790	5.499	18.790	--	--	3.42
F	8.0	7/12	Imp.	14.611	.586	14.585	--	--	24.93
F	16.0	7/12	Imp.	25.370	4.744	25.294	--	--	5.35
F	0.0	8/8	Imp.	4.988	1.789	4.977	--	--	2.79
F	0.5	8/8	Imp.	5.090	6.752	5.029	--	--	.75
F	2.0	8/8	Imp.	12.390	7.074	12.312	--	--	1.75
F	4.0	8/8	Imp.	13.416	5.499	13.350	--	--	2.44
F	8.0	8/8	Imp.	17.378	.586	17.348	--	--	29.65
F	16.0	8/8	Imp.	19.888	4.744	19.822	--	--	4.19
F	0.0	8/25	Imp.	6.248	.884	6.232	2,316	.269	7.40
F	2.0	8/25	Imp.	8.694	1.655	8.668	2,348	.370	5.25
F	4.0	8/25	Imp.	6.696	5.616	6.640	2,373	.282	1.19
F	0.5	8/29	Imp.	9.404	4.850	9.340	4,213	.223	1.94
F	1.0	8/29	Imp.	7.904	5.796	7.840	4,364	.181	1.36
F	3.0	8/29	Imp.	9.029	5.768	8.966	4,276	.211	1.56
H	2.0	9/15	.33	13.237	1.327	13.206	5,060	.261	9.97
G	2.0	9/15	.33	10.929	1.825	10.898	5,957	.183	5.99
H	2.0	9/15	.33	13.276	1.655	13.243	6,102	.217	8.02
G	2.0	9/15	.33	15.500	.664	15.473	6,171	.251	23.34
G	2.0	9/15	.33	10.929	.995	10.903	6,028	.181	12.08
H	2.0	9/15	.33	15.017	.664	14.989	5,661	.265	22.62
H	2.0	9/19	.33	7.540	.829	7.522	3,631	.207	9.09
G	2.0	9/19	.33	4.458	.664	4.446	3,758	.118	6.71
H	2.0	9/19	.16	4.398	1.127	4.381	3,370	.130	3.31
G	2.0	9/19	.16	11.751	.664	11.728	3,993	.294	17.69
G	2.0	9/19	.03	12.853	4.642	12.797	3,887	.330	2.77
H	2.0	9/19	.03	12.002	1.991	11.970	3,802	.315	6.03
H	2.0	9/27	.33	12.697	3.646	24.616	4,994	.254	3.48
G	2.0	9/27	.33	16.559	3.646	16.504	5,675	.291	4.54
G'	0.5	10/31	.33	3.332	.484	3.323	1,096	.304	6.88
H	1.0	10/31	.33	2.164	1.009	2.152	925	.233	2.14
G'	2.0	10/31	.33	1.807	1.983	1.787	1,143	.158	.91
H	4.0	10/31	.33	4.465	2.958	4.432	1,143	.391	1.51
G'	8.0	10/31	.33	3.099	4.444	3.059	971	.319	.69
H	16.0	10/31	.33	5.951	12.906	5.835	1,051	.566	.46
H	0.5	11/3	.33	4.038	1.129	4.022	12,273	.033	3.57
G'	1.0	11/3	.33	7.162	2.722	7.129	18,646	.038	2.63
H	2.0	11/3	.33	4.454	.995	4.439	18,250	.014	4.47
G'	4.0	11/3	.33	7.589	2.365	7.558	16,804	.045	3.21
H	8.0	11/3	.33	9.640	3.332	9.600	16,786	.057	2.89
G'	16.0	11/3	.33	14.059	2.149	14.020	12,193	.115	6.54
H	0.5	11/3	.33	4.038	1.129	4.022	12,273	.033	3.57
H	2.0	11/16	.33	3.904	.166	3.897	894	.436	23.52
G	2.0	11/16	.33	3.897	1.659	3.877	960	.405	2.35
H	2.0	11/16	.33	3.392	.829	3.380	1,068	.317	4.09
G	2.0	11/16	.33	3.865	.497	3.856	1,092	.354	7.77
G	2.0	11/16	.33	3.113	.166	3.107	1,031	.302	18.75
H	2.0	11/16	.33	4.215	.664	4.204	978	.430	6.35
H	2.0	11/21	.33	4.112	.116	4.105	2,112	.194	24.77
G	2.0	11/21	.33	4.356	1.659	4.336	2,402	.181	2.77
H	2.0	11/21	.33	4.127	1.829	4.160	2,777	.150	5.03
G	2.0	11/21	.33	5.193	.497	5.181	3,128	.166	10.45
G	2.0	11/21	.33	5.256	.166	5.247	2,336	.225	31.66
H	2.0	11/21	.33	5.447	.664	5.434	2,568	.212	8.20

[1] Imp. = Imperceptible.

gross production by the energy of incident solar radiation (15, p. 407).

The photosynthesis-respiration ratio was obtained by dividing the energy of gross production by the energy of daily respiration.

Net production was computed by subtracting an estimate of plant respiration from gross production. Estimates of plant respiration were based on the P/R ratios. It was assumed that plant respiration accounted for a large percentage of the total respiration when the P/R ratio was large, and conversely that plant respiration accounted for a small percentage of the total respiration when the P/R ratio was small. Plant respiration was estimated by arbitrarily assigning a value of 55 per cent of total respiration to plant respiration for a community with a P/R ratio of 32. A value of 10 per cent of total respiration as plant respiration was used for a community with a P/R ratio of 1. The percentages of plant respiration for particular P/R ratios were then taken from a straight line drawn on arithmetic graph paper with coordinates 1, 10 and 32, 55.

The proportions of the products of photosynthesis utilized in plant respiration vary widely. Hicks (8, p. 523) reported a coefficient of respiration of 15 per

cent for Lemna under cultural conditions. Juday (13, p. 448) reported lacustrine producers respired about 33 per cent of the organic matter they synthesized. Odum (17, p. 71) reported that in Silver Springs, Florida, the percentage of gross production utilized in plant respiration was 56.5 per cent. For the Sargasso Sea, Riley (28, p. 267-8) reported a one-year average of 53 per cent of gross production consumed by plant respiration. Verduin (34, p. 85) reported plant respiration as 80 per cent of gross production for lake plankton. Ryther (29, p. 134) reported that during exponential growth in Chlamydamonas, respiration was 5-10 per cent of photosynthesis, but in nutrient-starved, non-growing cultures, respiration equaled photosynthesis.

Gross production (Table 6) varied depending on the amount of light available, the nutrients and the type of community. On June 30, 1960, community F in stream 2 had a gross production of 21.21 grams per square meter per day with an exchange rate of 3.7 liters per minute and an imperceptible current. Community G' on October 31, 1960, had only 1.18 grams of gross production per square meter per day with an exchange rate of 2.0 liters per minute and a current velocity of .33 feet per second. The mean gross production for the experimental stream communities F, G

and H was 2.8 grams per square meter per day under all conditions of light, exchange rate and current velocity. This seems to be close to the average for the production rates in lakes and the sea (Table 7) but lower than some rich flowing water communities such as Silver Springs, Florida (20, p. 93), and the Pacific coral reefs (13, p. 248-251). Production rates of 43 grams per square meter were reported by Tamiya (32, p. 314) for cultures of Chlorella enriched with carbon dioxide. Odum (20, p. 93) recorded production rates of 64 grams per square meter per day from Homosassa Spring, Florida.

The range of efficiencies of utilization of light energy for the experimental stream communities (Table 6) was .014 to .566 per cent with a mean of .236 per cent. The efficiencies of the experimental stream communities were no doubt increased by the white walls of the streams and the shallow depth of only 4 inches of water over the periphyton-covered rocks. The algae attached to the sides of the stream troughs also may have increased the production rates and efficiencies of the experimental communities per unit of stream surface. The range of efficiencies may vary widely in the aquatic environment. Efficiencies ranging from .04 per cent for a Minnesota pond (7, p. 374) to 5.8 per cent for Eniwetok Reef (23, p. 291-320) are

TABLE 7. Average Gross Production Values as Grams per Square Meter per Day in Natural and Other Aquatic Ecosystems

Ecosystem	Gross Production	Reference
Values for long periods:		
Experimental streams	2.8	
Sargasso Sea, yr. av.	0.55	(28, p. 267-8)
Clear, deep lake, Wisconsin	0.7	(13, p. 446-8)
Lake Erie, winter	1.0	(34, p. 85)
Shallow lake, Japan	2.1	(10, p. 294)
Long Island Sound, yr. av.	3.2	(27, p. 341)
Lake Erie, summer	9.0	(34, p. 85)
Silver Springs, Florida	17.5	(17, p. 71)
Coral reefs, av. 3 in Pacific	18.2	(14, p. 248-251)
Values for short favorable periods:		
Experimental streams	21.2	
Pond with untreated wastes, South Dakota, summer	27.0	(3, p. 79-80)
Marine turtle grass flats, Florida, August	34.0	(20, p. 93)
Silver Springs, Florida, May	35.0	(21, p. 95)
Mass algal culture, *Chlorella* (extra CO_2 added)	43.0	(31, p. 314)
Homosassa Spring, Florida	63.8	(20, p. 93)

reported for natural aquatic ecosystems in Table 8. Tamiya (32, p. 314) has obtained efficiencies as high as 24 per cent in cultures of Chlorella elipsodea agitated with bubbles of carbon dioxide.

Figure 8 illustrates the relation between kilocalories of light energy at the stream surface and the per cent efficiency of utilization of light by communities F, G and H. The triangles represent the determinations made on community F grown at an exchange rate of 3.7 liters per minute with an imperceptible current. The circles and squares represent determinations made on communities G and H respectively grown at exchange rates of 2 liters per minute with .33 foot per second current produced by the paddlewheels.

In general, figure 8 shows a decrease in efficiency with an increase of light. Similar decreases have been shown by Odum (18, p. 593) (24, p. 341) (21, p. 107) and Verduin (34, p. 49). Tamiya's data (32, p. 314) on the efficiencies of Chlorella indicate an increase in efficiency with a decrease in light intensities under conditions of enrichment with carbon dioxide.

Differences in communities, biomass, and nutrient availability were responsible for much of the variation about the visually positioned line in figure 8. The number

TABLE 8. Efficiency in Per Cent of Light Utilization by Aquatic Plant Communities

Ecosystem	Efficiency	Reference
Experimental streams	.24	
Minnesota pond	.04	(7, p. 374)
Cedar Bog lake	.1	(15, p. 407)
Root Spring	.2	(33, p. 299)
Shallow lake, Japan	.22	(10, p. 290)
George's Banks	.3	(5, p. 333)
Lake Mendota	.4	(15, p. 407)
Silver Springs, Florida	1.1	(21, p. 109)
Pacific coral reef	1.1	(14, p. 248)
Eniwetok Reef	5.8	(23, p. 291-320)
Chlorella cultures, excess CO_2	24.0	(32, p. 314)
Av. terrestrial plants	.09	(26, p. 133-4)
"Best Forest"	.25	(26, p. 133-4)

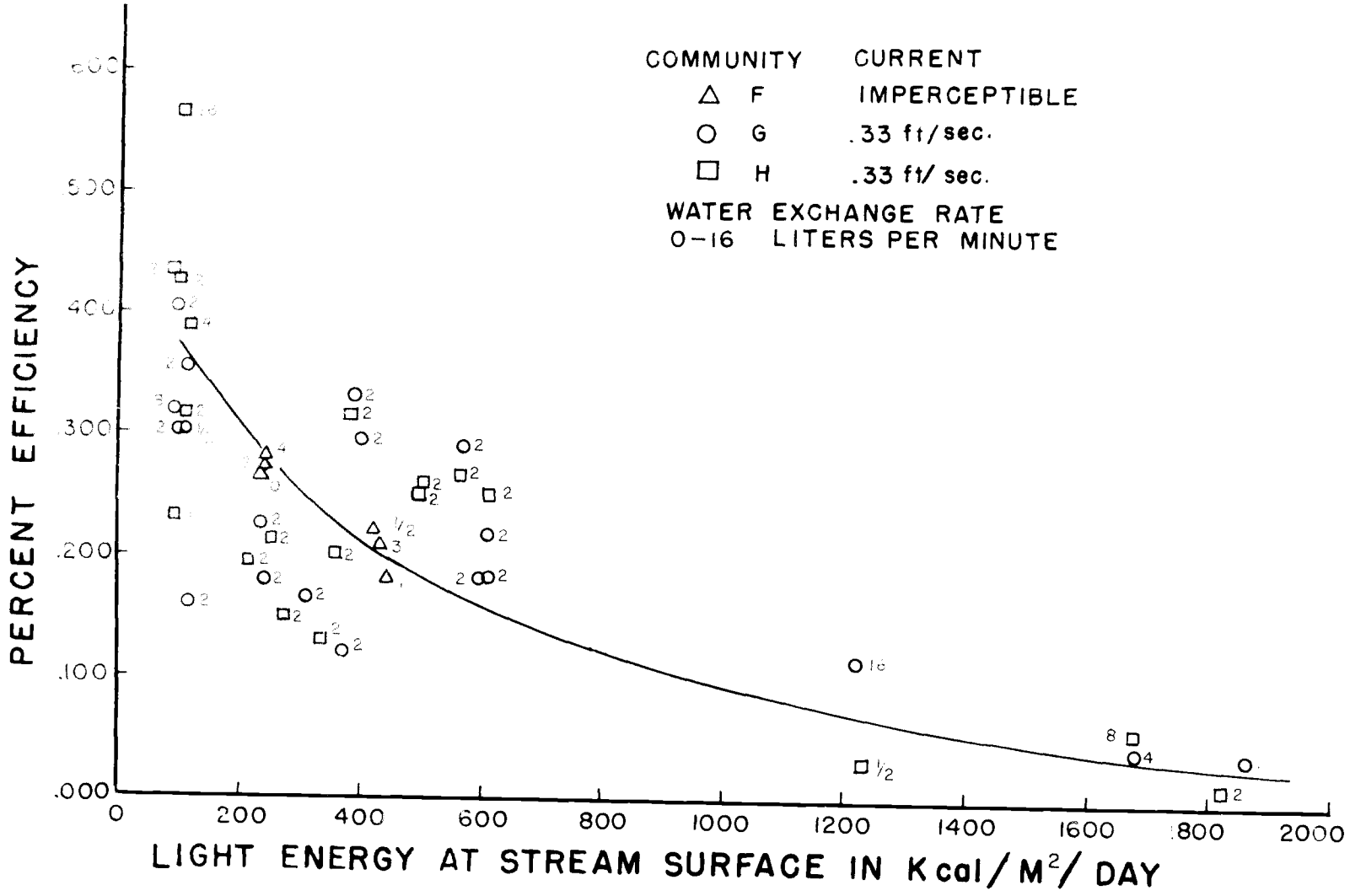

Figure 8. The influence of kilocalories of incident light per square meter per day on per cent of efficiency of light utilization.

by each symbol gives the exchange rate in liters per minute when the production estimates were made. High exchange rates usually resulted in higher efficiencies than did low exchange rates. A comparison can be made of the efficiencies of utilization of light at different exchange rates by community H, dominately diatoms, on a cloudy day, October 31, 1960. At one half liter per minute, an efficiency of .233 per cent resulted, at two liters per minute, .391 per cent, and at 16 liters per minute, .566 per cent. As might be expected, the efficiency of utilization of light by the diatoms, mainly Melosira, increased with increased nutrient availability at low light intensities. Community G', composed mainly of green algae, on a sunny day, November 3, 1960, at one liter of exchange water had an efficiency of .038 per cent, at four liters per minute, .045 per cent, and at 16 liters per minute, .115 per cent. Thus the efficiency of utilization of light by the green algae was increased by an increase of nutrients at high light intensities.

SUMMARY

1. A study was conducted during 1959 and 1960 at the Oak Creek Laboratory of the Pacific Cooperative Water Pollution and Fisheries Research Laboratories, Oregon State University, on the metabolism of algal communities in experimental streams.

2. The six artificial streams employed were equipped for exchange flow and current control. Trays were located in the bottom of the streams to permit removal of sections of the community to a photosynthesis-respiration chamber for more exacting control of some of the experimental variables.

3. Periphyton communities became established under a variety of conditions of light intensity, exchange rate of water, and current velocity.

4. The succession of organisms on glass slides suspended in the streams was studied. Diatoms became the dominant organisms early in succession in the communities grown at high light intensities; but these were later dominated by the green algae. In shaded communities, bacteria were the dominant organisms and diatoms the dominant autotrophs.

5. Primary production and respiration rates of the communities were estimated under varying conditions of

light, current velocity, exchange rate and nutrient level. The average gross production rate for all conditions for the experimental streams was 2.8 grams per square meter per day. It ranged from 1.18 to 21.21 grams per day.

6. Increased nutrient and light availability generally increased production rates.

7. Phosphate, nitrate, potassium or carbon dioxide did not appear to be the limiting nutrients at the time these experiments were performed.

8. The mean efficiency of utilization of light energy by the stream communities under all conditions was .24 per cent. Efficiencies seemed to decrease with increase in light intensity and increase with increases in nutrient availability. The diatoms were more productive than the green algae at low light intensities, and the green algae were more productive than the diatoms at the high light intensities.

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APPENDIX

TABLE A

Structure of Experimental Stream Communities in Terms of Groups as Per Cent by Number of Cells

Group	Community								
	A	B	C	D	E	F	G	G'	H
PLANTS									
Chlorophyta (green algae)	1.20	2.88	1.77	9.86	59.40	85.15	36.42	51.95	18.67
Stigeoclonium	.51	1.17	--	7.32	56.13	33.26	--	--	--
Oedogonium	--	.23	--	--	--	26.72	28.39	46.30	13.56
Hormidium	--	.35	--	--	--	--	2.91	2.46	1.53
Mougeotia	--	--	--	--	--	--	2.56	1.14	2.16
Spirogyra	--	--	--	--	--	--	.36	.19	.52
Closterium	--	--	--	--	--	1.15	2.06	1.86	.89
Gloeocystis	.17	--	--	--	--	--	--	--	--
Microspora	.06	--	--	--	--	--	--	--	--
Chlamydomonas	.46	1.13	1.77	2.54	3.27	24.02	.14	--	.01
Bacillariophyceae (diatoms)	65.66	29.99	4.07	50.99	33.61	10.53	47.73	31.06	74.47
Melosira	--	--	--	--	--	--	31.87	23.92	62.59
Fragilaria	.33	1.83	.26	.49	.52	1.01	9.88	5.43	9.74
Cocconeis	62.25	5.53	.75	8.38	5.30	.07	.17	.05	.10
Achnanthes	1.50	9.47	1.92	4.83	8.16	--	--	--	.03
Gomphonema	.21	1.84	.21	.97	.19	4.25	.04	--	.13

TABLE A (Continued)

Group	Community								
	A	B	C	D	E	F	G	G'	H
Pinnularia	.71	7.31	.30	24.03	11.94	--	1.00	.09	.38
Navicula	.46	1.02	.39	9.65	2.05	.87	.50	.27	.15
Nitzschia	.16	.49	.13	1.81	4.67	.05	--	--	--
Tabellaria	.04	2.44	.07	.83	.78	1.73	.46	.14	.66
Rhopalodia	--	--	--	--	--	--	2.75	1.16	.06
Surirella	--	--	--	--	--	2.48	.39	--	.02
Rhoicosphenia	--	--	--	--	--	--	.67	--	.50
Meridion	--	--	--	--	--	.07	--	--	--
Synedra	--	.06	.04	--	--	--	--	--	.13
Cyanophyta (blue green algae)	.80	2.46	.12	1.59	3.13	.25	8.73	14.63	5.98
Cylindrospermum	--	--	--	--	--	--	8.29	13.18	4.98
Oscillatoria	.26	.26	.12	--	--	--	--	--	--
Chroococcus	--	2.20	--	1.59	3.13	.25	--	--	--
Anabaena	--	--	--	--	--	--	.21	.09	1.00
Hormotila	.54	--	--	--	--	--	--	--	--
Heterohormogonium	--	--	--	--	--	--	.23	1.36	--
ANIMALS									
Ciliata	.80	.59	2.62	.30	.27	.43	.02	--	--
Chilodon	.42	.18	.27	.30	.27	.19	--	--	--
Linotus	.10	.14	.07	--	--	--	--	--	--
Amphileptus	.03	.09	--	--	--	--	--	--	--

TABLE A (Continued)

Group	Community								
Stylonychia	.03	.04	.04	--	--	--	.02	--	--
Euplotes	.04	--	.02	--	--	.24	--	--	--
Dysteria	.18	--	.07	--	--	--	--	--	--
Vorticella	--	.14	2.15	--	--	--	--	--	--
Mastigophora	.07	2.25	.68	1.23	.54	3.24	.02	--	--
Chryptomonas	.07	1.02	.57	1.23	.54	.17	.02	--	--
Bodo	--	1.23	.11	--	--	3.08	--	--	--
Rotifera	.05	.10	--	--	--	.06	--	--	--
Philodina	--	.10	--	--	--	--	--	--	--
Rotatoria	.05	--	--	--	--	.06	--	--	--
Bacteria	27.19	61.11	89.88	35.99	2.99	.21	--	--	.17
Date	Oct.-Jan.	Oct.-Jan.	Oct.-Jan.	July-Aug.	July-Aug.	May	Oct.-Dec.	Nov.	Oct.-Dec.
No. of Observations	100	100	100	260	260	60	180	30	180
No. of Streams	1	1	1	2	2	6	3	3	3

TABLE B

Mean Number of Organisms per Square Millimeter on Glass Slides During Succession for Communities D and E

Organism	Time of Count in Days after Beginning of Experiment												
	4	6	8	10	12	14	16	18	20	22	24	26	28
Community E (In Light)													
Diatoms	16	203	305	764	438	888	5,115	19,141	39,150	20,960	8,096	5,102	2,656
Greens			2	42	7	34	33	1,056	8,512	13,600	34,208	40,812	54,528
Bacteria				90	34	57	117	2,016	1,376	1,216	1,760	96	1,376
Community D (In Shade)													
Diatoms	9	24	20	32	28	27	772	2,432	2,988	2,464	3,456	3,840	8,255
Greens		2	3	4	9	3	43	416	372	640	544	864	1,056
Bacteria				43	48	105	496	2,656	5,376	5,440	2,656	1,216	1,407

TABLE C

Per Cent Phosphorus, Nitrogen, Crude Protein and Grams per Square Meter of Biomass for Experimental Streams

Date 1960	Stream Number	Community Type	Dry Weight	Crude Protein	Nitro-gen	Phos-phorus
			STILL WATER			
7/21	1	F	179	11.10	1.77	0.299
	2	F	82	15.60	2.49	0.329
	3	F	130	17.28	2.76	0.392
	4	F	67	17.50	2.80	0.310
	5	F	72	17.72	2.84	0.290
	6	F	71	13.40	2.14	0.297
8/17	1	F	166	13.32	2.13	0.276
	2	F	119	10.40	1.66	0.265
	3	F	155	14.34	2.29	0.301
	4	F	42	17.45	2.79	0.332
	5	F	41	28.47	4.55	0.347
	6	F	198	12.36	1.98	0.283
8/30	1	F	299	11.27	1.80	0.276
	2	F	102	13.97	2.24	0.294
	3	F	135	13.76	2.20	0.336
	4	F	52	17.98	2.88	0.278
	5	F	49	15.94	2.55	0.278
	6	F	128	15.88	2.54	0.343
			MOVING WATER			
9/29	1	H	51	8.82	1.41	0.211
	2	G	65	8.22	1.32	0.246
	3	H	60	9.78	1.56	0.260
	4	G	74	8.34	1.33	0.299
	5	G	58	9.98	1.59	0.258
	6	H	106	6.91	1.10	0.242
10/13	1	H	37	10.02	1.60	0.158
	2	G	78	9.80	1.57	0.297
	3	H	58	8.58	1.37	0.182
	4	G	77	8.21	1.31	0.296
	5	G	64	10.07	1.61	0.324
	6	H	52	8.07	1.29	0.286

TABLE C (Continued)

Date 1960	Stream Number	Community Type	Dry Weight	Crude Protein	Nitro-gen	Phos-phorus
11/8	1	H	77	7.88	1.26	0.235
	2	G	127	9.77	1.56	0.274
	3	H	175	7.13	1.14	0.271
	4	G	193	7.37	1.18	0.286
	5	G	147	7.51	1.20	0.120
	6	H	95	5.91	0.95	0.193
12/5	1	H	23	10.75	1.72	0.254
	2	G	45	12.87	2.06	0.200
	3	H	73	9.15	1.46	0.202
	4	G	130	10.29	1.65	0.219
	5	G	136	10.00	1.60	0.219
	6	H	146	8.27	1.32	0.196
12/23	1	H	129	9.07	1.45	0.160
	2	G	100	10.05	1.61	0.169
	3	H	106	9.25	1.48	0.207
	4	G	153	10.15	1.62	0.181
	5	G	162	9.45	1.52	0.173
	6	H	246	8.27	1.32	0.219

TABLE D

Chemical Constituents of Experimental Stream Water Supply in Milligrams per Liter[1]

Constituent	Date and Time of Collection					
	Oct. 31 1959 10:00 a.m.	Feb. 25 1960 1:45 p.m.	May 5 1960 3:00 p.m.	June 15 1960 11:00 a.m.	Aug. 30 1960 11:00 a.m.	Nov. 4 1960 10:30 a.m.
Silica (SiO_2)	40	33	33	35	39	38
Aluminum (Al)						
Iron (Fe)	0.14	0.22	0.22	0.24	0.21	0.21
Calcium (Ca)	22	15	17	18	23	23
Magnesium (Mg)	8.6	5.9	5.6	8.3	8.4	7.4
Sodium (Na)	8.8	6.5	6.9	7.8	9.0	8.5
Potassium (K)	0.8	0.6	0.4	0.6	0.5	0.5
TOTAL	80.34	61.22	63.12	69.94	80.11	87.61
Bicarbonate (HCO_3)	123	84	91	107	125	121
Carbonate (CO_3)	0.0	0.0	0.0	0.0	0.0	0.0
Sulfate (SO_4)	0.8	1.1	0.4	2.2	0.6	0.4
Chloride (Cl)	5.8	4.8	5.0	4.5	5.0	6.0
Fluoride (F)	0.1	0.1	0.1	0.1	0.1	0.1
Nitrate (NO_3)	0.0	0.2	0.1	0.1	0.1	0.3
Phosphate (PO_4)	0.01	0.13	0.09	0.13	0.11	0.10
TOTAL	124.71	90.33	96.69	114.03	130.91	127.90
DISSOLVED SOLIDS:						
Calculated	143	109	114	130	148	144
Residue on evaporation at 180° C.	147	107	112	127	154	147

TABLE D (Continued)

Constituent	Oct. 31 1959 10:00 a.m.	Feb. 25 1960 1:45 p.m.	May 5 1960 3:00 p.m.	June 15 1960 11:00 a.m.	Aug. 30 1960 11:00 a.m.	Nov. 4 1960 10:30 a.m.
Hardness as $CaCO_3$	90	62	66	79	92	88
Non-carbonate	0.0	0.0	0.0	0.0	0.0	0.0
Specific conductance: (Micromhos at 25° C.)	207	148	160	178	204	199
Appearance when collected	Clear	Clear	Slightly turbid	Clear		
pH	7.6	7.6	7.7	7.2	7.9	7.9
Color units	5	10	10	5	5	10

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

TABLE E

Nitrate Concentrations in Inflow and Outflow Water of Experimental Streams in Milligrams per Liter

Date[1] 1960	Inflow to all Streams	Outflow Stream Number					
		1	2	3	4	5	6
7/15	.040	.040	.060	.070	.050	.100	.050
8/1	.180	.200	.200	.200	.190	.190	.190
8/8	.043	.050	.032	.050	.064	.088	.078
8/9	.070	.085	.050	.065	.100	.065	.072
8/22	.202	.182	--	.175	--	--	.170
8/30	.055	.040	--	.050	--	--	.030
9/15	.075	.055	.055	.065	.056	.055	.057
9/19	.068	.048	.048	.042	.042	.048	.052
9/27	.060	.050	.055	.050	.055	.055	.050
10/31	.080	.090	.067	.064	.088	.110	.078
11/3	.038	.036	.036	.053	.037	.048	.050
11/16	.204	.168	.160	.140	.144	.135	.152
11/21	.233	.242	.241	.265	.247	.180	.177
12/5	.036	--	--	--	--	--	--
12/7	.031	--	--	--	--	--	--
12/8	.050	--	--	--	--	--	--
12/12	.026	--	--	--	--	--	--
12/13	.018	--	--	--	--	--	--
12/15 (8:00 a.m.)	.028	--	--	--	--	--	--
12/15 (4:30 p.m.)	.005	--	--	--	--	--	--

[1] Water samples taken at 2:00 p.m. except where specified.

TABLE F

Phosphate Concentrations in Inflow and Outflow Water of Experimental Streams in Milligrams per Liter

Date[1] 1960	Inflow to all Streams	Outflow Stream Number					
7/8	.680	.275	.275	.275	.150	.275	.275
8/1	.514	.714	.382	.788	.365	.818	.694
8/8	.645	.680	.620	.630	.600	.760	.688
8/9	.652	.645	.972	.644	.718	.718	1.022
8/22	1.130	1.105	--	1.085	--	--	.901
8/25	.870	.830	--	.542	--	--	.520
8/29	.575	.555	--	.530	--	--	.520
9/15	.064	.128	.105	.105	.105	.105	.105
9/19	.060	.075	.107	.085	.075	.095	.107
9/27	.183	.085	.085	.043	.043	.061	.085
10/31	.284	.178	.144	.135	.157	.150	.165
11/3	.192	.165	.088	.108	.143	.178	.180
11/16	.145	.100	.122	.560	.735	.440	.530
11/21	.145	.088	.100	.088	.135	.157	.157

[1] Water samples taken at 2:00 p.m.

TABLE G

Phosphate and Nitrate Concentrations in Inflow and Outflow Water of Photosynthesis-Respiration Chamber

Prod. Est.	Date 1960	Time	Nitrate in mg./l. Inflow	Nitrate in mg./l. Outflow	Phosphate in mg./l. Inflow	Phosphate in mg./l. Outflow	Remarks
	12/7	10:30 p.m.	.031	.042	.180	.135	Respiration Est.
G	12/8	9:45 p.m.	.050	.042	.180	.157	Control Est.
H	12/9	2:00 p.m.	.040	.031	1.200	1.100	Plus .8 ppm PO_4
	12/12	7:00 p.m.	.026	.042	.205	.307	Respiration Est.
I	12/13	8:30 a.m.	.018	.000	.270	.198	Control Est.
J	12/13	7:30 p.m.	.062	.050	.198	.850	Plus .8 ppm NO_3
K	12/14	8:40 a.m.	.525	.462	.145	.123	Plus 4.8 ppm NO_3
	12/15	8:45 a.m.	.028	.017	.130	.115	Respiration Est.
L	12/15	4:30 p.m.	.005	.004	.130	.115	Control Est.
M	12/17	9:30 a.m.	.034	.012	--	--	Plus .8 ppm NO_3
N	12/17	10:00 p.m.	--	.775	--	--	Plus 4.8 ppm NO_3
O	12/18	9:00 a.m.	.630	.835	--	--	Plus CO_2 and 4.8 ppm NO_3

TABLE H

Gross and Net Production and Respiration Rates as Milligrams of Oxygen per Square Meter per Hour and per Day

Comm. Type	Date 1960	Stream Number	Ex. R. l/min.	Vel. ft./sec.	mg. O_2/m^2/day			mg. O_2/m^2/hr.[1]	
					Gross P.	Resp.	Net P.	Gross P.	Resp.
F	6/30	1	3.7	Imp.[2]	5,421	1,202	5,305	408	50
F	6/30	2	3.7	Imp.	6,008	1,517	5,871	461	63
F	6/30	3	3.7	Imp.	5,731	1,435	5,601	473	60
F	6/30	4	3.7	Imp.	4,285	656	4,231	340	27
F	6/30	5	3.7	Imp.	5,294	3,238	5,064	395	135
F	6/30	6	3.7	Imp.	4,817	984	4,725	363	41
F	7/7	4	0.0	Imp.	1,413	507	1,374	33	21
F	7/7	2	0.5	Imp.	2,328	1,913	2,204	171	80
F	7/7	5	2.0	Imp.	3,817	2,004	3,674	287	84
F	7/7	3	4.0	Imp.	5,219	1,558	5,088	392	65
F	7/7	1	8.0	Imp.	3,740	166	3,727	259	7
F	7/7	6	16.0	Imp.	6,234	1,344	6,104	460	56
F	7/12	4	0.0	Imp.	1,260	507	1,224	88	21
F	7/12	2	0.5	Imp.	1,662	1,913	1,550	120	80
F	7/12	5	2.0	Imp.	4,447	2,004	4,304	348	84
F	7/12	3	4.0	Imp.	5,323	1,558	5,192	406	65
F	7/12	1	8.0	Imp.	4,139	166	4,090	305	7
F	7/12	6	16.0	Imp.	7,187	1,344	7,048	506	56
F	8/8	4	0.0	Imp.	1,419	507	1,377	104	21
F	8/8	2	0.5	Imp.	1,442	1,913	1,330	90	80
F	8/8	5	2.0	Imp.	3,510	2,004	3,367	287	84
F	8/8	3	4.0	Imp.	3,696	1,558	3,575	287	65
F	8/8	1	8.0	Imp.	4,923	166	4,867	350	7
F	8/8	6	16.0	Imp.	5,634	1,344	5,512	451	56

TABLE H (Continued)

Com. Type	Date 1960	Stream Number	Ex. R. l/min.	Vel. ft./sec.	Mg. $O_2/m^2/day$			Mg. $O_2/m^2/hr.$[1]	
					Gross P.	Resp.	Net P.	Gross P.	Resp.
F	8/25	3	0.0	Imp.	1,770	239	1,744	107	10
F	8/25	6	2.0	Imp.	2,463	469	2,420	217	20
F	8/25	1	4.0	Imp.	1,897	1,591	1,808	148	66
F	8/29	6	0.5	Imp.	2,664	1,374	2,572	217	57
F	8/29	3	1.0	Imp.	2,239	1,642	2,137	173	69
F	8/29	1	3.0	Imp.	2,558	1,634	2,457	213	68
H	9/15	1	2.0	.33	3,750	376	3,704	334	16
G	9/15	2	2.0	.33	3,096	517	3,049	269	22
H	9/15	3	2.0	.33	3,761	469	3,711	330	20
G	9/15	4	2.0	.33	4,391	188	4,350	310	8
G	9/15	5	2.0	.33	3,096	282	3,057	271	12
H	9/15	6	2.0	.33	4,254	188	4,213	297	8
H	9/19	1	2.0	.33	2,136	235	2,108	179	10
G	9/19	2	2.0	.33	1,263	188	1,245	105	8
H	9/19	3	2.0	.16	1,246	376	1,200	88	16
G	9/19	4	2.0	.16	3,329	188	3,295	280	8
G	9/19	5	2.0	.03	3,641	1,315	3,559	317	55
H	9/19	6	2.0	.03	3,400	564	3,352	296	24
H	9/27	1	2.0	.33	3,597	1,033	3,325	319	43
G	9/27	2	2.0	.33	4,691	1,033	4,614	418	43
G'	10/31	5	0.5	.33	944	137	1,332	42	57
H	10/31	1	1.0	.33	613	286	598	59	12
G'	10/31	4	2.0	.33	516	562	492	49	23
H	10/31	3	4.0	.33	1,265	838	1,226	118	35
G'	10/31	2	8.0	.33	878	1,259	829	83	53
H	10/31	6	16.0	.33	1,686	3,656	1,672	294	15

TABLE H (Continued)

Comm. Type	Date 1960	Stream Number	Ex. R. l/min.	Vel. ft./sec.	mg. $O_2/m^2/day$			mg. $O_2/m^2/hr.$[1]	
					Gross P.	Resp.	Net P.	Gross P.	Resp.
H	11/3	6	0.5	.33	1,144	320	1,126	112	13
G'	11/3	2	1.0	.33	2,029	771	1,991	198	32
H	11/3	3	2.0	.33	1,262	282	1,244	119	12
G'	11/3	4	4.0	.33	2,150	670	2,114	201	28
H	11/3	1	8.0	.33	2,731	944	2,684	248	39
G'	11/3	5	16.0	.33	3,983	609	3,938	370	25
H	11/16	1	2.0	.33	1,106	47	1,097	107	2
G	11/16	2	2.0	.33	1,104	470	1,081	107	20
H	11/16	3	2.0	.33	961	235	948	93	10
G	11/16	4	2.0	.33	1,095	141	1,085	105	6
G	11/16	5	2.0	.33	882	47	875	86	2
H	11/16	6	2.0	.33	1,194	188	1,181	114	8
H	11/21	1	2.0	.33	1,165	47	1,156	110	2
G	11/21	2	2.0	.33	1,234	470	1,211	118	20
H	11/21	3	2.0	.33	1,182	235	1,169	114	10
G	11/21	4	2.0	.33	1,471	141	1,457	141	6
G	11/21	5	2.0	.33	1,489	47	1,478	142	2
H	11/21	6	2.0	.33	1,543	188	1,528	148	8

[1] Mean from 9:00 a.m. to 3:30 p.m.

[2] Imp. = Imperceptible.