OXYGEN BALANCE IN A SOUTHERN GREAT PLAINS STREAM IN SOUTHEASTERN OKLAHOMA

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PREFACE

The objectives of the present study of unpolluted Blue River were to determine: (1) the magnitude of community metabolism; (2) the effects of channel strata upon community metabolism; (3) efficiency of photo-autotrophic organisms in the stream in converting solar energy to chemical energy; (4) seasonal changes in community metabolism and environmental conditions. Communities of the stream were compared with other flowing aquatic communities on the basis of metabolism and chlorophyll.

Dr. Troy C. Dorris served as major advisor. Drs. L. Herbert Bruneau, Roy W. Jones, Rudolph J. Miller, and R. R. Walton served on the advisory committee and criticized the manuscript. Dr. Richard Tubb, Ray Baumgardner, Kenneth Beadles, Gene Dorris, Kenneth Graham, Herbert Hannan, Richard Harrell, Bill Mathis, Fred Spangler, James Stribling, and Jerry Wilhm helped make field collections. My wife, Sally, typed the rough draft and Mrs. Frank Roberts typed the manuscript. The assistance of all these people is appreciated.

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I. INTRODUCTION

Oxygen balance in a stream is dependent upon plant photosynthesis, oxygen consumption and exchange of oxygen with the air. Chlorophyll-bearing plants produce oxygen by photosynthesis, and oxygen may be consumed by respiration of the biota or through chemical oxidation. Rates of oxygen production and utilization can be used to ascertain community metabolism. The rate at which oxygen content of water changes must be corrected for atmospheric oxygen exchange in order to estimate photosynthetic productivity.

Primary or photosynthetic productivity is the rate at which light energy is fixed by photo-autotrophic organisms. Primary production rate in the flowing aquatic community is influenced by physico-chemical environmental variables, particularly temperature, light intensity, dissolved solids concentration and types of underlying strata; and by biotic elements of the ecosystem such as kinds and numbers of producer and consumer organisms.

High productivity is common in the early recovery zone of streams receiving effluents of high organic content, but high productivity is not limited to such waters. Odum (1956b) cited a Pacific coral reef, Caribbean turtle grass communities, and Florida artesian springs as areas of high productivity in flows of low organic content. Production rates were high in Eniwetok Atoll (24 g O_2/m^2 day) where extremely low nutrient concentration was compensated by large current velocity (Odum and Odum, 1955). The current renewed the depleted substances required by the producer organisms and removed accumulating metabolic by-products.

Current also overcame low nutrient content in Florida springs and the marine turtle grass. These communities were uniquely characterized by relatively constant thermal conditions with high temperatures ranging from 21 to 25 C in the various springs. Production rates reached a maximum of 35 g $0_2/m^2$ day in beds of turtle grass on Long Key, Florida. Light was thought to be the main factor controlling productivity (Odum, 1956b, 1957a).

Unpolluted streams generally have lower productivity. In the Neuse River System in the mountains, piedmont and coastal plain of North Carolina production rates were very low, reaching a maximum of only 9.8 g $0_2/m^2$ day (Hoskin, 1959). In the canyon section of Logan River in the Middle Rocky Mountains of Northern Utah productivity was about 7 g $0_2/m^2$ day (McConnell and Sigler, 1959). In the Ivel River, Bedfordshire, England, productivity generally was low, with a maximum of 17.6 g $0_2/m^2$ day. Gross production rate in the Itchen River, England, was also low, reaching a maximum of 14.0 g $0_2/m^2$ day (calculated by Odum, 1956, from oxygen data of Butcher, Pentelow and Woodley, 1930).

A variety of explanations might be offered to account for the unusually high productivity in certain streams. Environmental variables such as nutrient concentration, current velocity, light intensity and temperature have been proposed. In the present study of an unpolluted Southern Great Plains stream, one section was observed which had very high productivity, especially in summer. Light intensity and water temperature were about the same as in near-by stream sections where production rates were low. Production rates in all observed stream reaches were closely correlated with the nature of bottom materials. The most productive region was in granite, whereas other regions in limestone and sand were not as productive. These bottom materials provided different opportunities for attachment of benthic producer organisms and thus influenced primary production rates. Attachment surfaces seem to be an important environmental variant.

II. PHYSICAL DESCRIPTION

Stream Order and Drainage Basin

Blue River, a tributary of the Red River, is located in Pontotoc, Johnston and Bryan counties in southeastern Oklahoma. The length of the channel approaches 225 km and the area of the drainage basin is approximately 2,000 square km. The gradient averages 1.1 m/km and ranges from 9.5 m/km in the headwaters to 0.4 m/km near the mouth. The average annual precipitation is 96.7 cm, with an average spring high of 13.3 cm and an average winter low of 5.3 cm (Hornuff, 1957).

West Blue Creek originates as a small tributary stream in a tall grass prairie area north of Roff. It flows southeastward, becoming a fifth order stream 7 km northwest of Connerville (Horton, 1945). East Blue Creek, a third order stream, joins West Blue Creek 3 km southeast of Connerville, about 96 km from the origin of the stream. In this distance the elevation drops from 437 to 183 m. Blue River continues as a fifth order stream for 128 km, flowing into the Red River at an elevation of 137 m.

The Blue River basin has a form factor of 0.12 and a compactness coefficient of 1.98. The form factor is the ratio of the average width to the axial length of the basin. The compactness coefficient is the ratio of basin perimeter to the circumference of a circle whose area is equal to that of the basin (Reid, 1961). Both of these values give some indication of the tendency toward flooding. A basin with a low form factor value or a high compactness coefficient value is less likely to receive intense rainfall simultaneously over its entire area than a basin of equal area having a high form factor value or a low compactness coefficient value.

Minor floods occur in the Blue River drainage basin about every four years while they occur every other year in the more circular Skeleton Creek drainage basin (Wilhm, 1965). Skeleton Creek is a sixth order stream in North Central Oklahoma whose basin receives an average annual rainfall of about 81 cm and has a form factor of 0.20 and a compactness coefficient of 1.79.

Geological Strata as Related to Bottom Type

Four geological formations occur in the study area outcropping primarily as limestone, granite and sand (Fig. 1). The Arbuckle group of rock formations, of Cambrian and Ordovician age, consists of limestones, dolomites, and some sandstones having an aggregate thickness of 1,980 m in some places. The limestones and sandstones in the upper part of the group are among the most productive aquifers in the state. The portion of the Blue River flowing through this formation has many springs and the stream bottom contains eroded limestone boulders of various sizes.

The Simpson group, of Ordovician age, overlies the Arbuckle groups in a portion of the stream basin. It has an average thickness of 460 m and consists of limestones, sandstones and shales. The sandstones and limestones of this group also have water-bearing properties.

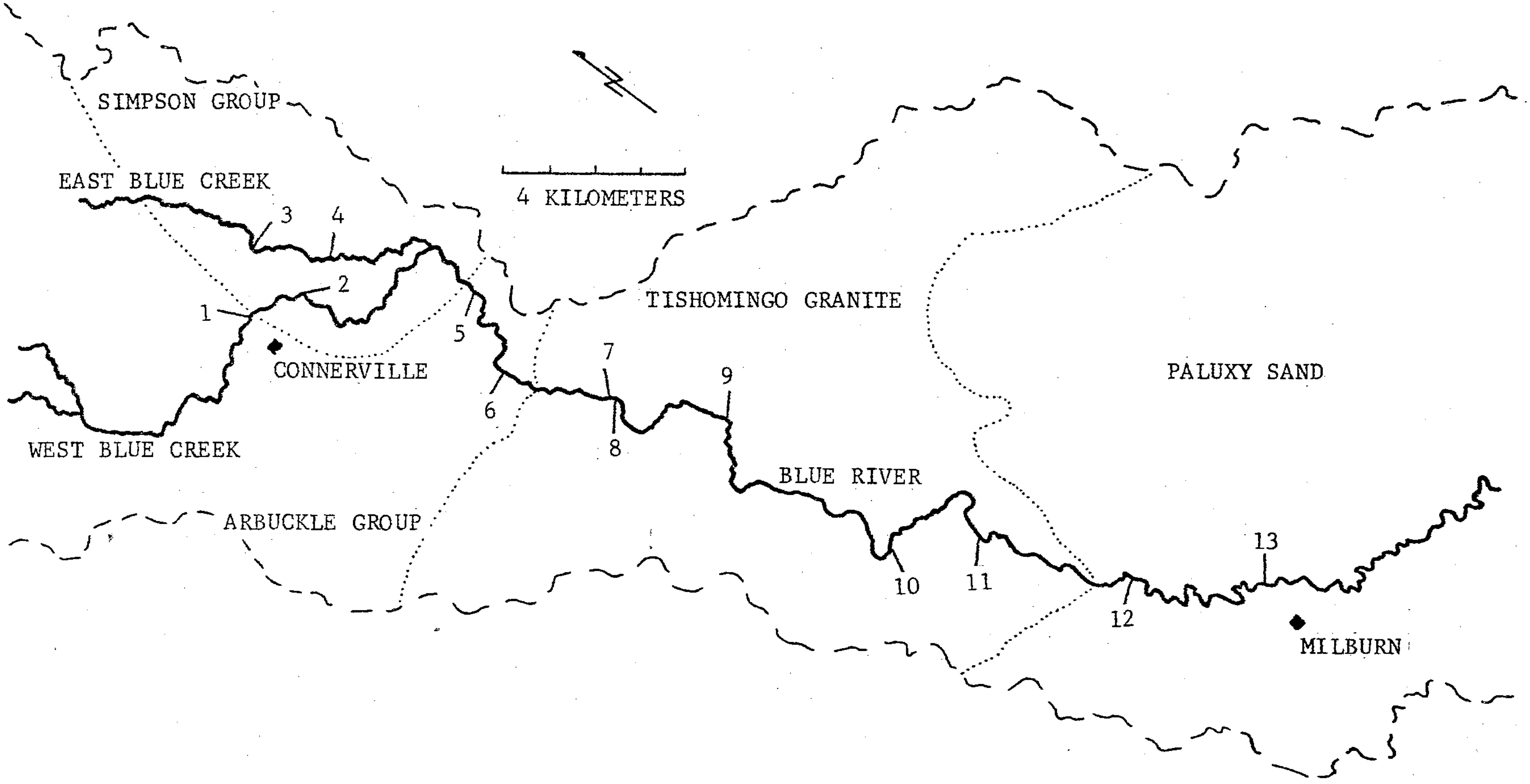

Fig. 1. Map of upper Blue River. Geological boundaries = (⋯⋯), sampling stations = (1-13), watershed boundary = (∼ ⌒).

In this formation, the stream channel also contains eroded limestone boulders.

Tishomingo granite, of Precambrian age, is an igneous basement rock. It is a coarse-grained, pinkish granite and consists essentially of microcline, plagioclase, quartz and biotite. The channel bed in this formation is composed of a series of exposed granite scarps separated by deeper pools where sediment has been deposited. Riffles and low falls are characteristic of the exposed granite areas.

The Paluxy sand belongs to the Trinity group of Cretaceous formations. In southern Oklahoma this formation consists of 120 to 215 m of conglomerate, fine sand, and clay. It dips toward the Gulf of Mexico, having a slope of about 13 m/km. The Paluxy sand is overlain by Goodland limestone, a nearly pure limestone formation 6 to 9 m in thickness, downstream from the study area. Water enters the sand formation in its outcrop and percolates down the slope. Artesian pressure is created since the water is confined by the overlying limestone.

Description of Reaches

Thirteen stations were selected for study along a stretch of Blue River, about 48 km in length, beginning about 88 km from the source (Fig. 1). This stretch was characterized by continuous flow as contrasted to the intermittent flow of the headwaters and it did not receive municipal sewage effluents as was true farther downstream.

Since discharge is the product of cross-sectional area and velocity, an increase in discharge may be accommodated by an increase in either or both of these factors. Cross-sectional areas of

Reaches 5-6 and 6-7 were approximately equal and increase in discharge was accommodated by the increase in velocity (Table 1). The decrease in discharge between Reaches 6-7 and 12-13 was slight compared to the decrease in cross-sectional area and this accounted for the large increase in velocity between them. Discharge increased between Reaches 5-6 and 6-7 because of accrual from the many springs of the limestone formation. Discharge decreased between Reaches 6-7 and 12-13 as a result of seepage into the Paluxy sand formation. The decrease in discharge, associated with seepage, was accompanied by a decrease in channel.

TABLE 1

MEAN CHARACTERISTICS OF REACHES

Reach	Width (m)	Depth (m)	Velocity (m/sec)	Discharge (m^3/sec)
5-6	18.2	0.37	0.16	1.09
6-7	15.8	0.42	0.21	1.35
12-13	10.8	0.34	0.34	1.17

Effects of geological formation on discharge in Blue River are further illustrated by flow data during a period of severe drought in 1956. Stream flow was the lowest on record in most of the state and widespread shortages of water occurred during the late summer and early fall. Near Blue, downstream from the Paluxy sand formation, there was no flow in Blue River from September 19 to October 16 (United States Geological Survey, 1960). However, near Connerville in the limestone formation, West Blue Creek had a discharge of approximately 0.40 m^3/sec for this same period.

III. MATERIALS AND METHODS

Sampling Procedures

Oxygen measurements were made at seasonal intervals between June 1963 and August 1964. Measurements were made at stations 5, 6, 7, 12 and 13 on days of full light intensity. Measurements were made at all stations during a period of low light intensity in the spring, 1964. Water temperature, stream flow, diffusion rate, pH, conductivity, turbidity and alkalinity were measured at the same time oxygen measurements were made.

Duplicate dissolved oxygen samples were taken at 3-hour intervals at each station and fixed by the Alsterberg (Azide) modification of the Winkler method (A.P.H.A., 1960). Samples were fixed in 126 ml bottles and the entire contents was titrated with 0.016 N sodium thiosulfate. Water temperature was measured at each sampling with a mercury thermometer so that per cent saturation of dissolved oxygen could be determined. Saturation values were taken from the tables of Truesdale, Downing and Lowden (1955).

Volume of stream flow was estimated according to the method proposed by Robins and Crawford (1954). Diffusion rates were measured by the use of a clear plastic dome and a Scholander device modified for field use (Copeland and Duffer, 1964).

Hydrogen-ion concentration was determined by use of a Hellige Comparator. Conductivity was measured with an Industrial Instruments

Conductivity Bridge and turbidity with a Bausch and Lomb Spectronic 20 Colorimeter. Phenolphthalein and methyl orange alkalinity were determined by titration with 0.02 N sulfuric acid. Chlorides were determined by the Mohr method and sulfates by the turbidimetric method (A.P.H.A., 1960).

Stream Metabolism

Stream metabolism was estimated following methods described by Odum (1956) and Odum and Hoskin (1958). Upstream and downstream stations in a stretch were sampled at about the same time and the diurnal rate of oxygen change was computed from oxygen concentration curves plotted for both stations. The upstream curve was shifted to the right on the time axis an amount corresponding to the time required for the water mass to travel between the two stations. The difference between the two curves at each hour was plotted to obtain the oxygen rate of change curve. The area under the curve was measured to determine the amount of oxygen produced. Oxygen production was converted to an areal basis by multiplying volumetric values by depth.

Upstream-downstream percentage saturation curves were adjusted in the same manner as the oxygen curves. The mean saturation value of the reach for any one time was obtained by averaging the saturation values at the two sampling stations. The mean saturation deficit was multiplied by the diffusion constant to obtain the diffusion correction.

Gross primary production and total respiration were estimated graphically from rates of oxygen change after corrections were made for the exchange of oxygen between the water and the atmosphere. Community respiration was determined by drawing a straight line through the average of the nighttime rate of change points and extrapolating this across the daytime period. This assumes constant community respiration day and night. Respiration studies on Chlorella with an 0^{17} enriched atmosphere, indicate that respiration is essentially independent of light (Brown, 1953).

Chlorophyll and Organic Matter

Water samples for suspended chlorophyll and organic matter analyses were taken at stations 5, 6, 7, 12 and 13 at the time of oxygen measurements. Benthic chlorophyll and organic matter samples were taken from these stations during the summer, 1963.

Samples of 500 ml were filtered through membrane filters of 0.45-micron pore size for suspended chlorophyll analysis. Benthic samples of 6 cm^2 were also analyzed. The residues were extracted in 10 ml of 90% acetone for 24 hr in the dark at about 5 C and centrifuged. Optical density of the liquid was determined with a Bausch and Lomb Spectronic 20 Colorimeter at a wavelength of 665 millimicrons using the 2.54 cm tube.

The method of Odum, et al., (1958) was used to estimate chlorophyll a concentration, where chlorophyll a in mg/liter of 90% acetone = 13.4 d_{665}. After correction for acetone and sample volumes this equation became:

$$\text{Chlorophyll } a \text{ in mg/liter} = 0.27\ d_{665}. \qquad (1)$$

Volumetric values were multiplied by depth to convert to an areal basis.

Since 6 cm^2 benthic samples were analyzed, equation (1) was converted to an areal basis for determination of benthic chlorophyll a concentrations. Equation (1) then became:

$$\text{Chlorophyll } \underline{a} \text{ in mg/m}^2 = 223\ d_{665}. \tag{2}$$

To determine suspended and dissolved organic matter, 50 ml samples were evaporated to oven dryness, cooled, weighed and ashed at red heat in a muffle furnace. The ash was cooled in a desiccator and weighed. Ash weight was subtracted from the dried weight to calculate ash-free dry weight or organic content.

Benthic organic matter was determined as the ash-free dry weight of channel bed samples of 25 cm^2.

IV. RESULTS AND DISCUSSION

Physico-chemical Conditions

Observed water temperature exhibited considerable seasonal fluctuation with a maximum of 34 C in July and a minimum of 6.5 C in March (Table 2). There was only a slight variation among reaches for each season, except for the wider range and higher summer values at Reach 12-13.

TABLE 2

SEASONAL RANGE OF WATER TEMPERATURE (C)

Season	Reach 5-6	6-7	12-13
Spring	18.0 - 26.5	18.0 - 26.0	18.5 - 27.0
Summer	23.0 - 31.0	23.0 - 30.5	23.0 - 34.0
Fall	10.0 - 15.0	9.0 - 15.0	8.0 - 14.0
Winter	7.0 - 16.0	7.0 - 16.0	6.5 - 15.5

Chlorides and sulfates were measured once during the study. Water samples from Reaches 5-6, 6-7 and 12-13 contained 4 ppm chlorides and only a trace of sulfates.

Differences in mean annual turbidity and pH among reaches were slight (Table 3). Turbidity varied from 5 to 23 ppm and pH from 8.0 to 8.5.

TABLE 3

MEAN ANNUAL PHYSICO-CHEMICAL CONDITIONS

Reach	Turbidity ppm	pH	Specific Conductance micromhos/cm	Alkalinity HCO_3^- ppm	$CO_3^{=}$ ppm	Total Residue ppm
5-6	14	8.2	543	300	8	323
6-7	12	8.3	530	286	12	296
12-13	13	8.3	472	224	21	300

Specific conductance and total alkalinity decreased downstream. Specific conductance measurements are proportional to dissolved or filtrable residue in a water sample and the downstream decrease in these measurements resulted from a decrease in the filtrable portion of the total residue. Conductivity decreased as a result of bicarbonate conversion to monocarbonate.

Free carbon dioxide is absent or present at very low concentrations above pH 8. The absence of free carbon dioxide does not limit photosynthesis of many algae and higher plants which are adapted for utilization of carbon dioxide from bicarbonates. The effect of carbon dioxide removal from the system is to split off carbon dioxide from soluble bicarbonate which brings about precipitation of calcium carbonate.

Due to the low solubility product of calcium carbonate, 0.48×10^{-8}, this substance generally precipitates from a calcareous water when the pH is raised beyond 8.3 to permit existence of appreciable carbonate ions (Hutchinson, 1957). However, metastable conditions may exist where there is apparent supersaturation with calcium carbonate. Steidtmann (1935) has suggested that colloidal calcium salts accounted for the apparent supersaturation of a travertine-depositing water. The downstream increase in carbonate alkalinity in the present study may be attributed to excess calcium carbonate in a relatively stable colloidal form.

Chlorophyll and Organic Matter

The principal primary producers and chlorophyll bearers of the stream were bryophytes, algae and diatoms. Dominant genera in the reaches were _Fontinalis_, _Diatoma_, _Melosira_, _Synedra_, _Spriogyra_, _Rhizoclonium_, _Schizothrix_, and _Cladophora_. In the upstream reaches epiphytes were attached to bryophytes and sessile algae and there was a continual release of pseudoplankton from these thick benthic communities.

Chlorophyll and organic matter measurements were made during the summer, 1963 (Table 4). Benthic chlorophyll _a_ and organic matter concentrations were greater than the suspended concentrations except at Reach 12-13, where organic matter samples were taken from large rocks sparsely scattered in the sandy channel bed. There was no variation in suspended chlorophyll _a_ concentration and only a slight variation in suspended organic residue among reaches. Average benthic chlorophyll _a_ concentration was highest at Reach 6-7. High chlorophyll _a_ concentration in the upstream reaches was associated with the presence of large boulders in the channel bed and low concentration at Reach 12-13 was associated with shifting sand in the stream channel.

McConnell and Sigler (1959) found that larger rocks supported greater amounts of chlorophyll. In the canyon section of Logan River, Utah, the average quantity of chlorophyll _a_ was 0.30 g per m^2 of bottom. Most of this was contributed by algae attached to larger rocks having a minimum dimension of 12 cm or greater. Smaller rocks with a minimum dimension of 2.5 to 12 cm yielded 0.15 to 0.25 g/m^2. Less than 6% of all chlorophyll was supported by bottom material having a minimum dimension less than 2.5 cm.

TABLE 4

SUMMER CHLOROPHYLL AND ORGANIC MATTER

Reach	Suspended Organic Residue g/m^2	Benthic Organic Matter g/m^2	Suspended Chlorophyll *a* g/m^2	Benthic Chlorophyll *a* g/m^2
5-6	40	250	0.004	0.26
6-7	41	212*	0.004	0.39
12-13	35	46*	0.004	0.02

*From scattered rocks and not representative of channel bed

There is a wide variation of chlorophyll concentration among stream communities (Table 5). Suspended chlorophyll concentration in unpolluted streams is much lower than benthic concentration. In Silver Springs where primary producers were large macrophytes, Odum (1957b) found benthic chlorophyll concentration much higher than suspended concentration. The values for benthic chlorophyll concentration from Silver Springs are comparable to values from polluted Mission River where the primary producers were algae (Odum, et al., 1958). In unpolluted streams benthic algal communities have a lower chlorophyll concentration than communities composed of large macrophytes.

Suspended chlorophyll concentration is higher in quasi-flowing oil refinery effluent holding ponds than in unpolluted streams. Summer chlorophyll a concentration in oil refinery effluent holding ponds, Oklahoma, was as high as 0.5 g/m^2 (Copeland, 1963). About ten days were required for water to travel through the ten-unit pond system. In oil refinery effluent holding ponds suspended chlorophyll concentration was closely correlated with sunlight and water temperature and dependent upon the amount of nutrients available.

TABLE 5

CHLOROPHYLL a IN FLOWING AQUATIC COMMUNITIES

Source	Chlorophyll a g/m^2
Silver Springs, Florida, (Odum, 1957b)	
Suspended pseudoplankton.	0.002 - 0.003
Benthic eelgrass.	3.0
Blue-green algal mat, polluted stream, Mission River, Texas (Odum, et al., 1958)	2.5
Canyon section of Logan River, Utah, benthic algae (McConnell and Sigler, 1959).	0.3
Blue-green algal mat in flowing microcosm (Odum and Hoskin, 1957)	0.03 - 0.38
Blue River, Oklahoma, 1963-64	
Suspended pseudoplankton.	0.004
Benthic bryophytes and algae.	0.02 - 0.39

In stream communities, the maximal amount of chlorophyll occurs in the benthos where materials in suspension or solution do not significantly decrease the radiation penetrating the water. In a stream where the primary producer components of the benthos are bryophytes, algae and sessile diatoms, it appears that a firm stony bottom is optimal for maximal chlorophyll production.

Community Metabolism

Mean oxygen exchange rates in Blue River varied from 1.3 to 2.9 g/m^2 hr at 100% saturation deficit. Exchange rates were higher at Reach 12-13 due to greater velocity and shallow water.

Measurements of oxygen production and respiration are indicative of energy relationships of the community since approximately one gram of carbohydrate material is synthesized or respired for each gram of oxygen produced or utilized.

Photosynthetic productivity at Reach 5-6 varied from 2.4 g/m^2 day in winter to 12.0 g/m^2 day in summer (Fig. 2). Community respiration varied from 6.1 to 16.4 g/m^2 day. Respiration always exceeded photosynthesis. Primary productivity was about 2.5 kg/m^2 year and total oxygen consumption of the community was about 4.0 kg/m^2 year.

Metabolism on the limestone strata at Reach 5-6 was comparable to that of the unpolluted, calcareous Itchen River, England. Odum (1956) calculated the seasonal course of community metabolism for the Itchen River from data given by Butcher, Pentelow and Woodley (1930) and found that community respiration almost always exceeded primary productivity.

At Reach 6-7, high primary productivity and respiration values were produced by large populations of benthic producers growing on the granite formations in the stream, and photosynthetic productivity always exceeded community respiration (Fig. 3). Differences were least from November 1963 through March 1964. Photosynthetic productivity varied from 10.1 g/m^2 day in winter to 48.0 g/m^2 day in summer. Community respiration, ranging from 9.0 to 19.9 g/m^2 day, was low in fall and early winter. Gross primary productivity and total oxygen

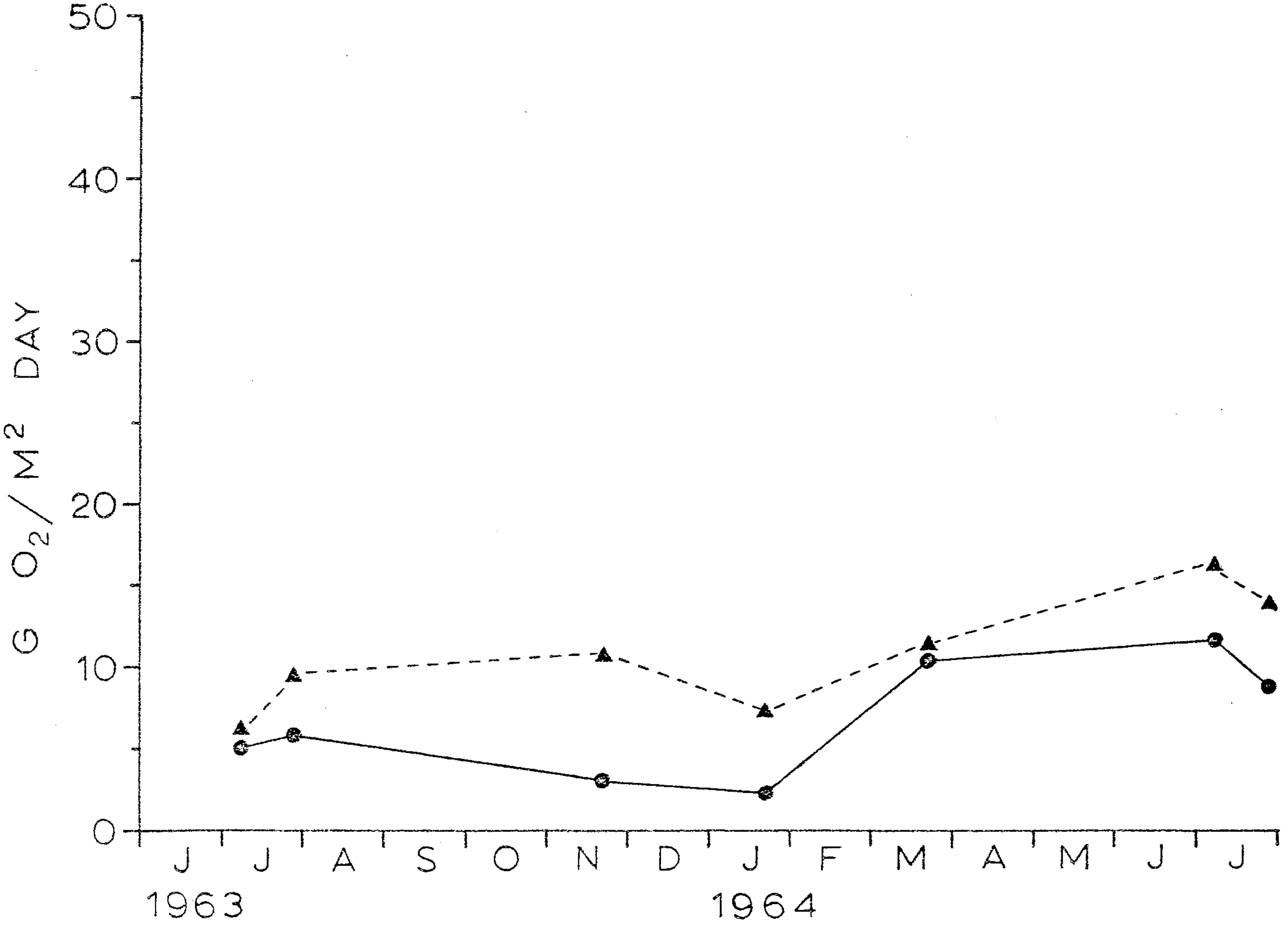

Fig. 2. Seasonal metabolism at Reach 5-6. Photosynthetic productivity = (—●—), community respiration = (–▲–).

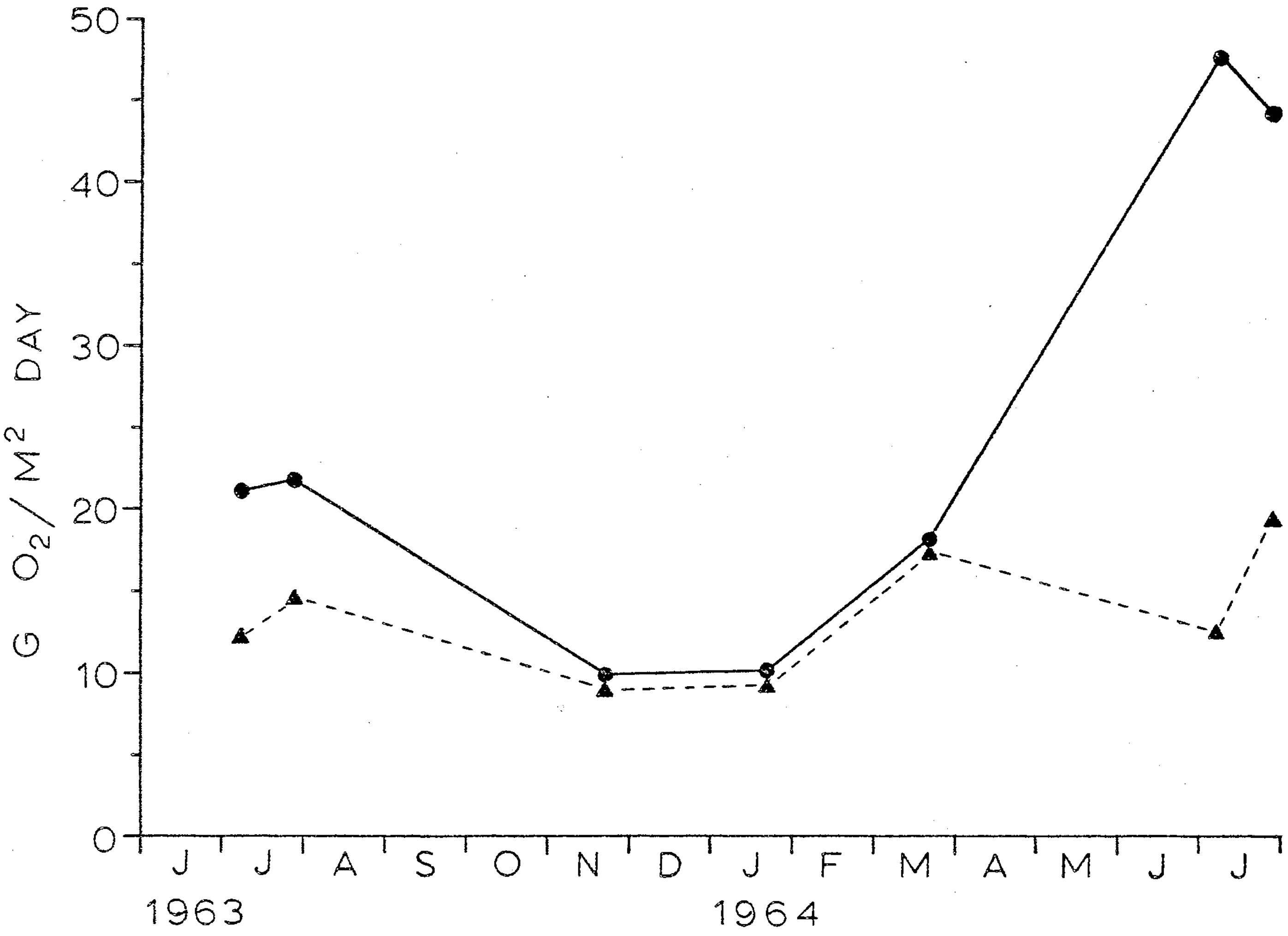

Fig. 3. Seasonal metabolism at Reach 6-7. Photosynthetic productivity = (—●—), community respiration = (-▲-).

consumption of the community were about 7.8 and 4.6 kg/m^2 year, respectively.

The difference between primary productivity and respiration was greatest during the spring bloom period. Community respiration was high in late winter, but declined in early summer when primary productivity was maximal. Copeland (1963) reported low respiration and high productivity during the spring bloom of algae in oil refinery effluent holding ponds, and Odum, et al., (1958) reported that net productivity and gross productivity were almost similar in spring bloom periods because of low respiration demand. It would seem that spring algal populations have high efficiency of assimilation and exert very little respiratory demand.

The large summer values of primary productivity at Reach 6-7 are similar to those found at high light intensities in the early recovery zone of streams below sewage discharge and in some artesian calcareous springs. However, different factors must have caused the various high productivity values.

Odum (1956b) estimated the downstream sequence of productivity and respiration for White River, Indiana, from oxygen data collected by Denham (1938) and found that primary production rates greatly exceeded decomposition processes in the early recovery zone because additional nutrients permitted producers to make organic matter faster than it was utilized.

Artesian springs in Florida maintained a relatively constant water temperature of about 23 C. Odum (1957a) felt that high productivity in the thermostatic springs was dependent upon high light intensity and dense populations of large benthic macrophytes rather than levels of nutrient materials. Light intensity obviously was not the factor responsible for high productivity on Blue River since upstream and downstream reaches had the same light but lower productivity. On Blue River high productivity was associated with an abundant benthic algal and bryophyte flora attached to rock surfaces in the channel. Submerged populations of larger rooted macrophytes were not established in the stream. Wide seasonal fluctuations in water temperature may have favored the smaller bryophytes rather than larger macrophytes.

In the Florida springs having maximum productivity, long streamers of rooted plants extended to within a few centimeters of the water surface. The aufwuchs encrusting these long streamers was thought to be the major producing component. Blue River and the Florida springs were alike in supporting large populations of macrophytes which in turn supported large populations of aufwuchs. It would appear that the major factor promoting high productivity in streams is favorable attachment surface.

At Reach 12-13, photosynthetic productivity was highest in summer and fall and lowest in winter and spring, ranging from 1.5 to 5.1 g/m^2 day (Fig. 4). Community respiration was low in the cooler months and high in the warmer months, varying from 6.1 to 11.0 g/m^2 day. Total oxygen consumption of the community was about 2.8 kg/m^2 year and primary productivity was about 1.1 kg/m^2 year, indicating that the community produced only about 39% of what it consumed.

Low primary productivity values resulted from small populations of benthic producers on the shifting sand in the stream channel. The relatively high respiration values may have been caused by the continual influx of decomposing organic material from upstream reaches. Odum

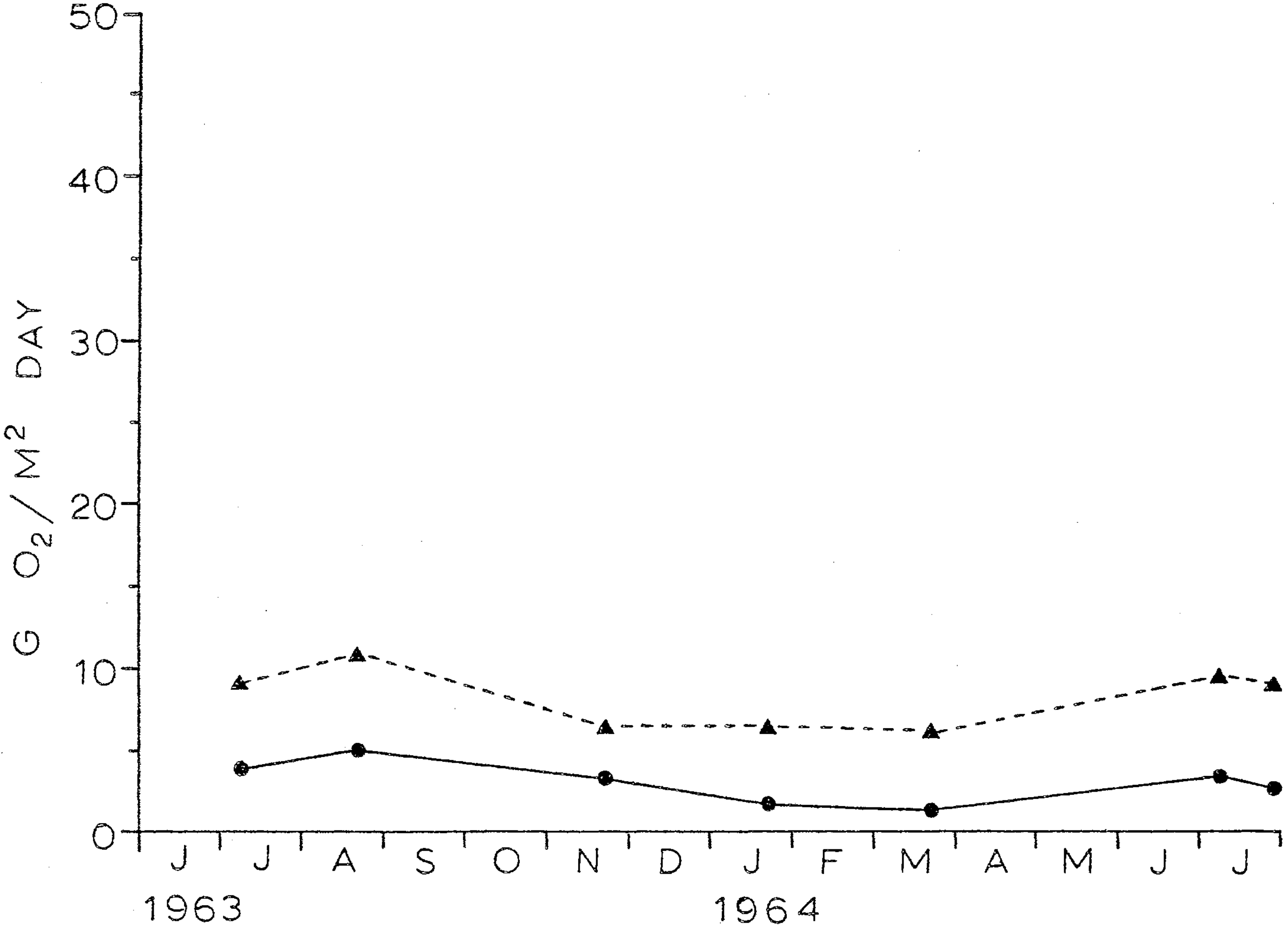

Fig. 4. Seasonal metabolism at Reach 12-13. Photosynthetic productivity = (—●—), community respiration = (-▲-).

and Hoskin (1958) asserted that it is necessary to have a steady flow of organic matter into a community in order to maintain respiration constantly in excess of productivity.

The ratio of productivity to respiration (P/R ratio) provides a meaningful index by which flowing aquatic communities can be classified (Odum, 1956b). When oxygen production exceeds oxygen demand (P/R ratio greater than one) as at Silver Springs, Florida (Odum, 1957b) or in the zone of recovery from pollution of White River, Indiana (Odum, 1956b), the community is autotrophic, producing organic matter faster than it is being consumed (Table 6). When oxygen demand exceeds oxygen production (P/R ratio less than one) as at Itchen River, England or the pollution outfall zone of White River, Indiana (Odum, 1956b), the community is heterotrophic, consuming organic matter faster than it is being produced.

The P/R values at Reaches 5-6 and 12-13 were always less than one, while the values at Reach 6-7 always exceeded one (Fig. 5 and Table 7). Longitudinal stream succession tends toward a steady state condition downstream. Steady state metabolism in a community results in a P/R ratio of one unless an outside source of organic matter is supplied to the community. The autotrophic community at Reach 6-7 produced organic matter which was continually exported (only 59% of the production was consumed) and in the heterotrophic reaches there was import of organic matter. Longitudinal succession at downstream Reach 12-13 had not progressed to the steady state condition due to the relatively high particulate organic matter, and small populations of benthic producers (Fig. 6). High community respiration and low productivity resulted

TABLE 6

COMPARATIVE ANNUAL COMMUNITY METABOLISM

Flow	Reference	Gross Production kg O_2/m^2 yr	Community Respiration kg O_2/m^2 yr	P/R
Silver Springs Headwater area	(Odum, 1957b)	6.8	6.4	1.06
Ivel River	(Edwards and Owens, 1962)	3.5	3.1	1.13
Itchen River	(Odum, 1956b)	2.0	3.7	0.54
Logan River Canyon section	(McConnell and Sigler, 1959)	1.3*	-	-
Blue River	--			
Reach 5-6		2.5	4.0	0.64
Reach 6-7		7.8	4.6	1.70
Reach 12-13		1.1	2.8	0.39

*Estimated from relation of chlorophyll to photosynthesis in light and dark bottle experiments.

TABLE 7

RATIO OF PHOTOSYNTHETIC PRODUCTIVITY TO RESPIRATION

Date		Reach 5-6	6-7	12-13
1963				
July	7	0.86	1.74	0.44
July	28	0.60	1.49	--
Aug.	19	--	--	0.47
Nov.	22	0.30	1.11	0.54
1964				
Jan.	23	0.32	1.06	0.29
March	21	0.93	1.01	0.24
July	5	0.73	3.92	0.38
July	26	0.65	2.23	0.31

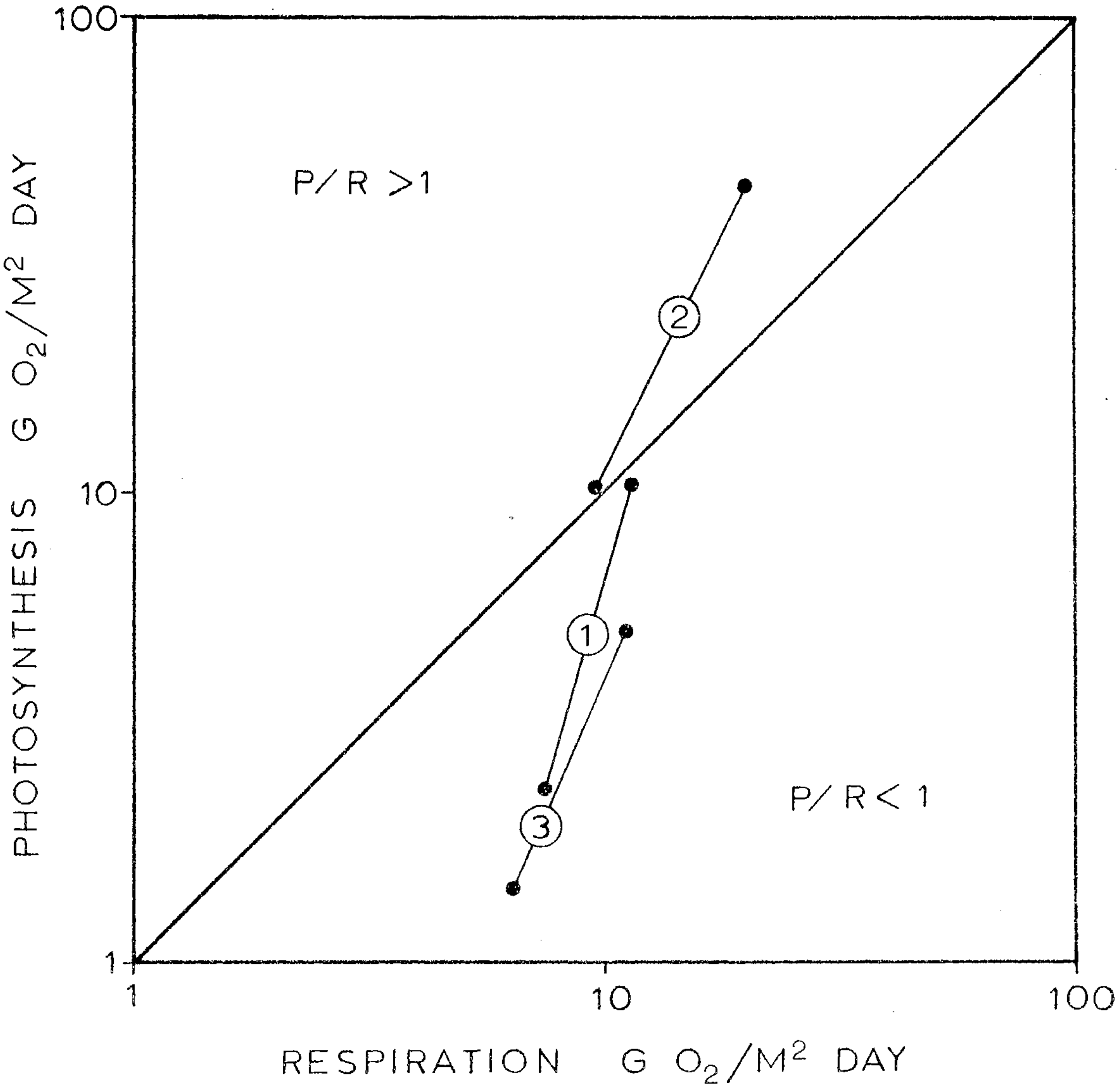

Fig. 5. Range and relative dominance of autotrophic and heterotrophic metabolism. Reach 5-6 = (1), Reach 6-7 = (2), Reach 12-13 = (3).

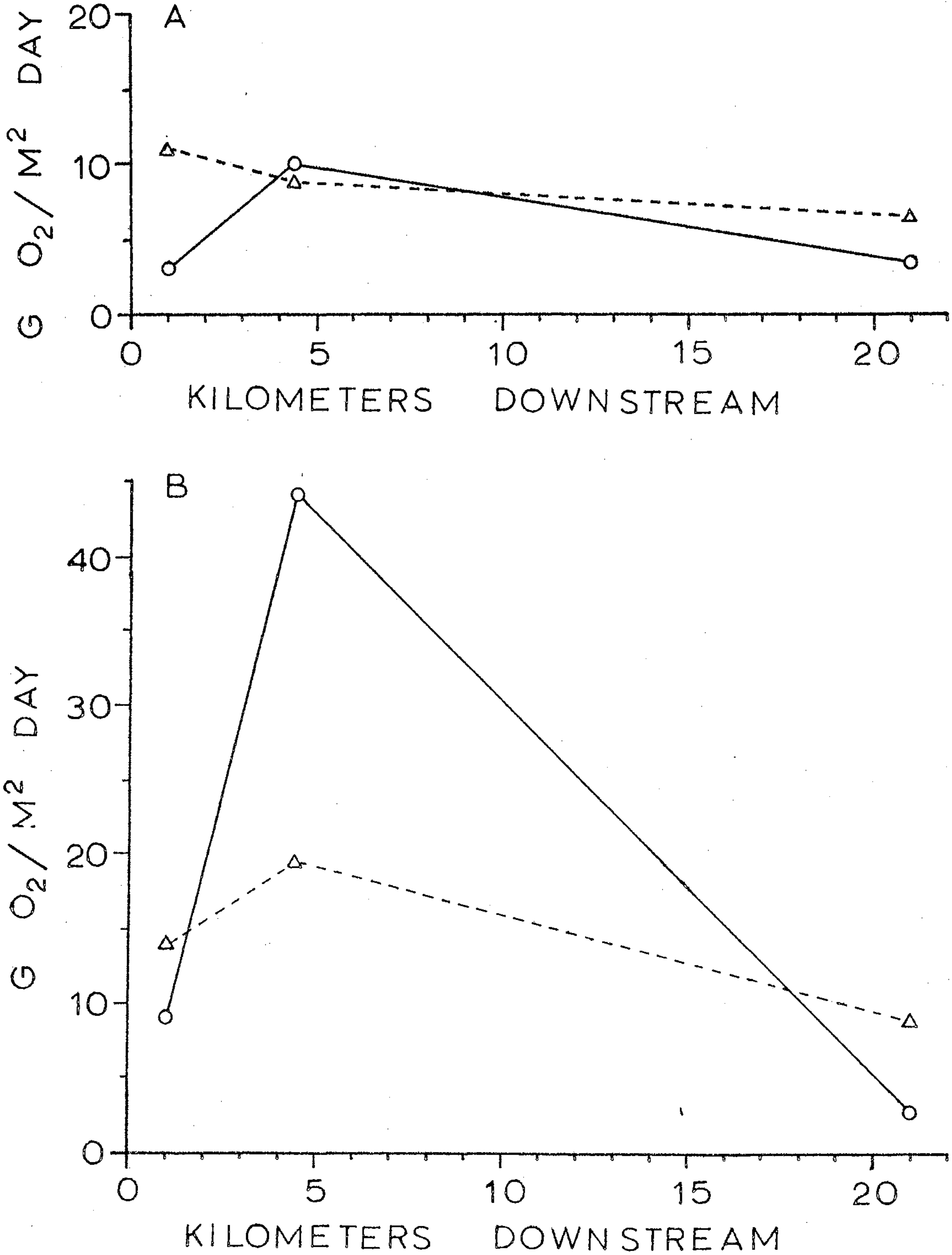

Fig. 6. Downstream sequence of production (-○-) and community respiration (--△--) below Station 5. (A) 22 Nov 1963, (B) 26 July 1964.

because of the above factors, yielding a heterotrophic range of annual metabolism.

Efficiency

Efficiency of photo-autotrophic organisms in converting solar energy to chemical energy was computed from photosynthesis and radiation data (Table 8). Total solar radiation in cal/cm^2 hr was measured by the Oklahoma State University weather station. Efficiency was calculated as percentage of total surface radiation utilized, assuming that 112 kcal is required to form glucose equivalent to one mole oxygen (Krauss, 1956).

Daily photosynthetic efficiencies ranged from 0.1 to 2.7%. Highest efficiency occurred in May at Reach 8-9 and the lowest in March at Reach 12-13. Similar efficiencies were reported by Edwards and Owens (1962) in Ivel River, England (1.0 to 2.2%) and by Copeland (1963) in oil refinery effluent holding ponds (0 to 2.0%). In oil refinery effluent holding ponds, when calculations were based on percentage of photosynthetically active radiation utilized (50% of total radiation), efficiencies were higher and ranged from 0 to 3.9%. Odum (1957b) reported 1.6% efficiency for Silver Springs, Florida (5.2% in terms of photosynthetically active radiation and with shading correction).

As solar radiation increased during the day photosynthetic productivity increased, but efficiency of utilization of solar radiation decreased (Fig. 7). Solar radiation was partially limiting to photosynthetic productivity at all observed surface intensities up to the maximum of 72 cal/cm^2 hr. The rate of increase in photosynthetic productivity per additional unit of solar radiation began to decline at intensities greater than 20 cal/cm^2 hr. The lag in productivity in relation to solar radiation was approximately correlated with decreased efficiency above 30 cal/cm^2 hr. Photosynthetic efficiency of the plant community in per cent of solar radiation utilized declined rapidly up to 30 cal/cm^2 hr (3.7 to 1.3%). The rate of decline was less at intensities from 30 to 72 cal/cm^2 hr.

TABLE 8

PHOTOSYNTHESIS, SOLAR RADIATION AND PHOTOSYNTHETIC EFFICIENCY

Date		Reach	Photosynthesis g/m^2 day	Total Solar Radiation cal/cm^2 day	Photosynthetic Efficiency %
1963					
June	16	5-6	3.3	192	0.6
June	16	12-13	4.9	192	0.9
July	28	5-6	5.9	563	0.4
July	28	6-7	22.0	563	1.4
Aug.	8	12-13	5.1	654	0.3
1964					
Jan.	23	5-6	2.4	296	0.3
Jan.	23	6-7	10.2	296	1.2
Jan.	23	12-13	1.9	296	0.2
March	21	5-6	10.5	539	0.7
March	21	6-7	18.2	539	1.2
March	21	12-13	1.5	539	0.1
May	28	1-2	4.0	160	0.9
May	28	5-6	5.4	160	1.2
May	28	6-7	10.6	160	2.3
May	28	8-9	12.3	160	2.7
May	28	10-11	4.3	160	0.9
May	28	12-13	3.7	160	0.8

The relationship between efficiency of utilization and total surface intensity of solar radiation each hour in Blue River is similar

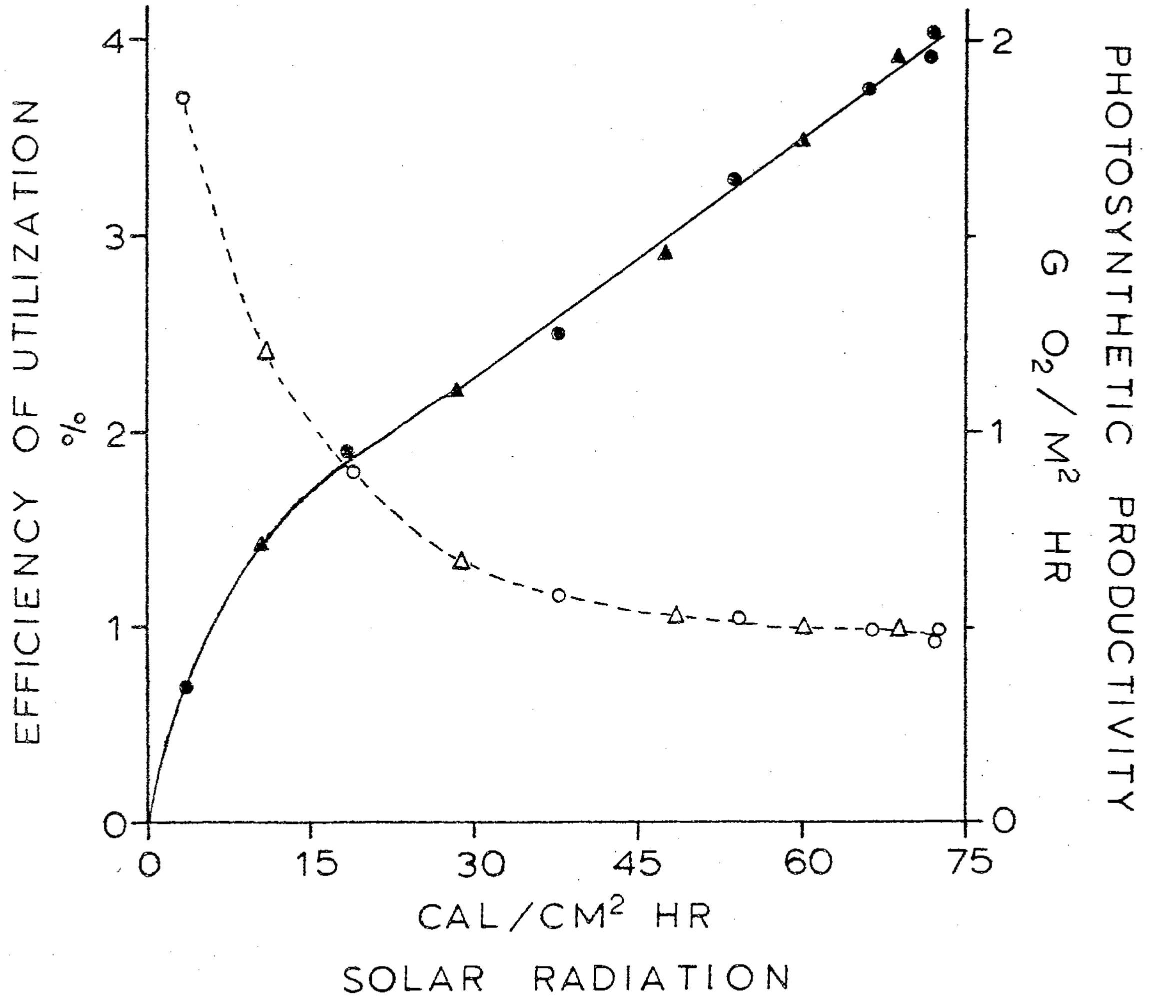

Fig. 7. Relationship of solar radiation, efficiency of utilization (△–○) and rate of photosynthesis (▲–●) 21 March 1964 at Reach 6-7. Morning = (△ ▲), afternoon = (○ ●).

to results of Edwards and Owens (1962) on a chalk stream in which there was also decreasing efficiency at high light intensities. In general, efficiency calculated from daily total solar radiation indicates the same relationship as that calculated from total radiation each hour (higher efficiency with low light intensity, compare Table 7 and Fig. 7).

In general, efficiency calculated from daily total solar radiation was directly related to productivity. Highest efficiency occurred in the stream community with the greatest productivity. Copeland (1963) and Butler (1964) also reported that community efficiency, based on daily total solar radiation was maximal with high productivity and minimal with low productivity. In contrast, the relationship between photosynthetic productivity and total surface intensity each hour in the most productive community on granite indicates that efficiency was maximal with low productivity.

According to the optimum efficiency-maximum power hypothesis, natural systems perform maximum power output at an optimum efficiency which is always less than the maximum efficiency (Odum and Pinkerton, 1955). Efficiency up to 50% has been obtained in experiments on the quantum requirements of algal cultures where low light intensities were used, but the energy flow was small and production was low. At the higher light intensities common to natural communities, production is greater, but efficiency is much lower (Odum, 1956a).

V. SUMMARY

1. A study of physico-chemical conditions and community metabolism in a Southern Great Plains stream in southeastern Oklahoma was conducted between June 1963 and August 1964. Seasonal environmental changes, effects of underlying strata upon community metabolism, the annual course of community metabolism and efficiency of photo-autotrophic organisms in converting solar energy to chemical energy were determined. Principal primary producers and chlorophyll bearers of the stream were bryophytes, algae and diatoms.

2. Water temperature fluctuated from 34 C in July to 6.5 C in March. Total solar radiation varied from 160 to 654 cal/cm^2 day. Total alkalinity decreased and carbonate alkalinity increased downstream. The increase in carbonate alkalinity was attributed to excess calcium carbonate. Specific conductance decreased downstream as a result of bicarbonate conversion to carbonate.

3. Benthic chlorophyll *a* concentration was greater than suspended concentration. Summer chlorophyll concentration was highest on the granite outcrop. High chlorophyll concentration occurred in upstream reaches on large boulders in the channel bed and low concentration occurred downstream on shifting sand.

4. Oxygen exchange rates varied from 1.3 to 2.9 g/m^2 at 100% saturation deficit. Exchange rates were higher in areas of greater velocity and shallow water.

5. Gross photosynthesis varied from 10.1 g O_2/m^2 day in winter to 48.0 g O_2/m^2 day in summer on the granite outcrop, and always exceeded respiration. High primary productivity and respiration resulted from large populations of benthic algae and bryophytes growing on these granite formations. Community respiration always exceeded photosynthetic productivity at reaches in limestone and sand formations. Annual primary production varied from 1.1 kg/m^2 on the sand to 7.8 kg/m^2 on the granite.

6. Ratio of productivity to respiration for the autotrophic community on the granite formation varied from 1.01 to 3.92. The P/R ratio of the heterotrophic community on the limestone varied from 0.30 to 0.93, while that on the sand varied from 0.24 to 0.50.

7. Daily photosynthetic efficiencies ranged from 0.1 to 2.7%. As solar radiation increased during the day photosynthetic productivity increased, but efficiency of utilization of solar radiation decreased. Solar radiation partially limited photosynthetic productivity at all observed surface intensities up to the maximum of 72 cal/cm^2 hr. Photosynthetic efficiency of the plant community as per cent of solar radiation utilized decreased from about 3.7% at low intensity to 1.0% at 72 cal/cm^2 hr.

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