

MACROPHYTE STANDING CROP AND METABOLISM IN A
CONSTANT TEMPERATURE RIVER

By

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PREFACE

A 567-m stretch of the spring-fed San Marcos River, Texas, was studied to ascertain the relationship of community metabolism to community structure. Macrophyte standing crop (g/m^2) was reported as fresh weight, dry weight, ash weight, organic weight and organic carbon. Quantitative relationships between macrophytes and stream bed materials were determined. Biomass units were used in determining species diversity. Efficiency of conversion of solar input to chemical energy by photo-autotrophic organisms in the river and photosynthesis: respiration ratios were calculated.

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TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION.	1
II. STUDY AREA.	3
III. METHODS	8
IV. RESULTS AND DISCUSSION.	11
Physicochemical Conditions	11
Primary Producers.	16
Species Diversity.	28
Community Metabolism and Light Intensity	28
Efficiency, Structure and Ecosystem Maturity	32
Community Metabolism, Structure and Ecosystem Maturity	35
V. SUMMARY	41
LITERATURE CITED	44

LIST OF TABLES

Table	Page
I. Physical Characteristics of Plots for Macrophyte Sampling	6
II. Chemical Conditions in the San Marcos River	7
III. Mean Physicochemical Conditions at Stations A and B	12
IV. Mean Nutrient Conditions for Stations A and B	17
V. Chlorophyll <u>a</u> of Epilithic Algae and Phytoplankton in Plots 4, 5 and 11 of the Study Area	19
VI. Conversion Factors for Converting Fresh Weight to Dry Weight and Dry Weight to Ash Weight, Organic Carbon and Organic Weight.	22
VII. Percentages of Dry Weight, Ash Weight, Organic Carbon and Organic Matter from Mean Standing Crop (g/m ²) of Sub- mersed Aquatic Plants in the Study Area	23
VIII. Annual Plot and Bed-Type Standing Crop Means (g/m ²) With Variances for the Study Area.	24
IX. Maximum Standing Crops of Submersed Macrophytes in Rivers	27
X. Gross Photosynthesis, Respiration and Light Intensity on Successive Days	30
XI. Metabolism of Lotic Waters Calculated From Diurnal Oxygen Curves.	36

LIST OF FIGURES

Figure	Page
1. Plan of Study Area, San Marcos River, Texas	5
2. The pH in the Study Area and Upstream Falls Between Spring Lake and the San Marcos River 26 Jan 65	13
3. Diurnal Carbon Dioxide and Daytime Oxygen Rate-of-Change Curves on 4 Oct 1964.	15
4. Number of Species and Accumulated Weight of Macrophytes Beginning One Week After Dredging Operations.	20
5. Species Diversity of Macrophytes.	29
6. Photosynthetic Efficiency	33
7. Community Metabolism Under Clear Skies.	34
8. Photosynthesis/Respiration Ratios of Community Metabolism . . .	39

CHAPTER I

INTRODUCTION

Efforts to determine the relationship between submersed macrophyte standing crop and community metabolism in natural rivers have been limited, although much work has been done on primary productivity in natural waters. Quantitative estimations of macrophyte standing crop have been made from summer samples (Odum, 1957; Edwards and Owens, 1960; Westlake, 1961), quaterly samples (Owens and Edwards, 1961), spring and summer samples (Owens and Edwards, 1962), benthic chlorophyll (Duffer and Dorris, 1966) and several spring-river systems (Natelson, 1955). Only in the studies of Odum (1957), Edwards and Owens (1962), and Duffer and Dorris (1966) were community metabolism measurements made.

This study differs from those mentioned above in that changes in community metabolism were related to the development of the macrophyte community. The study was made in a 567-m stretch of the spring-fed San Marcos River, San Marcos, Texas, during a period of reestablishment of plants from a dredging operation. Plants are dredged annually from the headwaters of the river which has relatively constant flow, temperature and chemical conditions.

The river's source is the San Marcos Springs which emerge from the Edwards Underground Reservoir at the base of the Balcones fault zone.

into a 18-ha lake. The water leaves the lake over a small dam and flows southeasterly for approximately 98 km to join the Guadalupe River below Gonzales, Texas.

CHAPTER II

STUDY AREA

A 567-m stretch of the San Marcos River, Texas, beginning 650 m below the San Marcos Springs was selected for study. The site was located between the Jeff Davis Bridge (Station A) and the Hutchinson Street Bridge (Station B) in San Marcos (Fig. 1). To obtain an estimation of plant biomass, the study area was divided according to stream bed types and to width and depth intervals within bed types (Table I). Bed types were silt-pebble, gravel, mud and mud-gravel transition. Five width intervals and four depth intervals were specified. Width deviation within each plot was no more than 7.62 m, while depth deviation was no more than 0.51 m. Mean width and depth were 27.1 and 1.0 m, respectively. Velocity varied throughout the stretch; however, it remained relatively constant at 0.24 m/sec for the entire stretch as measured with fluorescein dye. Mean discharge was $4.84 \text{ m}^3/\text{sec}$. Chemical conditions were relatively constant at the springs and more variable downstream (Table II).

Total precipitation was 1.09 m for the duration of the study and varied from 0.02 m during July, 1964, to 0.19 m during June, 1964. Mean wind velocity during the study period was 15.29 km/hr and mean monthly velocity varied from 12.71 km/hr during September, 1964, to 18.67 km/hr during April, 1964. The sky was clear 35% of the time,

partly cloudy 32% and cloudy 33% (Local climatological data, U.S.
Department of Commerce Weather Bureau, Austin, Texas).

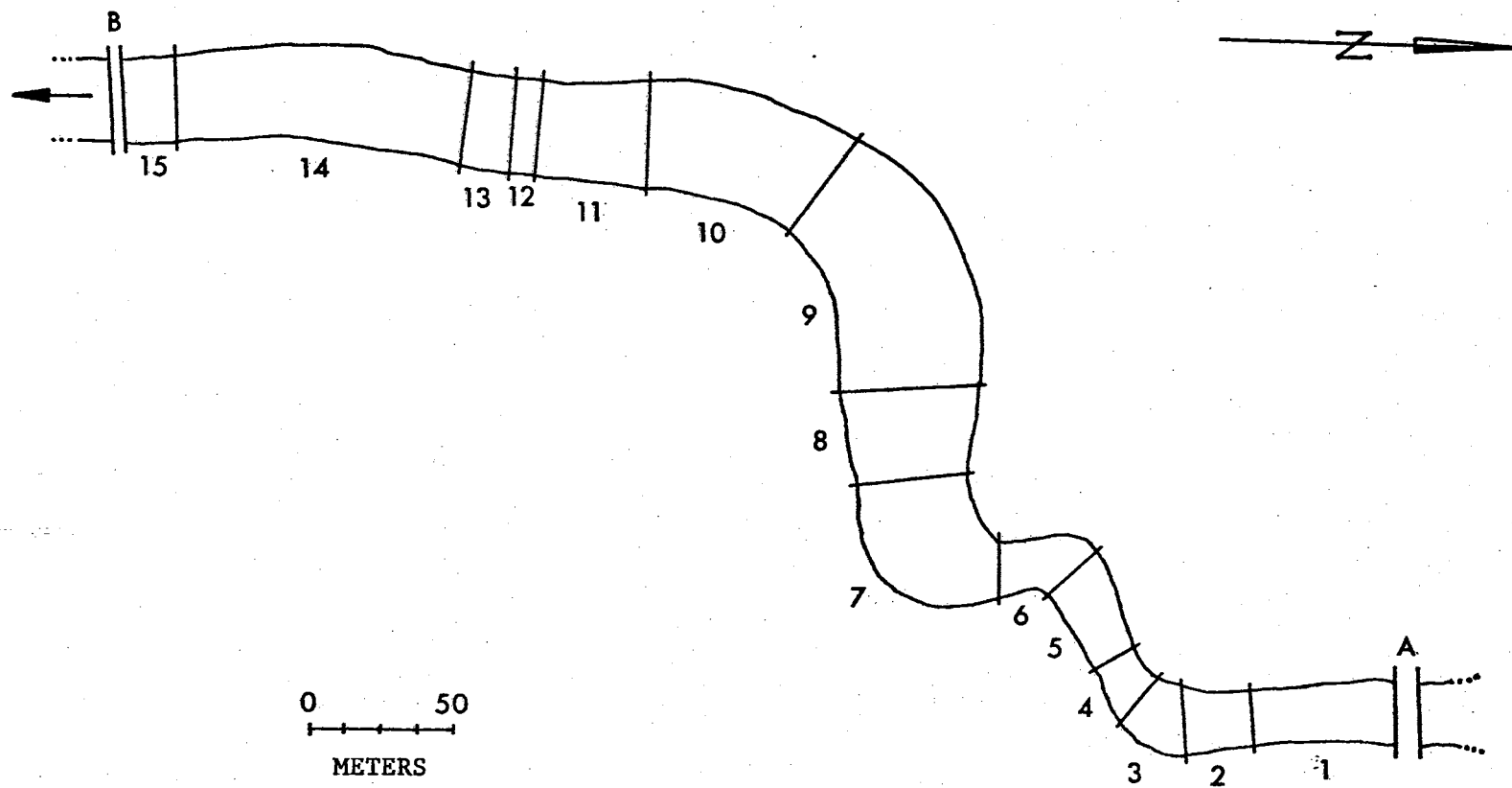


Fig. 1. Plan of Study Area, San Marcos River, Texas. Numbers Indicate Plots for Sampling Macrophytes. A = Station A, Jeff Davis Bridge; B = Station B, Hutchinson Street Bridge.

TABLE I
 PHYSICAL CHARACTERISTICS OF PLOTS FOR MACROPHYTE SAMPLING

Bed Type	Plot	Depth Interval (0.51 m)	Width Interval (7.62 m)	Mean * Velocity (m/sec)
				**
Silt-Pebble	1	0.52 - 1.03	12.19 - 19.81	0.18 ± 0.07
	2	1.04 - 1.55	12.19 - 19.81	0.12 ± 0.02
	3	1.56 - 2.07	12.19 - 19.81	0.11 ± 0.07
Gravel	11	0.00 - 0.51	27.45 - 35.07	0.30 ± 0.06
	5	0.52 - 1.03	12.19 - 19.81	0.24 ± 0.15
	4	1.04 - 1.55	12.19 - 19.81	0.17 ± 0.05
Mud	7	0.52 - 1.03	27.45 - 35.07	0.11 ± 0.03
	8	0.52 - 1.03	35.08 - 42.70	0.07 ± 0.04
	9	0.52 - 1.03	42.71 - 50.33	0.11 ± 0.03
	10	0.52 - 1.03	35.08 - 42.70	0.12 ± 0.05
	14	0.52 - 1.03	27.45 - 35.07	0.14 ± 0.05
	15	1.04 - 1.55	19.82 - 27.44	0.11 ± 0.03
	6	1.56 - 2.07	12.19 - 19.81	0.13 ± 0.07
13	1.56 - 2.07	27.45 - 35.07	0.10 ± 0.06	
Mud-Gravel transition	12	0.51 - 1.03	27.45 - 35.07	0.12 ± 0.14

* Velocity was measured with a Price mechanical current meter in the quadrat from which the plants were cropped from March through October, 1964.

** Mean ± standard deviation.

TABLE II
CHEMICAL CONDITIONS IN THE SAN MARCOS RIVER

Location	Date	SiO ₂	Ca	Mg	Na&K	HCO ₃	CO ₃	SO ₄	Cl	NO ₃	Specific Conductance	pH
San Marcos Springs, San Marcos, Texas	Mar 1955	13.0	82	21	10.7	309	0.0	20	16	4.6	556	7.4
	June 1959	9.2	84	18	11.3	317	0.0	25	20	8.5	557	7.1
	Feb 1963	-	-	-	-	308	-	-	20	8.5	-	-
	Sept 1963	-	-	-	-	300	-	-	20	-	-	-
Luling, Texas (U.S.G.S. gage station, 33 km below San Marcos Springs)	Mar 1963	8.9	76	20	28.0	266	0.0	33	55	3.0	637	6.9
	July 1963	12.0	61	18	18.0	231	0.0	26	32	3.2	478	7.0
Ottine, Texas (Below Hwy. 2091 bridge, 41 km below San Marcos Springs)	Mar 1963	9.1	84	19	41.0	288	0.0	40	70	0.0	728	6.5
	July 1963	11.0	62	18	29.0	236	0.0	28	47	2.8	531	7.3

Concentrations are in mg/l, except specific conductance (micromhos at 25° C) and pH.

Data from United States Geological Survey reports, Austin, Texas

CHAPTER III

METHODS

Solar input was determined from continuous measurements made with a pyrhelimeter at the San Antonio Weather Station, San Antonio, Texas. Light intensities at stations A and B were measured every two hours on the day of oxygen sampling with a Tri-Lux foot-candle meter. Stream flow for the entire study area was measured every month during the study with fluorescein dye. Within each quadrat from which standing crop samples were taken, stream velocity was measured with a Price current meter from March through October, 1964.

Methyl orange and phenolphthalein alkalinity were determined by titration with 0.02 N sulphuric acid. Specific conductance was determined with an Industrial Instruments Conductivity Bridge (A.P.H.A., 1960). A Beckman Zeromatic pH meter was used for pH determinations. Nitrate-N, Nitrite-N, ammonia-N and orthophosphates were analyzed by Hach colorimetric methods.

Free carbon dioxide was determined from pH measurements (Byers, 1963a) and graphically from bicarbonate concentration (Moore, 1939). Total dissolved solids were determined from water filtered through Millipore filters of 0.45 μ pore size. The filtrate was evaporated at 106° C, and the residue weight determined as total dissolved solids. Temperature was measured with a mercury thermometer.

Benthic and planktonic chlorophyll was extracted in 90% aqueous acetone for 24 hr at 5° C in the dark. Samples were filtered through Millipore filters with 0.45 μ pore size. Optical density was read on a Beckman DU spectrophotometer at 665, 645, 630 m μ for chlorophyll a concentration and at 750 m μ for turbidity correction (Holmes, Schafer and Shimada, 1957). Calculations were based on the formulae of Richards and Thompson (1952).

Macrophytes were sampled from each of the 15 plots along the 567-m stretch at monthly intervals. Randomly chosen transects were divided into three equal parts, and one 0.25 m² quadrat was randomly selected from each part. Plants were cropped at the stream bed surface and transported to the laboratory in polyethylene bags; sorted by species into water to prevent dehydration; washed free of animals and debris; spun for 2.5 minutes in a domestic washing machine (centrifugal force at 136 G) and fresh weight determined (Edwards and Owens, 1960). Since the spun-dry fresh weight (FW): oven-dry weight (DW) relationship was linear for each species of macrophytes, dry weight was determinable for each species as a percentage of the fresh weight. Ash content for each species was determined as the residue of ignition in a muffle furnace at 550° C. Organic carbon was determined by the wet combustion method (Scott, 1947).

Community metabolism was estimated by methods described by Odum and Hoskin (1958) and Odum and Wilson (1962). Primary productivity measurements were made under clear as well as overcast skies. Duplicate samples were taken every two hours in daylight and every three hours at night at each station and analyzed for dissolved oxygen by the

Alsterberg (azide) modified Winkler method (A.P.H.A., 1960). Oxygen saturation values were taken from tables by Churchill (1962).

Gas bubbles rising to the surface from the river bed were trapped and analyzed for oxygen content by the Scholander method (Scholander, 1942). The bubbles contained an average 16.5% oxygen (Range 16.4 - 16.6%) amounting to an oxygen loss of only 0.1 g/m^2 day. The loss of oxygen to the atmosphere from this source was omitted from productivity calculations.

CHAPTER IV

RESULTS AND DISCUSSION

Physicochemical Conditions

The mean of physicochemical conditions at stations A and B was determined from January, 1964, to February, 1965 (Table III). Temperature, alkalinity, specific conductance and total dissolved solids were only slightly different between stations, and were relatively constant throughout the study period. Specific conductance varied only between 546 and 593 $\mu\text{mhos/cm}$. Total dissolved solids fluctuated from 300 to 379 mg/l. For most natural waters the ratio of total dissolved solids to specific conductance is about 0.65 ± 0.1 (Rainwater and Thacher, 1960). In the present study this ratio ranged from 0.51 to 0.68, with a mean of 0.60. River temperature ranged from 21.0°C in December, 1965, to 23.3°C in July, 1964, and was uniform throughout the stretch during each sampling period.

Diurnal pH measurements were made at stations A and B. The mean of minimum and maximum values ranged from 7.27 to 7.70 pH units. Actual minimum and maximum values were 7.17 and 7.90 pH units. The pH was always higher downstream, indicating a constant loss of carbon dioxide from the river (Fig. 2). Carbon dioxide was lost from the river at the falls upstream from Station A as indicated by the increase in pH. The importance of falls on the oxygen balance of river waters has been

TABLE III
 MEAN PHYSICOCHEMICAL CONDITIONS AT STATIONS A AND B

Date	Temperature (°C)	pH	Specific Conductance (μmhos/cm)	Alkalinity HCO ₃ ⁻ ** (mg/l)	Total Dissolved Solids (mg/l)	Dissolved Solids/Specific Conductance
25 Jan 64	22.5*	7.52*	-	-	-	-
22 Feb	22.3	7.70	-	-	-	-
21 Mar	22.5	7.27	556	244	379	0.68
26 Apr	22.5	7.57	557	247	339	0.61
29 May	23.3	7.54	571	248	357	0.63
24 June	23.3	7.41	553	248	344	0.62
18 July	23.3	7.48	582	252	314	0.54
16 Aug	23.3	7.47	583	253	373	0.64
26 Sept	22.5	7.52	592	253	300	0.51
4 Oct	22.3	7.54	593	244	331	0.56
21 Nov	21.5	-	558	245	309	0.55
19 Dec	21.0	-	546	245	333	0.61
26 Jan 65	22.2	7.58	554	247	372	0.67
26 Feb 65	22.3	-	548	247	328	0.60

* Mean of minimum and maximum values taken every two hours during the day and every three hours during the night during a 24-hour period. Temperature did not vary more than 2.5°C during any 24-hour period.

** Total alkalinity was bicarbonate.

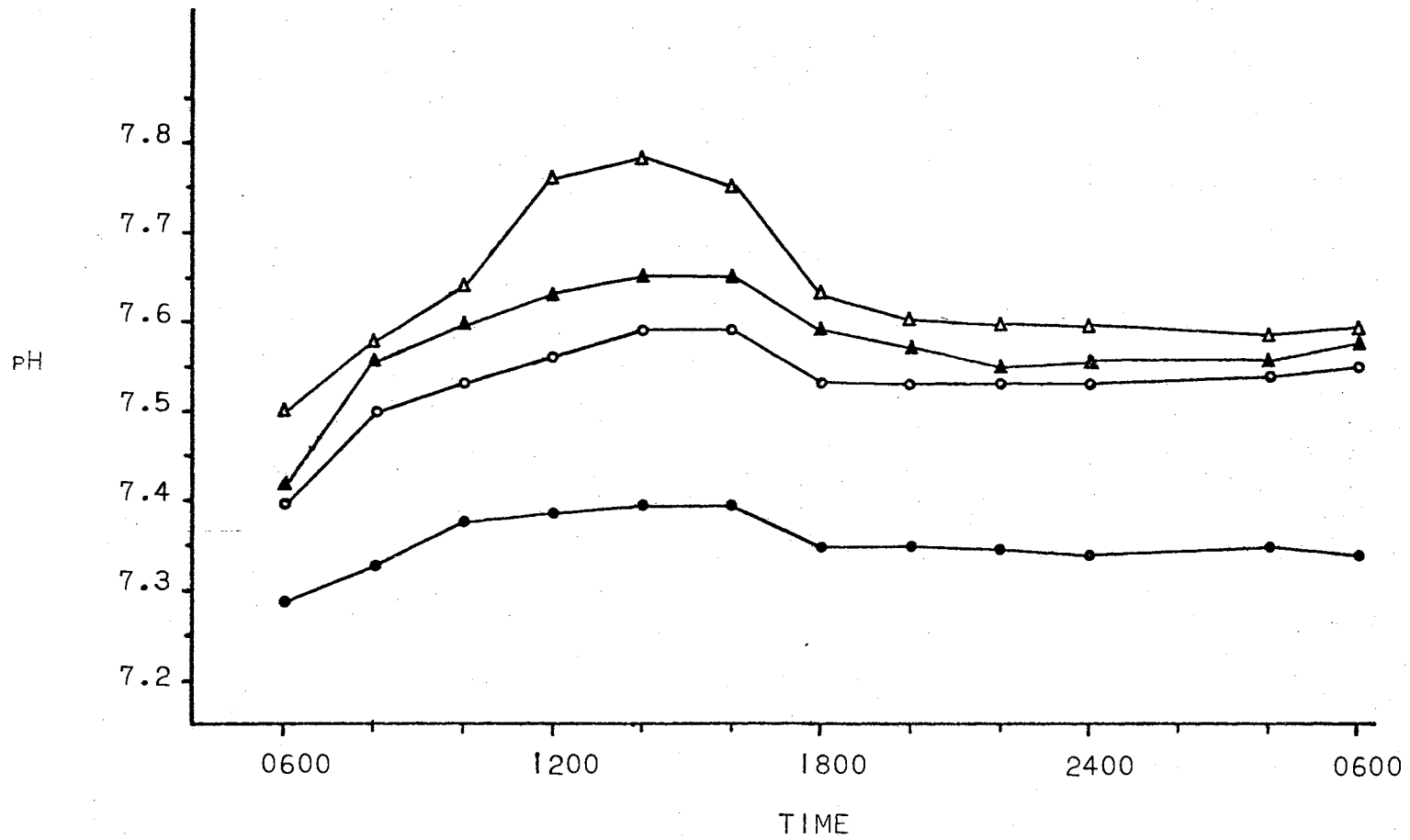


Fig. 2. The pH in the Study Area and Upstream Falls Between Spring Lake and the San Marcos River 26 Jan 65. Above Spillway = (●), Below Spillway = (○), Station A = (▲), Station B = (△).

recognized (Owens and Edwards, 1963), but the effect on carbon dioxide concentration appears not to have been given much consideration.

Carbon dioxide rate-of-change curves were not symmetrical with respect to oxygen rate-of-change curves for the same day. A daytime increase of carbon dioxide occurred at midday on several occasions indicating a depression of photosynthetic activity (Fig. 3). However, the oxygen concentration increased during the same period as if photosynthetic activity had increased. This apparent anomaly in symmetry may be due to differences in diffusion rates of gases between the plants and the surrounding water. In submersed aquatic plants, carbon dioxide diffuses readily in comparison to oxygen (Gorski, 1929). Carbon dioxide frequently decreased to a nighttime depression point, followed by an increase to the post-sunset level by dawn. No reason for the nighttime reduction is apparent, and it was not associated with changes in wind velocity.

Bicarbonate alkalinity ranged between 244 and 253 mg/l. Constancy of bicarbonate may be attributed to an excess of free carbon dioxide, a relatively constant calcium ion concentration and the use by plants of free carbon dioxide. Calcium ion concentration of the water was about 84 mg/l. An excess of only 2.5 mg/l free carbon dioxide is required to retain the calcium bicarbonate in solution under these conditions (Ruttner, 1963). Free carbon dioxide was greater than 5.5 mg/l throughout the study period.

The lack of diurnal change in bicarbonate concentration further confirmed that free carbon dioxide was the main carbon source in photosynthesis. Aquatic plants seldom utilize bicarbonate as a nutrient in photosynthesis when a sufficient supply of free carbon dioxide is

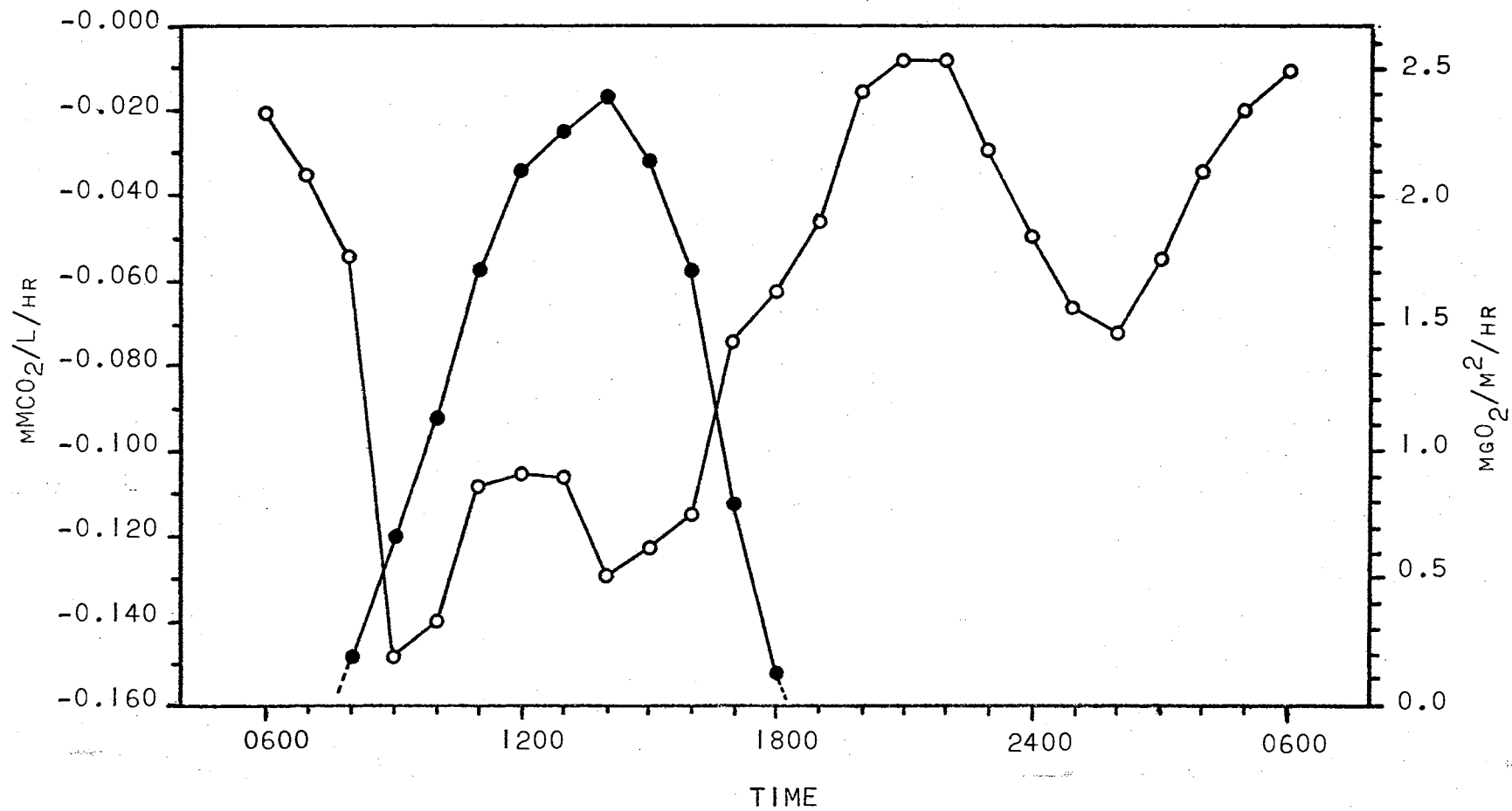


Fig. 3. Diurnal Carbon Dioxide and Daytime Oxygen Rate-of-Change Curves on 4 Oct 1964.
Carbon Dioxide = (○), Oxygen = (●).

present (Steeman-Nielsen, 1946, 1952a, 1952b). Apparently, a positive relationship exists between alkalinity and productivity in natural waters only when free carbon dioxide is limiting and bicarbonate is the carbon source (Cushing, 1964).

Nitrite-N, nitrate-N, ammonia-N and orthophosphates were monitored at stations A and B from May, 1964, to April, 1965 (Table IV). Only slight differences in concentration existed between stations throughout the study. No differences in concentration were found during diurnal and stratification measurements. Ammonia-N was present only in May and June, 1964, with concentrations of 0.27 and 0.23 mg/l, respectively. Nitrite-N ranged from 0.001 to 0.006 mg/l and nitrate-N from 0.64 to 1.65 mg/l. Orthophosphate concentration varied from 0.20 to 0.47 mg/l.

Primary Producers

Fifteen species of submersed angiosperms, two bryophytes and one filamentous alga occurred in abundance in the study area (Table VI). These 18 species are treated as macrophytes. Potamogeton nodus was observed on occasions but was never collected in any sample. Diatoms and desmids were part of a macrophyte-Aufwuchs algae complex. However, the quantity of Aufwuchs attached to the macrophytes was small and was not weighed separately. Dominant genera of epilithic algae were Stigeoclonium, Oscillatoria, Anabaena, Spirogyra, Cladophora, Terpsinae and Microthamnion.

Benthic Algae and Phytoplankton

Chlorophyll a concentration of epilithic algae on flat rocks and gravel was measured during January, March, May, August and November, 1965. Benthic algae were sparse in other bed types because of

TABLE IV
MEAN NUTRIENT CONDITIONS FOR STATIONS A AND B

Date	Nitrite-N (mg/l)	Nitrate-N (mg/l)	Ammonia-N (mg/l)	Orthophosphates (mg/l)
1964				
May	0.006	1.36	0.27	0.25
June	0.006	1.65	0.23	0.28
July	0.006	0.71	0.00	0.20
Aug	0.006	1.00	0.00	0.20
Sept	0.004	0.64	0.00	0.47
Oct	0.004	1.15	0.00	0.42
Nov	0.004	1.18	0.00	0.20
Dec	0.003	1.08	0.00	0.35
1965				
Jan	0.002	1.33	0.00	0.27
Feb	--	--	--	--
Mar*	0.001	1.42	0.00	0.25
Apr	0.002	1.50	0.00	0.27

* After cropping in March, 1965

vegetation-cover. Chlorophyll a concentration was not correlated with primary productivity (Table V and Fig. 7). Mean chlorophyll a ranged from 0.12 g/m^2 in May, 1965, to 0.57 g/m^2 in January, 1965. In January a few samples, atypical of the area, had chlorophyll a concentrations above 0.67 g/m^2 due to dense growths of Spirogyra sp. When the Spirogyra samples were omitted from the calculations, the chlorophyll a concentration was 0.44 g/m^2 . The minimum in May occurred five weeks after dredging operations. Waters (1961) found that the chlorophyll a concentration of periphyton growing on concrete blocks in a stream reached a maximum in three to eight weeks, after which seasonal differences occurred. Seasonal changes were not apparent in the present study.

Traces of phytoplankton were present only in May and August, 1965, with a mean chlorophyll a concentration of 0.003 and 0.007 g/m^2 , respectively (Table V).

Macrophytes

The number of macrophyte species following dredging increased from nine in March, 1964, to 18 in September, 1964, and remained constant throughout the remainder of the study period (Fig. 4). Conversion factors for fresh weight, dry weight, ash weight, organic weight and organic carbon were determined for each species on at least three occasions. No sign of seasonal variation was found. These factors were used in converting the fresh weight of each species to the other parameters. Converted weights of each species were then summed and means for the entire community were plotted (Fig. 4). Factors for a particular conversion (e.g. fresh weight to dry weight) varied considerably

TABLE V
 CHLOROPHYLL a OF EPILITHIC ALGAE AND PHYTOPLANKTON
 IN PLOTS 4, 5 AND 11 OF THE STUDY AREA

Date	Phytoplankton Mean \pm SD (g/m ²)	Epilithic Algae Mean \pm SD (g/m ²)
1965		
Jan	0.000 (6)	0.57 \pm 0.33 (16)* 0.44 \pm 0.12 (13)**
Mar	0.000 (6)	0.42 \pm 0.19 (9)
River dredged free of plants March 25-30, 1965		
May	0.003 \pm 0.003 (6)	0.12 \pm 0.13 (19)
Aug	0.007 \pm 0.002 (6)	0.32 \pm 0.19 (17)
Nov	0.000 (6)	0.28 \pm 0.06 (16)

() Number of samples

* Observations above 0.67 g/m² were due to dense growths of Spirogyra which were atypical of the plots.

** Algae excluding Spirogyra

SPECIES OF
MACROPHYTES

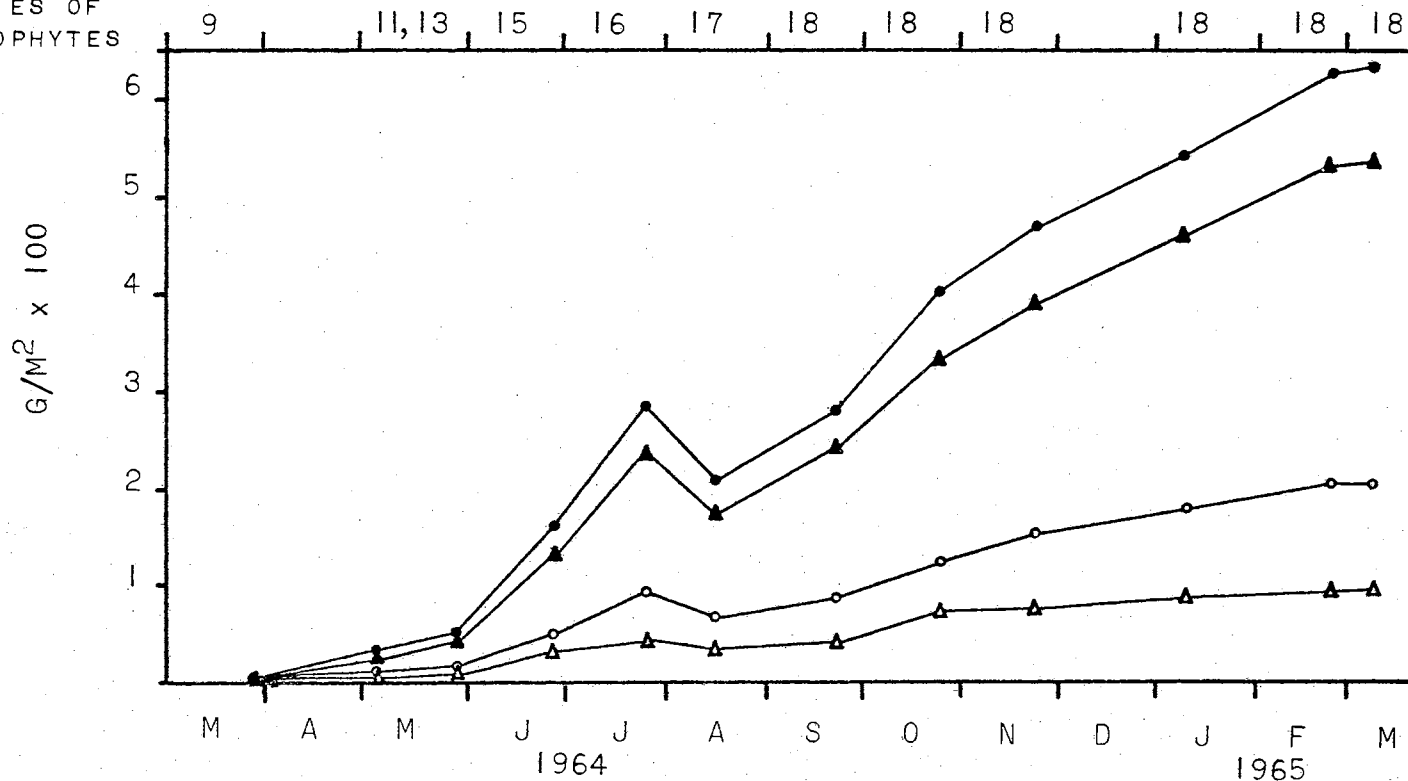


Fig. 4. Number of Species and Accumulated Weight of Macrophytes Beginning One Week After Dredging Operations. Dry Weight = (●), Organic Weight = (▲), Organic Carbon = (○), Ash Weight = (△).

among species (Table VI). However, the means of conversion factors for all species (Table VI) and the annual means calculated from monthly standing crop (Table VII) varied only 10.5%, 12.5%, 2.2% and 2.7% for dry weight, ash weight, organic carbon and organic weight, respectively. Conversion factors for bryophytes and Rhizoclonium were considerably different from the other species, but these plants constituted less than 2% of any monthly crop. If conversion factors for these plants are omitted from the species means, the resultant angiosperm means and means calculated from the monthly macrophyte standing crop differed only 3.4%, 3.0%, 0.2% and 0.5% for dry weight, ash weight, organic carbon and organic weight, respectively. In a heterogeneous plant community, the mean of the conversion factors can be applied to total biomass with accuracy. Laborious and time-consuming sorting of species and weighing of numerous samples thus may be eliminated. However, the common practice of approximating percentage factors for converting plant wet weight to dry weight and dry weight to other weight parameters should be avoided (Wetzel, 1965).

Differences among the annual standing crop means of the four stream bed types were tested using a Cochran and Cox's (1962) approximate 't' value since the error variances were heterogeneous (Table VIII). All possible two-way comparisons for the four stream bed types were made on dry weight, organic weight and organic carbon at the 1% level. Differences between mud and silt-pebble beds were found not to be significant whereas differences between all other comparisons were found to be significant. The composition of the mud beds and the silt-pebble beds favored attachment of macrophytes.

TABLE VI

CONVERSION FACTORS FOR CONVERTING FRESH WEIGHT TO DRY WEIGHT AND DRY WEIGHT
TO ASH WEIGHT, ORGANIC CARBON, AND ORGANIC WEIGHT

	Dry Weight (Per Cent of Fresh Weight)	Ash Weight (Per Cent of Dry Weight)	Organic Carbon (Per Cent of Dry Weight)	Organic Weight (Per Cent of Dry Weight)
CHLOROPHYCEAE				
<u>Rhizoclonium hieroglyphicum</u> (Aq.) Kuetz	27.43 ± 1.80*	29.17 ± 0.47*	25.84 ± 0.41*	70.83**
MUSCI				
<u>Amblystegium riparium</u> Brit. Sch.	30.57 ± 0.82	29.24 ± 0.15	27.12 ± 0.29	70.76
HEPATICAЕ				
<u>Riccia fluitans</u> L.	8.87 ± 0.42	27.06 ± 0.13	28.66 ± 0.24	72.94
ANGIOSPERMAE				
<u>Cabomba caroliniana</u> Gray	7.47 ± 0.56	22.80 ± 0.85	28.36 ± 0.74	77.20
<u>Ceratophyllum demersum</u> L.	8.90 ± 0.36	8.78 ± 0.20	34.34 ± 0.81	91.22
<u>Anacharis canadensis</u> (Michx) Planchon	10.47 ± 1.75	16.77 ± 0.97	30.84 ± 0.74	83.23
<u>Heteranthera dubia</u> (Jacq.) Mac M.	6.53 ± 0.41	19.71 ± 2.77	27.18 ± 0.59	80.29
<u>Ludwigia palustris</u> (L.) Ell.	13.50 ± 0.50	25.32 ± 1.60	29.54 ± 0.67	74.68
<u>Myriophyllum brasiliense</u> Cambess.	20.00 ± 0.20	10.08 ± 1.17	35.28 ± 1.19	89.92
<u>Myriophyllum heterophyllum</u> Michx.	12.77 ± 0.22	8.89 ± 0.40	37.61 ± 0.43	91.11
<u>Najas guadalupensis</u> (Spreng.) Morong.	10.83 ± 1.12	18.28 ± 1.37	31.92 ± 0.79	81.72
<u>Potamogeton illinoensis</u> Morong.	14.20 ± 0.26	15.85 ± 1.04	32.73 ± 0.76	84.15
<u>Potamogeton pectinatus</u> L.	15.56 ± 0.20	15.35 ± 1.08	30.49 ± 0.86	84.65
<u>Potamogeton crispus</u> L.	13.66 ± 0.31	19.27 ± 0.76	30.74 ± 0.71	80.73
<u>Sagittaria platyphylla</u> (Engelm.) J. G. Sm.	6.40 ± 0.26	22.60 ± 3.07	33.30 ± 0.56	77.40
<u>Vallisneria americana</u> Mich.	6.50 ± 0.45	24.33 ± 2.38	28.60 ± 0.77	75.67
<u>Zannichellia palustris</u> L.	12.86 ± 0.16	10.60 ± 0.37	34.83 ± 0.58	89.40
<u>Utricularia subulata</u> L.	13.47 ± 0.16	19.92 ± 0.17	29.69 ± 0.79	80.08
Mean (Angiosperms)	11.5	17.2	31.7	82.8
Mean (All species)	13.3	19.1	31.0	81.0

* Mean ± standard deviation calculations for dry weight, ash, and carbon are based on three, four, and five samples, respectively.

** Dry weight - Ash = Organic weight.

TABLE VII
 PERCENTAGES OF DRY WEIGHT, ASH WEIGHT, ORGANIC CARBON AND
 ORGANIC MATTER FROM MEAN STANDING CROP (g/m²) OF
 SUBMERSED AQUATIC PLANTS IN THE STUDY AREA

Date	Dry Weight (Per Cent of Fresh Weight)	Ash Weight (Per Cent of Dry Weight)	Organic Carbon (Per Cent of Dry Weight)	Organic Weight (Per Cent of Dry Weight)
1964				
27 Mar	11.5	17.7	30.8	82.0
2 May	10.3	16.3	31.5	83.6
28 May	12.3	16.6	32.0	83.4
27 June	14.8	19.4	30.6	80.6
25 July	13.2	16.4	31.9	83.3
15 Aug	13.1	15.8	32.4	84.2
22 Sept	11.0	16.1	31.9	83.9
24 Oct	11.9	18.0	31.2	82.0
21 Nov	11.4	16.6	32.1	83.5
1965				
1 Jan	10.7	16.2	32.4	83.9
21 Feb	11.7	15.3	32.8	84.8
Annual mean	11.9	16.7	31.8	83.2

TABLE VIII
ANNUAL PLOT AND BED-TYPE STANDING CROP MEANS (g/m^2) WITH VARIANCES FOR THE STUDY AREA

Bed Type	Silt-Pebble			Gravel			Mud						Mud-Gravel		
Plot Number	1	2	3	4	5	11	6	7	8	9	10	13	14	15	12
	Dry Weight														
Plot mean	236	464	363	53	54	21	277	361	579	349	329	281	372	290	174
Bed-type mean		354			43					355					174
Variance		79,005			8,820					71,065					51,662
	Organic Weight														
Plot mean	191	402	308	43	44	17	228	302	506	296	275	237	290	222	148
Bed-type mean		301			35					295					148
Variance		63,467			5,794					51,159					37,229
	Carbon Weight														
Plot mean	74	155	118	17	17	7	85	116	198	115	106	91	111	84	57
Bed-type mean		116			13					113					57
Variance		9,951			884					7,594					5,575

Analysis of variance (factorial arrangement) of dry weight, organic weight and organic carbon was determined for the different stream bed types testing the null hypothesis that the means of plots, months, samples, and plots by months were equal (0.01 level). No significant difference was found among sample means within plots. A significant difference was found with time for the mud and the silt-pebble beds, which was due to continuous macrophytic growth and increase in number of species. Plants growing in gravel and mud-gravel transition beds had shorter shoots than plants growing in the other bed types. No significant plots by months interaction was shown for any bed type. This indicates similar growth trends among plots within each bed type during the months.

A significant difference was found among plots within beds. Duncan's multiple range test was used to compare annual plot means of biomass within bed types (0.01 level). Significant differences which were found might be associated with stream velocity. Among mud plots, Plot 8 had a significantly greater biomass than other plots. Mean velocity of 0.07 m/sec in Plot 8 was lower than in any other plot in the study area. Among gravel plots, Plot 11 had the highest velocity, 0.30 m/sec, and significantly less biomass than Plots 4 and 5. Among the silt-pebble plots, Plot 1 had the highest velocity, 0.18 m/sec, and less biomass than Plots 2 and 3.

In most rivers, submersed macrophytes demonstrate a seasonal partial or complete die-off leaving only underground organs. If the biomass is negligible at the beginning of the season, cumulative net production of macrophytes, assuming no losses, can be estimated by sampling the seasonal maximum biomass (Westlake, 1965). This method of

measurement seems not to be applicable to the present study since growth was nearly continuous, and there was undoubtedly considerable export of broken and partially decayed plants. Following dredging in March, 1964, macrophytic growth exhibited certain aspects of a hypothetical growth curve (Fig. 4). A lag phase occurred from March through May, 1964, followed by a period of accelerated growth which resulted in a July maximum. A decline in biomass occurred in August, and then biomass increased throughout the remainder of the study period at a lower rate. This lower rate could be attributed to increased density due to biomass accrual and the increase in number of species.

The July maximum of dry weight in this study was similar to the seasonal peak standing crop for several other rivers (Table IX). The decline in biomass in August may correspond to the pattern of plant death and decay following seasonal maximum growth typical in other rivers. Many authors have assumed that maximum biomass occurs at about the time of flowering. In San Marcos River, flowering was prevalent during July, 1964, but continued to a lesser degree throughout the study period.

The 638 g/m^2 of dry weight of macrophytes which accumulated during the 361 days was greater than that reported for most other rivers (Table IX), but it was similar to the Sagittaria weight reported for Silver Springs, Florida (Odum, 1957). Obviously, the greater biomass in these two spring-fed rivers was due to the longer growing season permitted by the constant chemical, hydrological and thermal conditions. The mean net gain of cumulative standing crop (organic) for 361 days of growth was 1.2 g/m^2 day. This estimate does not include grazing, mortality, roots and downstream export.

TABLE IX
 MAXIMUM STANDING CROPS OF SUBMERSED MACROPHYTES IN RIVERS

River	Reference	Dry Weight (g/m ²)
River Ivel, England	(Edwards and Owens, 1960)	520
River Ivel, England	(Owens and Edwards, 1962)	320
Test, England		385
Yare, England		381
Chess, England		322
Maple Lodge Channel, England	(Westlake, 1961)	123*
Silver Springs, Florida	(Odum, 1957)	621
Three spring-river systems, Florida	(Natlson, 1955; from Penfound, 1956)	526 412 424
San Marcos River, Texas	(Present study)	638

* Polluted

Species Diversity

Species diversity in the ecological community is a measure of the distribution of organisms into species. Numerous diversity indices have been proposed which utilize numbers of species and individuals. Biomass units have been found preferable to numbers for populations with differences in weight among species and were used in this study (Wilhm, 1967). Species diversity (\bar{H}) was calculated from the pooled biomass of each species for all 15 plots for each monthly collection by the equation of Patten (1962).

Diversity varied between 1.99 and 2.81 (Fig. 5). In general, diversity increased sharply in the immature community to a maximum in June, 1964. The June maximum was due to a relatively even distribution of weight among species. After June, 1964, diversity generally decreased throughout the remainder of the study period. This was the result of the continuous increase in weight of a few species. Species added to the community after June, 1964, contributed relatively little weight to the total biomass. These findings are in accord with Odum's (1963) model for ecological succession of autotrophs, that is, species diversity increases initially in the immature community, then becomes stabilized or declines in the more mature community.

Community Metabolism and Light Intensity

The magnitude of primary productivity varied with light intensity as observed from successive clear and cloudy day measurements made intermittently during the study (Table X). In May, the cloudy day was 52% as productive as the clear day, whereas in December, the cloudy day was 80% as productive as the clear day. Light intensity was

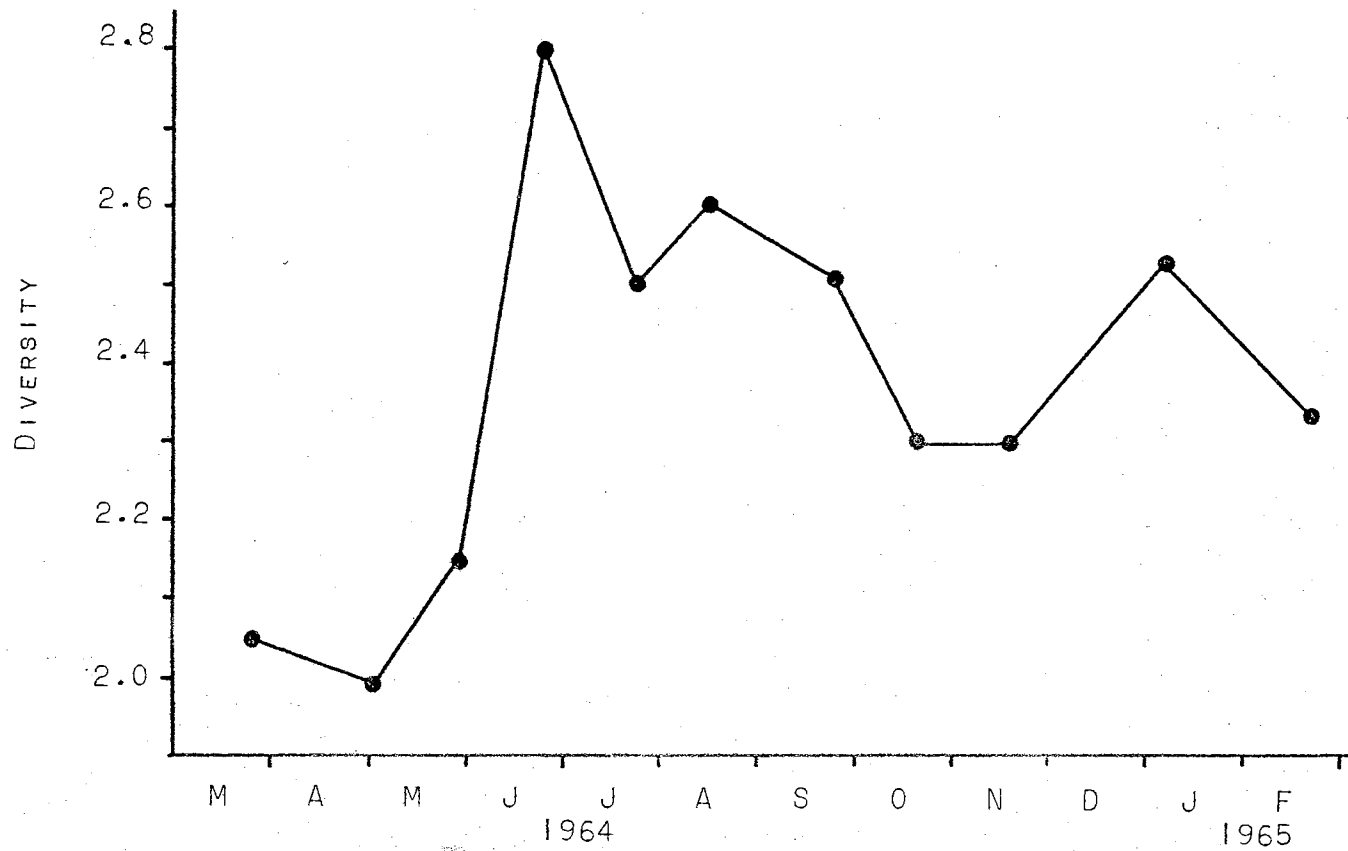


Fig. 5. Species Diversity of Macrophytes.

TABLE X
 GROSS PHOTOSYNTHESIS, RESPIRATION AND LIGHT INTENSITY
 ON SUCCESSIVE DAYS

Date	Gross Photosynthesis (g O ₂ /m ² day)	Community Respiration (g O ₂ /m ² day)	Light Intensity Langleys/day
1964			
29 May	15.9	12.9	576
30 May	8.4	12.8	312
16 July	25.9	17.3	647
17 July	27.4	19.9	586
18 July	21.2	19.7	516
19 July	16.6	19.4	337
15 Aug	21.5	19.2	459
16 Aug	21.9	19.6	450
19 Dec	13.7	12.1	156
20 Dec	17.1	13.3	344

limiting during three consecutive days, 17-19 July. With total solar input of 586 langleys, gross photosynthesis was $27.4 \text{ g O}_2/\text{m}^2$ day, but at 337 langleys, it was only $16.6 \text{ g O}_2/\text{m}^2$ day. Inhibition by high intensity of 647 langleys on 16 July caused a reduced photosynthetic productivity at $25.9 \text{ g O}_2/\text{m}^2$ day. Limiting and inhibitory effects of light on photosynthesis have been shown extensively for algal communities in lentic waters (Ryther, 1956, Talling, 1961, Copeland and Dorris, 1964). However, few studies report inhibition of primary productivity in macrophytes in natural waters. Copeland and Gloyna (1965) have considered the possibility of light saturation in a flume ecosystem containing macrophytes and algae, and Felfoldy (1960) has shown inhibition in Potamogeton perfoliatus in a lake.

Light intensity had no obvious effect on community respiration under limiting intensities, but it appeared to influence respiration under inhibitory conditions. Respiration remained relatively constant between 19.4 and $19.9 \text{ g O}_2/\text{m}^2$ day (16-19 July) with light intensity limiting photosynthesis. High light intensity of 647 langleys which inhibited photosynthesis on 16 July was accompanied by reduced community respiration at $17.3 \text{ g O}_2/\text{m}^2$ day. By contrast, Odum and Wilson (1962) found a close correspondence between primary productivity and community respiration in grass beds of Redfish Bay, Texas, for successive clear and cloudy days. Laboratory studies indicate that photosynthetic activity has a regulatory effect on cellular respiration (Forti, 1965), and differences in temperature and oxygen concentration have been shown to influence the rates of oxygen consumption by aquatic plants (Owens and Maris, 1964; Phinney and McIntire, 1965). Considerable difference in temperature and oxygen regimes existed between the San Marcos River

and Redfish Bay. Possibly, under the constant temperature conditions prevailing in the San Marcos River, respiration rate was not affected by oxygen concentration and noninhibitory light intensity.

Efficiency, Structure and Ecosystem Maturity

In determining efficiency of conversion of solar energy to protoplasm, it was assumed that 3,500 cal of solar radiation are required to produce one gram of oxygen (Kraus, 1956). The amount of solar input used in photosynthesis is uncertainly known. Values used in calculating efficiency range from 42.6 to 100%. Copeland and Gloyna (1965) determined that an average 63.4% of total solar input was available for photosynthesis in the arid southwest. This value was used in calculating efficiency in the present study.

Daily photosynthetic efficiency ranged from 0.2 to 4.8% (Fig. 6). Similar efficiencies were reported in Silver Springs, Florida, 5.3% (Odum, 1957); in Ivel River, England, 2.04-4.0% (Edwards and Owens, 1962); in Blue River, Oklahoma, 0.2-5.4% (Duffer and Dorris, 1966); and in a flume, 0.3-4.8% (Copeland and Gloyna, 1965).

Efficiency was plotted for four different ranges of light intensity (Fig. 6). Efficiency was low one week after dredging and increased as the ecosystem matured to a maximum between July and September, 1964. A slight decrease occurred during the later stages of succession through the fall and winter months.

In general, an inverse relationship existed between photosynthetic efficiency and light intensity. Similar results have been reported by Odum and Hoskin (1958). Efficiency tended to parallel the general trend of primary productivity (Figs. 6 and 7). Copeland (1963), Butler (1964)

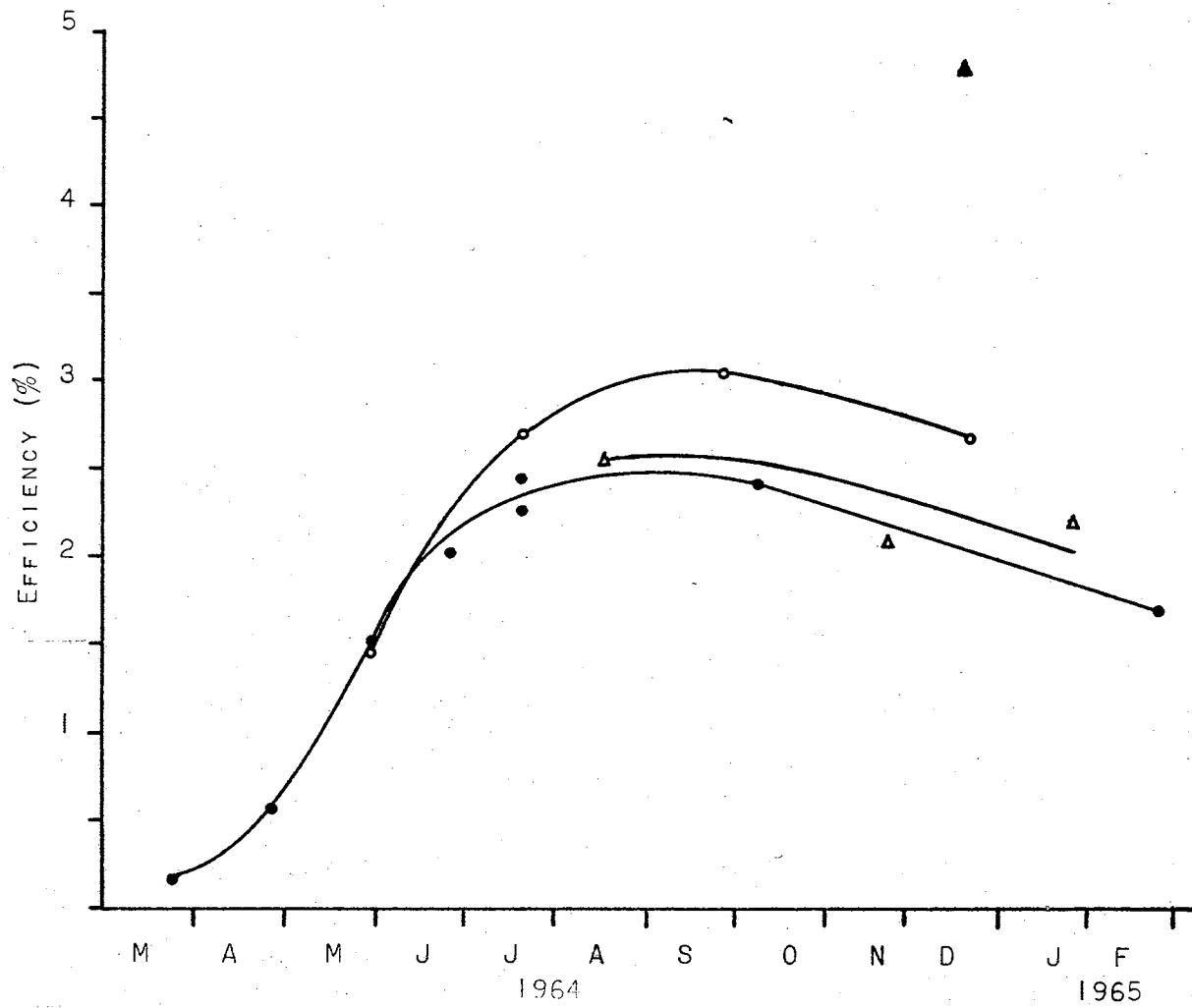


Fig. 6. Photosynthetic Efficiency. Langleys: 100-200 = (▲), 301-400 = (○), 401-500 = (△), 501-600 = (●).

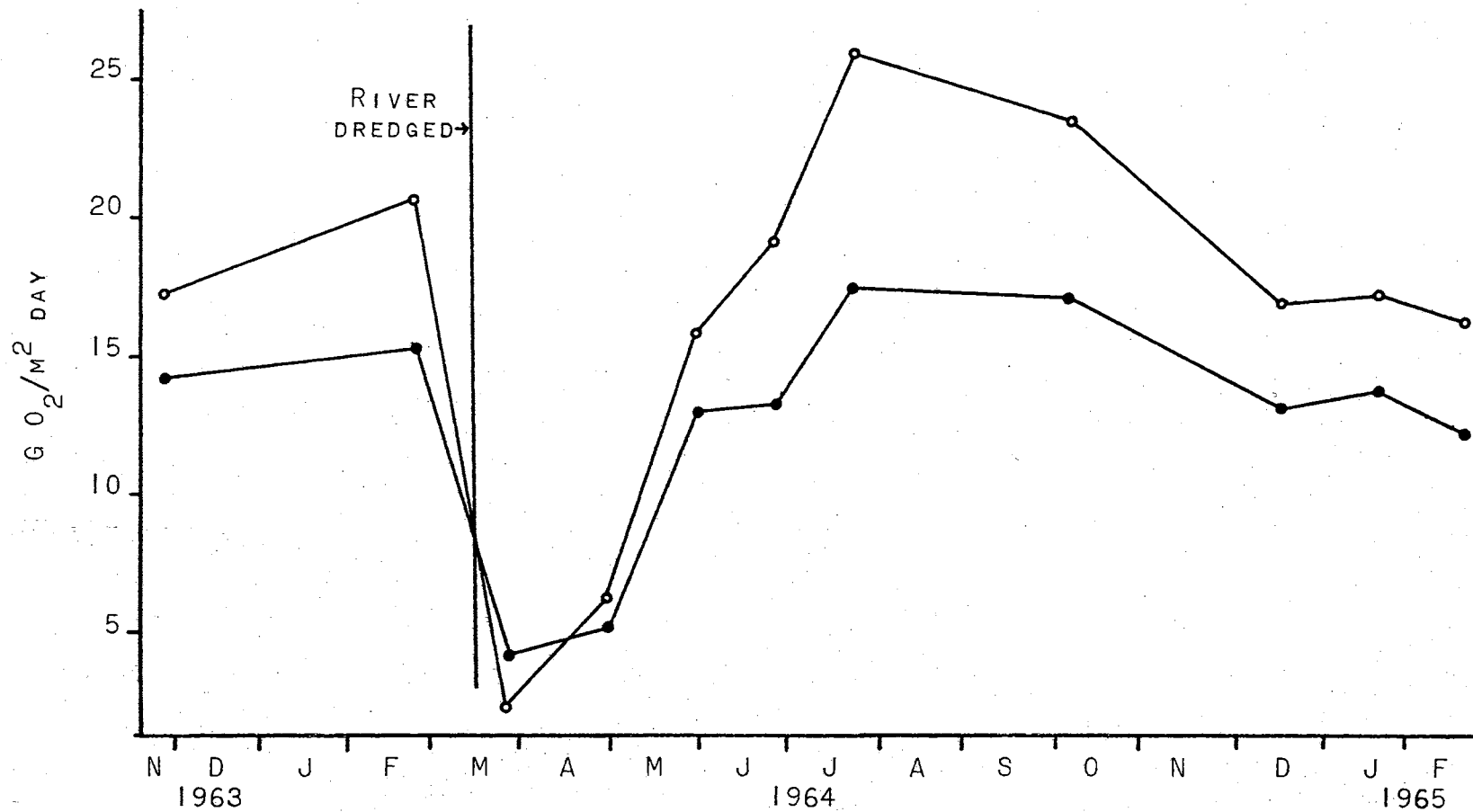


Fig. 7. Community Metabolism Under Clear Skies. Gross Photosynthesis = (\circ), Community Respiration = (\bullet).

and Duffer and Dorris (1966) also reported that the magnitude of community efficiency, based on daily total solar radiation, was directly related to the magnitude of productivity.

Macrophytes increased from nine species in March, 1964, to 18 in September, 1964, while dry weight increased from 3.3 g/m^2 to 287 g/m^2 . The increase in number of species and quantity of macrophytes as the community developed enhanced community efficiency to what may have been an optimum level. Biomass increased from about 300 g/m^2 during the summer months to about 600 g/m^2 in February, 1965, but efficiency decreased slightly. Efficiency did not parallel biomass beyond an optimum level since the complexity of the ecosystem did not change after the summer months and photosynthesis was restricted by shading.

Community Metabolism, Structure and Ecosystem Maturity

Primary productivity and community respiration were plotted for days with clear skies (Fig. 7). Gross photosynthesis decreased to a minimum $2.5 \text{ g O}_2/\text{m}^2$ day as a result of dredging in March, 1964, and increased rapidly in the immature ecosystem to a maximum in July, 1964, at $25.9 \text{ g O}_2/\text{m}^2$ day. After July primary productivity decreased progressively to $17 \text{ g O}_2/\text{m}^2$ day in December and was relatively stable throughout the winter. Respiration followed a similar trend as photosynthesis but at a lower magnitude. Community respiration increased from $4.1 \text{ g O}_2/\text{m}^2$ day after dredging to $17.3 \text{ g O}_2/\text{m}^2$ day in July, 1964, and then decreased to $13 \text{ g O}_2/\text{m}^2$ day in December, 1964, and was relatively stable during the winter. Similar ranges of community metabolism have been reported in other studies (Table XI).

TABLE XI
METABOLISM OF LOTIC WATERS CALCULATED FROM DIURNAL OXYGEN CURVES

Source	Reference	Gross Photosynthesis g O ₂ /m ² day	Community Respiration g O ₂ /m ² day	P/R
Itchen River, England	Butcher (1930)*	0.4-14	4.2-20.2	0.1-1.1
Ivel River, England	Edwards and Owens (1962)	3.2-17.6	6.7-15.4	1.13
Silver Springs, Florida	Odum (1956)			
Spring		35.0	5.0**	7.0
Winter		8.0	2.8**	2.9
Headwaters area	Odum (1957)	18.6	17.6	1.06
Neuse River, North Carolina	Hoskins (1959)	0.3-9.8	0.7-21.5	-
Blue River, Oklahoma	Duffer and Dorris (1966)			
Limestone bed		6.8	11.0	0.64
Granite bed		21.3	12.6	1.70
Sand bed		3.0	7.7	0.39
San Marcos River, Texas	Present study	2.5-27.4	4.1-19.9	0.59-1.50

* Calculated by Odum (1956)

** From bell jars

Dry weight of macrophytes had increased to 287 g/m^2 at the time of maximum primary productivity in July. Macrophyte accrual and an increased number of species increased the capacity of the plant community for photosynthesis. Surface area for Aufwuchs algae attachment enhances productivity in lotic waters (Odum, 1957; Duffer and Dorris, 1966). Edwards and Owens (1965) have found the relation of plant surface to dry weight for four species of aquatic macrophytes to be 1 mg DW of plant equivalent to 1 cm^2 of plant surface. If it is assumed that the ratio $1 \text{ cm}^2:1 \text{ mg DW}$ applies to submersed macrophytes in general, the ratio of plant surface to that of river bed was 29:1 at maximum productivity. This may be an approximation to the optimum ratio for maximum utilization of solar energy by the macrophyte-Aufwuchs complex. Beyond this point, photosynthesis may be restricted through enhanced mutual shading. Although biomass generally increased during the fall and winter months, productivity decreased from the July maximum to a winter minimum. The decrease in productivity can be attributed to decrease in solar influx with season (Odum, 1957) and morphological changes of the plants during growth (Wetzel, 1964). Growth of the macrophytes occurred from small rooted area as elongation of shoots extending downstream. Plant shoots extended six-tenths of the way to the water's surface in October, 1964. By January, 1965, Potamogeton illinoensis had reached the water's surface in isolated patches. Death and decay of shoot tips was evident and could account for decrease in primary productivity during January and February, 1965.

The ratio of primary productivity to respiration (P:R ratio) has been used to classify communities (Odum, 1956). When photosynthesis exceeds respiration (P:R ratio greater than one) the community is

autotrophic, and when photosynthesis is less than respiration (P:R ratio less than one) the community is heterotrophic. The nature of community metabolism as indicated by the P:R ratio may also serve as an indicator of the degree of stability (Odum, 1959). The P:R ratio ranged from 0.59 to 1.50 with a mean 1.17 (Fig. 8). Similar ranges have been found in other studies (Table XI).

In the immature community, fluctuation in light intensity had more effect on community metabolism than in the more mature community. Respiration exceeded photosynthesis even with high energy input of 600 langley immediately after the river was dredged free of plants in March, 1964. Respiration exceeded photosynthesis in the immature community under a light intensity of 312 langley in May, 1964, whereas photosynthesis was greater than respiration on the following day under a light intensity of 576 langley. A similar fluctuation was found on successive days in July. As the community continued to mature, fluctuations in metabolism, as indicated by the P:R ratio, were less pronounced. Photosynthesis exceeded respiration in November and December even though light intensity was lower (363, 156 langley) than the intensity which had caused respiration to exceed photosynthesis in the immature community. It is evident that fluctuation in community metabolism in the immature community was due to differences in light intensity acting on low biomass and few species. As succession developed in the ecosystem by an increase in species and biomass, homeostasis increased until only autotrophic conditions existed even under low light intensity. This exemplifies Margalef's (1963) ecological principle, "The relative amount of energy necessary for maintaining an ecosystem

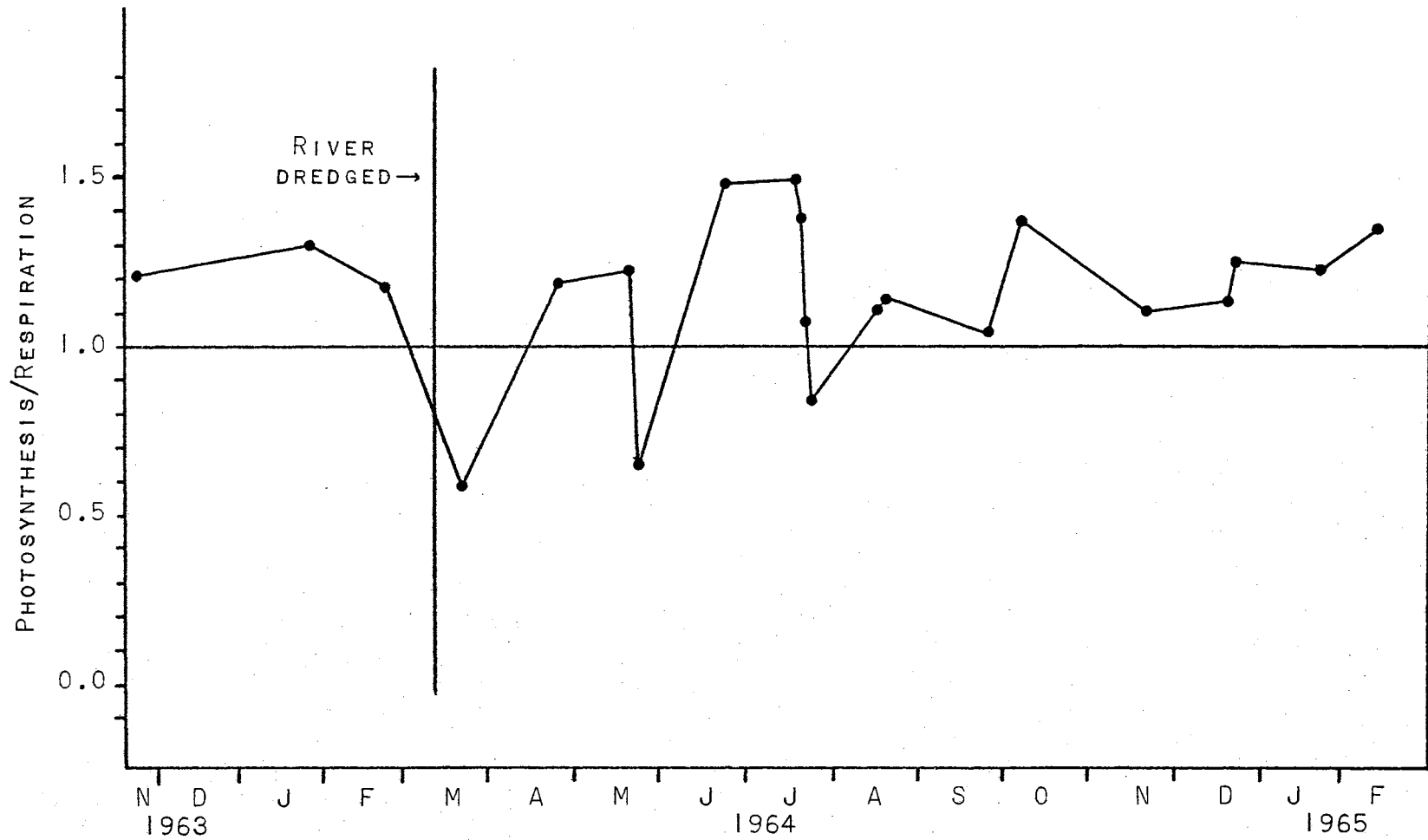


Fig. 8. Photosynthesis/Respiration Ratios of Community Metabolism.

is related to the degree of structure or organization of this ecosystem. Less energy is necessary for a more mature complex."

Photosynthesis exceeded respiration in Blue River, Oklahoma, even with low energy input (Duffer and Dorris, 1966). A complex bryophyte-algal community was present, whereas adjacent reaches with limestone and sand beds lacked macrophytes and respiration always exceeded photosynthesis. A macrophyte-Aufwuchs complex existed in Silver Springs, Florida, and autotrophic conditions prevailed (Odum, 1957).

It has been shown in aquatic laboratory microecosystems (Beyers, 1963b) and coral reef communities (Odum and Odum, 1955) that with time an ecosystem stabilizes and the P:R ratio approaches one. Autotrophic succession occurred in the study area. It is assumed that photosynthesis would equal respiration if the macrophytes were permitted to grow undisturbed year after year or that photosynthesis would exceed respiration with export as occurs in Silver Springs, Florida (Odum, 1957).

CHAPTER V

SUMMARY

1. A study of physicochemical conditions, community metabolism and community structure was conducted in a 567-m stretch of the spring-fed San Marcos River, San Marcos, Texas, during a period of reestablishment of plants following a dredging operation. Mean width and depth of the study area were 27.1 and 1.0 m, respectively. Velocity was a constant 0.24 m/sec. Mean discharge was $4.84 \text{ m}^3/\text{sec}$.

2. Fifteen species of submersed angiosperms, two bryophytes and one filamentous alga constituted the macrophyte biomass. Diatoms and desmids were part of the macrophyte-Aufwuchs complex. Seven dominant genera of benthic algae occurred.

3. Conversion factors for fresh weight, dry weight, ash weight, organic weight and organic carbon were determined for each species of macrophyte. Converted weights of each species for monthly samples were summed and means for the study area plotted. In general, standing crop increased throughout the study period to $541 \text{ g organic matter/m}^2$, which represents a mean net gain of cumulative standing crop of $1.2 \text{ g/m}^2 \text{ day}$. Differences between the annual standing crop means of dry weight, organic weight and organic carbon for mud and silt-pebble beds were found not to be significant (0.01 level), whereas differences between all other comparisons of bed types were found to be significant. No significant difference (0.01 level) was found among sample means within

plots. A significant difference for dry weight, organic weight and organic carbon was found with time for the mud and silt-pebble beds, which was due to continuous macrophytic growth and increase in number of species. Significant difference (0.01 level) found among plots within beds might be associated with stream velocity.

4. Chlorophyll a concentration of benthic algae on gravel beds was not correlated with primary productivity, and seasonal changes were not apparent. Chlorophyll a was sparse on other bed types.

5. Species diversity varied between 1.99 and 2.81. In general, diversity increased sharply in the immature community to a maximum in June, 1964. After June, 1964, diversity generally decreased throughout the remainder of the study period.

6. Light intensity exhibited both limiting and inhibitory effect on gross photosynthesis. Light had no obvious effect on community respiration under limiting intensities; however, it appeared to reduce respiration under inhibitory conditions.

7. Daily photosynthetic efficiency ranged from 0.2 to 4.8%. Efficiency reached a maximum between July and September, 1964, as the ecosystem matured. A slight reduction occurred during the fall and winter months. An inverse relationship existed between photosynthetic efficiency and light intensity. Efficiency tended to parallel the general trend of primary productivity.

8. Gross photosynthesis decreased to a minimum $2.5 \text{ g O}_2/\text{m}^2 \text{ day}$ as a result of dredging in March, 1964, and increased rapidly in the immature community to a maximum in July, 1964, at $27 \text{ g O}_2/\text{m}^2 \text{ day}$. After July, 1964, primary productivity decreased progressively to $17 \text{ g O}_2/\text{m}^2 \text{ day}$ in December and was relatively stable throughout the winter.

Respiration followed photosynthesis but at a lower magnitude. Community respiration increased from $4.1 \text{ g O}_2/\text{m}^2$ day in March, 1964, to about $20 \text{ g O}_2/\text{m}^2$ day in July, 1964, and then decreased to $13 \text{ g O}_2/\text{m}^2$ day in December, 1964, and remained relatively stable during the winter.

9. Carbon dioxide and oxygen rate-of-change curves were not symmetrical.

10. The ratio of plant surface area to stream bed was 29:1 at maximum productivity. This may be an approximation to the optimum ratio for maximum utilization of solar energy by the macrophyte-Aufwuchs complex. Beyond this point photosynthesis may be restricted by shading.

11. The P:R ratio ranged from 0.59 to 1.50 with a mean of 1.17. In the immature community, metabolism was heavily dependent on environmental conditions, and P:R fluctuated with variations in light intensity. This fluctuation was the result of solar intensity acting on low biomass and few species. As the ecosystem matured with an increase in species and biomass, homeostasis increased until only autotrophic conditions existed even under low light intensity.

LITERATURE CITED

- American Public Health Association. 1960. Standard methods for the examination of water and waste water. A.P.H.A. 11th Ed. 626 p.
- Butler, J. L. 1964. Interaction of effects by environmental factors on primary productivity in ponds and microecosystems. Ph.D. Thesis, Okla. State Univ. 110 p.
- Byers, R. J. 1963a. Directions for the determination of changes in carbon dioxide concentration from changes in pH. Publ. Inst. Mar. Sci., Texas, 9: 454-489.
- _____. 1963b. The metabolism of twelve aquatic laboratory microecosystems. Ecol. Monogr., 33: 281-306.
- Churchill, M. A. 1962. The prediction of stream reaeration rates. Tenn. Valley Author., Chattanooga, Tenn. 98 p.
- Cochran, W. G. and G. M. Cox. 1962. Experimental Design. 2nd. Ed. J. Wiley and Sons, Inc. 538 p.
- Copeland, B. J. 1963. Oxygen relations in oil refinery effluent holding ponds. Ph.D. Thesis, Okla. State Univ. 110 p.
- _____ and T. C. Dorris. 1964. Community metabolism in ecosystem receiving oil refinery effluents. Limnol. and Oceanog., 9: 431-447.
- _____ and E. F. Gloyna. 1956. Radioactivity transport in water - Structure and metabolism of a lotic community. Technical Report 8, The Univ. of Texas. 51 p.
- Cushing, C. E. 1964. Plankton and water chemistry in the Montreal River lake-stream system, Saskatchewan. Ecology, 45: 306-313.
- Duffer, W. R. and T. C. Dorris. 1966. Productivity in a great plains stream. Limnol. and Oceanog., 11: 143-151.
- Edwards, R. W. and M. Owens. 1960. The effects of plants on river conditions. I. Summer crops and estimates of net productivity of macrophytes in a chalk stream. J. Ecol., 48: 151-180.
- _____ and _____. 1962. The effects of plants on river conditions. IV. The oxygen balance of a chalk stream. J. Ecol., 50: 207-220.

- Edwards, R. W. and M. Owens. 1965. The oxygen balance of streams. Fifth Sympos. of the Brit. Ecol. Soc., 149-172.
- Felföldy, L. J. M. 1960. Apparent photosynthesis of Potamogeton perfoliatus in different depths of Lake Balaton. Ann. Biol. Tihany, 27: 201-208.
- Forti, G. 1965. Light utilization in photosynthesis, pp. 19-35. In C. R. Goldman (ed.) Primary productivity in aquatic environments. Mem. Ist. Ital. Idrobiol., 18 Suppl., University of Cal. Press, Berkeley.
- Gorski, F. C. 1929. Recherches sur les methodes de mesure de photosynthese chez les plantes aquatiques submergees. Acta Soc. Bot. Poloniae, 6: 1-29.
- Holmes, R. W., M. B. Schaffer and B. M. Shimada. 1957. Primary production, chlorophyll and zooplankton volumes in the tropical eastern Pacific Ocean. Bull. Inter-Am. Trop. Tuna Comm., 11: 129-169.
- Kraus, R. W. 1956. Photosynthesis in the algae. Ind. and Eng. Chem., 48: 1449-1458.
- Margalef, R. 1963. On certain unifying principles in ecology. Amer. Nat., 97: 357-374.
- Moore, E. W. 1939. Graphic determination of carbon dioxide and the three forms of alkalinity. Amer. Wat. Works Assoc. J., 31: 51-66.
- Natelson, D. 1955. Standing crops and community survey of submerged vegetation in seven springs. In W. T. Penfound, 1956, Primary productivity of vascular plants. Limnol. and Oceanog., 1: 92-101.
- Odum, E. P. 1959. Fundamentals of Ecology. 2nd. Ed. W. B. Saunders Co., Philadelphia. 546 p.
- _____. 1963. Ecology. Holt, Rinehart and Winston, New York. 152 p.
- Odum, H. T. 1956. Primary productivity in flowing waters. Limnol. and Oceanog., 1: 102-117.
- _____. 1957. Trophic structure and productivity of Silver Springs, Florida. Ecol. Monogr., 27: 55-112.
- _____ and C. M. Hoskin. 1958. Comparative studies on the metabolism of marine waters. Publ. Inst. Mar. Sci., Texas, 5: 16-46.
- _____ and E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr., 25: 291-320.

- Odum, H. T. and Wilson. 1962. Further studies on reoeration and metabolism of Texas bays. Publ. Inst. Mar. Sci., Texas, 8: 23-55.
- Owens, M. and R. W. Edwards. 1961. The effects of plants on river conditions. II. Further crop studies and estimates of net productivity of macrophytes in a chalk stream. J. Ecol., 49: 119-126.
- _____ and _____. 1962. The effects of plants on river conditions. III. Crop studies and estimates of net productivity of macrophytes in four streams in southern England. J. Ecol., 50: 157-162.
- _____ and _____. 1963. Some oxygen studies in the River Lark. Proc. Soc. Wat. Treatm. and Exam., 12: 126-144.
- _____ and P. J. Maris. 1964. Some factors affecting the respiration of some aquatic plants. Hydrobiologia, 23: 533-543.
- Patten, B. C. 1962. Species Diversity in net phytoplankton of Raritan Bay. J. Mar. Res., 20: 57-75.
- Phinney, H. K. and C. D. McIntire. 1965. Effect of temperature on metabolism of periphyton communities developed in laboratory streams. Limnol. and Oceanog., 10: 341-344.
- Rainwater, F. H. and L. L. Thacher. 1960. Methods for collection and analysis of water samples. U.S. Government Printing Office, Washington, D.C. 201 p.
- Richards, F. A. and T. G. Thompson. 1952. The estimation and characterization of plankton populations by pigment analyses. J. Mar. Res., 2: 156-172.
- Ruttner, F. 1953. Fundamentals of ecology. 3rd. Ed. Univ. of Toronto. 295 p.
- Ryther, J. H. 1956. Photosynthesis in the ocean as a function of light. Limnol. and Oceanog., 1: 61-70.
- Scholander, P. F. 1942. Analyzer for quick estimation of respiratory gases. J. Biol. Chem., 146: 159-162.
- Scott, W. W. 1947. Standard methods of chemical analysis. 5th Ed. D. Van Norstrand Co., Inc., New York. 648 p.
- Steeman, Nielsen E. 1946. Carbon sources in the photosynthesis of aquatic plants. Nature, 158: 594-596.
- _____. 1952a. Experimental carbon dioxide curves in photosynthesis. Physiol. Plant., 5: 145-159.
- _____. 1952b. On detrimental effects of high light intensities on the photosynthetic mechanism. Physiol. Plant., 5: 334-344.

- Talling, J. F. 1961. Photosynthesis under natural conditions. *Ann. Rev. of Plant Physiol.*, 12: 133-154.
- U. S. Geological Survey. 1959. Unpublished analytical statement of chemical conditions of Guadalupe River Basin. Austin, Texas. n.p.
- _____. 1963. Unpublished analytical statement of chemical conditions of Guadalupe River Basin. Austin, Texas. n.p.
- U. S. Weather Bureau. 1964. Climatological data. National Summary. Asheville, North Carolina. n.p.
- Waters, T. F. 1961. Notes on the chlorophyll method of estimating the photosynthetic capacity of stream periphyton. *Limnol. and Oceanog.*, 486-488.
- Westlake, D. F. 1961. Aquatic macrophytes and the oxygen balance of running water. *Verh. Internatl. Verein. Limnol.*, 15: 499-504.
- _____. 1965. Some basic data for investigations of the productivity of aquatic macrophytes, pp. 229-248. In C. R. Goldman (ed.) *Primary productivity in aquatic environments. Mem. Ist. Ital. Idrobiol.*, 18 Suppl., University of California Press, Berkeley.
- Wetzel, R. G. 1964. A comparative study of the primary productivity of higher aquatic plants, periphyton and phytoplankton in a large, shallow lake. *Int. Revue ges. Hydrobiol.*, 49: 1-61.
- _____. 1965. Techniques and problems of primary productivity measurements in higher aquatic plants and periphyton, pp. 249-267. In C. R. Goldman (ed.) *Primary productivity in aquatic environments. Mem. Ist. Ital. Idrobiol.*, 18 Suppl., University of California Press, Berkeley.
- Wilhm, J. L. 1967. Biomass units in Shannon's Formula. In manuscript. *Ecology*.

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