PRIMARY PRODUCTION, ENERGETICS, AND NUTRIENT UTILIZATION IN A WARM-WATER STREAM

Thesis for the Degree of Ph. D.

MICHIGAN STATE UNIVERSITY

Alfred Richard Grzenda

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This is to certify that the

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PRIMARY PRODUCTION, ENERGETICS, AND NUTRIENT UTILIZATION IN A WARM-WATER STREAM

presented by

Alfred Richard Grzenda

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Ph. D **degree in** Fisheries and Wildlife

Robert C. Ball
Robert C. Ball **Major professor**

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PRIMARY PRODUCTION, ENERGETICS, AND NUTRIENT UTILIZATION IN A WARM-WATER STREAM

by

ALFRED RICHARD GRZENDA

AN ABSTRACT

Submitted to the School for Advanced Graduate Studies of

Michigan State University of Agriculture and

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1960

Approved Robert C Ball

Alfred Richard Grzenda

Primary production, energetics, and nutrient fixation were investigated in a warm-water stream located in the south central portion of the Lower Pennisula of Michigan.

Gravimetric net production estimates were made from periphyton harvested from plexiglass substrata which had been submerged in the stream. Colorimetric productivity measurements were made by relating the absorbancy of phytopigments extracted from the periphyton colony to the ash-free dry weight of the colony. Good agreement was noted between the two methods. Diurnal oxygen curves were found to be unsuitable for year-round productivity measurements. Seasonal production maxima were observed in late spring, early summer, and late fall. The seasonal range in net primary production as measured by artificial substrata is 0.01 to 2.28 g m^{-2} day^{-1} with an annual mean of 0.56 g m^{-2} day^{-1}. The annual mean rate of gross production is estimated to be about 1 g m^{-2} day^{-1}.

A model describing primary energetics was synthesized from observed data and literature values. Photosynthetic efficiencies based on net production and surface radiation varied from 0.003 to 0.245% with an annual mean of 0.07%. The annual mean efficiency based on gross production and surface energy was estimated to be 0.1%.

The annual phosphorus import into the study area was 16 metric tons. During three flood periods collectively representing a time lapse of 30 days about 45% of the annual import was carried into the study area. The total inorganic nitrogen import for a nine month period was 84 metric tons. The effect of floods on the seasonal distribution of inorganic nitrogen was less pronounced than in the case of phosphorus. The data indicate

that sanitary drains are the major source of phosphorus and surface run-off the major source of inorganic nitrogen.

The phosphorus content of periphyton varied considerably throughout the year. In general, the slowest growing colonies had the highest phosphorus content. The ratio of phosphorus content to weight of the periphyton colony (x 1,000) varied from 1.54 to 33.63. During periods of maximal periphyton production the ratio of phosphorus to nitrogen within colony was approximately 1.

Seasonal phosphorus utilization efficiency quotients based on soluble phosphorus import and calculated for a 100 meter length of stream varied from 0.0007 to 0.61% depending upon the growth rate of the periphyton. The lowest efficiencies were observed during the mid-winter production minima. Similar quotients computed for inorganic nitrogen ranged from 0.03 to 0.19%.

The ratio of phytopigment absorbancy to periphyton colony weight can be used to differentiate between oligosaprobic and mesosaprobic communities. Such ratios obtained from a clean-water zone vary from 10.0 to 16.9. Similar values obtained from a polluted zone vary from 1.8 to 2.9. Ratios based on the phosphorus content of the colony are less reliable indices of pollution and appear to be limited to pollution detection rather than evaluation.

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I wish to thank Drs. Gordon Guyer, Gerald W. Prescott, and Peter I. Tack for the time they spent serving as members of my guidance committee. I am also grateful to Dr. Morris L. Brehmer and Mr. David L. Correll for their advice and assistance in conducting laboratory analyses.

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INTRODUCTION

In the study of community dynamics it is necessary to differentiate between the transfer of energy and the transfer or circulation of material. According to the Second Law of Thermodynamics spontaneous energy transfer (exothermic reactions) is always characterized by an enthalpy change accompanied by an increase in entropy. Qualitatively, an enthalpy change may be defined as the energy absorbed during a transfer process, and entropy as the unavailable energy in a thermodynamic system. Therefore, as the entropy of a system increases its capacity for spontaneous transfer is diminished. The number of spontaneous transfers possible within a system depends upon the entropy increase incurred at each successive transfer. When applying this law of thermodynamics to energy-flow models based on trophic structure, enthalpy change corresponds to the amount of energy transfered to trophic level n from trophic level n-1. Similarly, the entropy change corresponds to the energy changed to heat by the respiration of trophic level n.

In constrast to energy-flow, basic materials such as carbon, phosphorus, and nitrogen may undergo an infinite number of transformations and are freely recirculated among all trophic levels until lost by export or entombed by sedimentation. Even under such circumstances it is possible for the same material to re-enter the bio-dynamic cycle by import or changes in the redox potential of the postdepositional environment. Flowing waters appear to be the simplest expression of material circulation. Recirculation and sedimentation are kept to a minimum by downstream transport. On an annual basis only material retained by organisms having a life cycle greater than a year is available for recirculation. Therefore, in the long run import is approximately equal to export and recirculation of material among various trophic levels is temporary and minimal.

Periphyton is virtually the only autotrophic community in the Red Cedar River. It is also the only aggregation of organisms that can directly extract large quantities of dissolved material from the water. Much of the stream drift that becomes available for filter feeders originates from this community. In other words, periphyton serves as the primary vehicle for the transfer of energy and material. Therefore, the maximum biological productivity of the environment is ultimately determined by the efficiency of the periphyton community in utilizing available solar radiation and dissolved nutrients.

This investigation is an attempt to describe energy-flow and material circulation at the primary level in a warm-water stream. The findings are first presented as specific data and then expanded to fall within the framework of the principles stated in the introduction.

DESCRIPTION OF STUDY AREA

The Red Cedar River is a warm-water stream located in the south central portion of the Lower Pennisula of Michigan. The stream originates as an outflow from Cedar Lake (T. 1 N; R. 4 E; Sec. 28, 29; Livingston Co.) and flows for 49 miles before its confluence with the Grand River in the city of Lansing. The river has a gradient of 2.5 ft $mile^{-1}$ and a drainage area of 475 $miles^{2}$. The climatological and edaphic features of the watershed have been summarized by Meehan (1958). Brehmer (1958) made a detailed study of the physical, chemical, and biological characteristics of 5.3 miles of stream located 14 miles upstream from the confluence.

Most of this study was conducted at Dobie Road which is located 10 miles upstream from the mouth of the river. At base flow this area has a mean width of 72 ft, a mean depth of 1.6 ft, a mean cross sectional area of 110 ft^{2}, and a discharge of about 65 ft^{3} sec^{-1}. The stream bottom is composed predominately of sand with occassional patches of gravel. A thermograph was maintained by the Department of Fisheries and Wildlife, Michigan State University at this station. A detailed summary of the water temperature present during this study is reported by Brehmer (op. cit.). Pollution studies were made at stations located 25 and 50 meters downstream from the outfall of the Williamston sewage treatment plant.

METHODS AND EQUIPMENT

pH and alkalinity. pH was measured with a Beckman Model N portable pH meter. Alkalinity determinations were made in the laboratory using the method described by Welch (1948).

Turbidity. Turbidity was measured on a Klett-Summerson photoelectric colorimeter which had been calibrated with a Jackson Turbidimeter. The Fuller's earth standards used in the calibration were prepared in accordance with instructions given in "Standard Methods for the Examination of Water, Sewage, and Industrial Wastes" (APHA, AWWA, FSIWA 1955). Readings were taken using a number 42 filter (blue) having a spectral transmission of 400 - 465 mu. Corrections for intrinsic color were made by adjusting the colorimeter scale to zero with a water sample that was filtered through a Millipore membrane (HA type, 0.45 u pore size).

Seston. Crude estimates of seston were made by filtering 500 ml of river water through a Gooch crucible equipped with an asbestos filter mat. The crucible was then dried, weighed, ignited, and reweighed; thereby measuring both total and organic seston.

Absorbancy. The absorption properties of unfiltered river water to three spectral regions were studied in the laboratory using a Klett-Summerson colorimeter. The filters used were; numbers [1] 42 (blue), 54 (green), and 66 (red) having the approximate transmission ranges of 400 - 465, 500 - 570, and 640 - 700 mu respectively.

Phosphorus. Total phosphorus and total dissolved phosphorus were measured using methods modified from Ellis, Westfall, and Ellis (1948). The procedure differed in that the digested sample was split in half and the pH adjusted to the phenolphthalein end point with saturated NaOH before the color producing reagents were added (Taylor 1937). The

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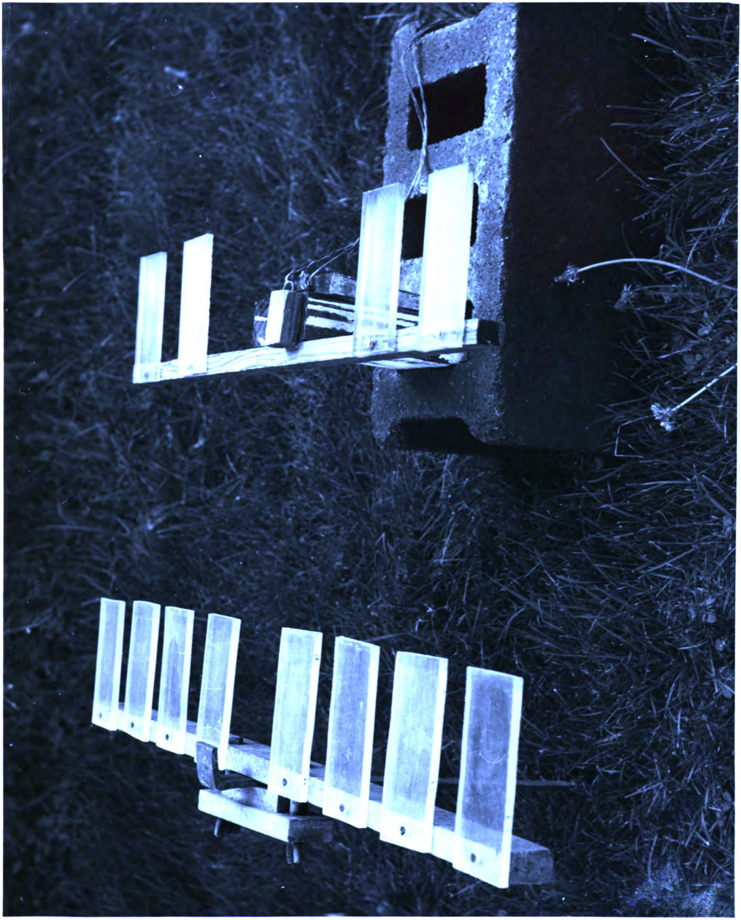
[1] Klett-Summerson Photoelectric Colorimeter - Industrial Manual Klett Manufacturing Co., N.Y.

absorbancy of the colored solution was measured on a Klett-Summerson colorimeter equipped with a number 66 filter (red). Prior to digestion the water samples used for the total dissolved phosphorus analyses were filtered through an HA type Millipore membrane having a pore size of 0.45 u.

Nitrogen. Ammonia nitrogen was determined using the distillation method given in "Standard Methods for the Examination of Water, Sewage, and Industrial Wastes" (APHA, AWWA, FSIWA 1955). Oxidized forms of nitrogen (NO_2 + NO_3) were measured using the reduction method described in the same source. Color produced by nesslerization in both of the above techniques was measured with a Klett-Summerson colorimeter using a number 54 filter (green). A micro-Kjeldahl procedure similar to the one described by Belcher and Godbert (1945) was used to determine the organic nitrogen content of periphyton. The catalyst mixture differed from the one given by these authors in that $CuSO_4$ was substituted for $HgSO_4$. Similarly, Na_2S was eliminated from the procedure. These changes permitted the nesslerization of samples having minimal nitrogen concentrations.

Periphyton. Periphyton productivity was studied by submerging artificial substrata in the stream. The substrata were plexiglass plates, 7 mm thick, having an exposed surface area of 1.4 dcm^2 when fastened to a horizontal crossbar. The crossbar was bolted to a steel post in the stream or attached to a vertical upright which was wedged into a concrete block (figure 1). Experiments conducted by the author and Dr. Morris L. Brehmer showed that periphyton samples collected from plexiglass plates exhibited considerably less variation than samples taken from wood shingles, glass microscope slides, and cinder bricks.

Figure 1. Plexiglass substrata and supporting devices.



The submersion period ranged from one to three weeks depending upon the accrual rate.

The substrata were transfered from the stream to the laboratory by means of individual plastic bags and then frozen. The freezing aided in releasing the growth from the plastic and facilitated pigment extraction by rupturing the cell walls.

The relationship between the absorbancy of extracted phytopigments and periphyton weight was studied by using the following technique. First, the growth was removed from the substrate by scraping and then washing it with 95% ethanol. Any macro-fauna, such as aquatic insects, were removed from the solution. The particulate fraction of the sample was separated from the extracted phytopigments by filtration through a Gooch crucible. The contents of the crucible were washed with dilute HCl followed by distilled water. The crucible was then dried to constant weight and organic weight estimated by loss on ignition. The absorbancy of the ethanol soluble pigments was determined with a Klett-Summerson colorimeter equipped with a red filter (transmission 640 - 700 mu) after the solution volume was adjusted to 50 ml. The solvent was evaporated from the extract and the weight of the organic residue determined by loss on ignition. The weight of the residue was added to the organic weight of the particulate fraction. This sum is the weight estimate obtained from one substrata.

In the preceeding technique constant weight is defined as two consecutive readings of $\pm$ 0.5 mg after an interval of 12 hours.

Productivity studies involving the use of artificial subtrata are not new. Cooke (1956) gives a comprehensive literature review on the subject. However, experiments (Grzenda 1955, Alexander 1956) directed by Drs. R.C. Ball and Frank F. Hooper were the first to combine phytopigment techniques used by Kreps and Verjbinskaya (1930), Harvey (1934), Manning and Juday (1941), and others with artificial substrata (cedar shingles, and cinder blocks) methods.

Diurnal oxygen curves. Primary production was measured using the diurnal oxygen curve method as given by Odum (1956). The rate of change in dissolved oxygen for an area where there is no drainage accrual is dependent upon three component rates; production, diffusion, and respiration. Before a gross production estimate can be made from a gas curve it is necessary to estimate both community respiration and diffusion. Odum (op. cit.) gives several methods for computing each of these rates. Therefore, the specific procedures used in this study will now be mentioned.

Odum (op. cit.) states the rate of gaseous transfer into water can be expressed by the relation.

$$D = K S$$

where

D = the diffusion rate per area (g O_2 m^{-2} hr^{-1}).

K = the gas transfer coefficient at 0% saturation (g O_2 m^{-2} hr^{-1}).

S = the saturation deficit between water and air.

The gas transfer coefficient (K) can be calculated using the following expression.

$$K = \frac{z(q_m - q_e)}{S_m - S_e}$$

where

S_m = the predawn saturation deficit.

S_e = the evening saturation deficit.

z = the mean depth (m).

q_m = the rate of oxygen change in the morning ($g\ O_2\ m^{-3}\ hr^{-1}$).

q_e = the rate of oxygen change in the evening ($g\ O_2\ m^{-3}\ hr^{-1}$).

Using the above relationships a correction for either inward or outward diffusion can be applied to each point on the gas curve.

Respiration was indirectly measured during darkness by subtracting the diffusion rate from the observed rate of change to obtain the estimate in $g\ O_2\ m^{-3}\ hr^{-1}$. This method, like all respiration estimates made in the darkness, assumes that community respiration is constant throughout the day and night.

In this study the gas curves were constructed using the "spot dye" method where the data carries the dimensions of $g\ O_2\ m^{-3}\ hr^{-1}$. Gross primary production in $g\ O_2\ m^{-2}\ day^{-1}$ is obtained by multiplying the mean depth (m) by the area under the diurnal gas curve ($g\ O_2\ m^{-3}\ day^{-1}$). Odum (1956) also gives equations suitable for calculating gross primary production when the rate is expressed as a difference between stations rather than a change per hour.

All dissolved oxygen determinations were made using the unmodified Winkler procedure as stated in "Standard Methods for the Examination of Water, Sewage, and Industrial Wastes" (APHA, AWWA, FSIWA 1955).

Units. The dimensions on all measurements presented in this thesis are in the exponential form. Using this system cubic centimeters of O_2 per square meter per day would be expressed as $cm^3\ O_2\ m^{-2}\ day^{-1}$. In the literature, particularly the European, chemical concentrations are very often expressed in terms of free radicals (i.e. NO_2, NO_3, etc.). In order to make comparisons among various authors all data is converted so that concentrations are expressed in terms of the essential element (i.e. mg $N.NO_3\ l^{-1}$.

RESULTS AND DISCUSSION

Physical and Chemical Environmental Factors

M.O. alkalinity and pH. The methyl orange alkalinity of water samples collected from the Red Cedar River is shown in table 1. Phenolphthalein alkalinity was observed only once, indicating carbonate is present predominately in the half-bound form ($X(HCO_3)_2$). At base flow m.o. alkalinity was in the vicinity of 250 ppm; however, during the 1957 flood a low of 112 ppm was recorded. When large fluctuations in discharge occur in a short time span, a plot of m.o. alkalinity vs. discharge approximates an inverse linear or curvilinear regression (figure 2). If a similar plot is made for the year this relationship is obscured by the scatter of the points. This variation is caused by seasonal changes in the absolute bicarbonate content of the river.

The pH values for the year ranged between 7.5 and 8.3 (table 1). No difference was noted among determinations obtained during periods of high and low productivity, demonstrating the photosynthetic utilization of bicarbonate does not contribute to large pH changes in the Red Cedar. This is to be expected because a high bicarbonate content functions as a pH buffer. The greatest fluctuations in pH were observed during floods when the values approached neutrality. It was shown in the preceeding paragraph that high discharge causes a dilution in the bicarbonate concentration. In water like that of the Red Cedar, containing only bicarbonate, carbonic acid, and free CO_2, the pH will be determined largely by the OH^- arising from the hydrolysis of HCO_3^- (Ruttner 1953). Therefore, the drop can be directly attributed to the dilution of the OH^- concentration.

Turbidity and seston. A summary of turbidity measurements, taken at Dobie Road, together with discharge data is shown in table 1. Maximal turbidities were recorded during times of high discharge. However, continous periods of maximal discharge were not accompanied by sustained high

Figure 2. The relationship between discharge and methyl orange alkalinity following two flood periods.

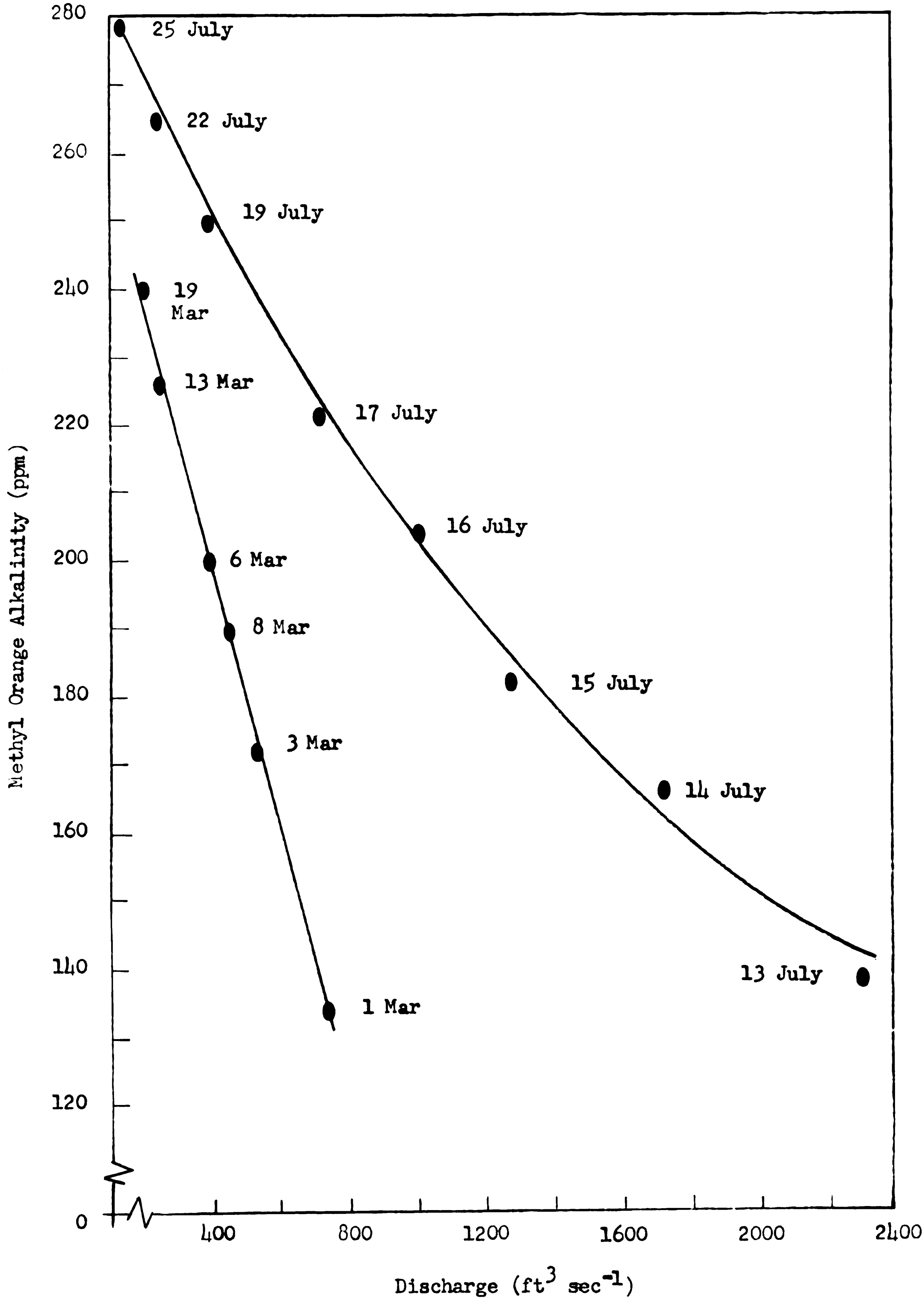

280
260
240
220
200
180
160
140
120
0
400
800
1200
1600
2000
2400
Methyl Orange Alkalinity (ppm)
Discharge (ft3 sec-1)
25 July
22 July
19 July
17 July
16 July
15 July
14 July
13 July
19 Mar
13 Mar
6 Mar
8 Mar
3 Mar
1 Mar

TABLE 1

THE TURBIDITY, pH, AND METHYL ORANGE ALKALINITY OF WATER SAMPLES COLLECTED AT DOBIE ROAD

Collection Date	pH	M.O. Alkalinity (ppm)	Turbidity Units	Discharge ◁ (ft^3sec^{-1})
1957				
3 July	—	—	24	92
11 July	—	—	200	706
12 July	7.5	112	238	1,940
13 July	7.6	138	140	2,290
14 July	7.7	166	74	1,740
15 July	7.8	182	85	1,290
16 July	7.9	204	65	1,020
17 July	8.0	221	73	728
19 July	8.0	250	73	400
22 July	8.1	265	73	259
25 July	8.0	279	42	218
29 July	8.1	279	41	139
31 July	8.0	290	28	111
6 Aug	8.1	268	22	68
9 Aug	8.2	280	19	66
16 Aug	8.3	269	13	54
27 Aug	8.1	272	14	50
3 Sept	7.9	250	9	66
10 Sept	8.0	250	7	48
16 Sept	8.1	270	7	54
23 Sept	7.9	270	7	46
1 Oct	8.1	264	6	41
14 Oct	8.0	282	15	54
25 Oct	7.9	220	22	228
16 Nov	8.0	298	39	473
27 Nov	8.0	240	15	142
5 Dec	7.9	278	25 **	116
11 Dec	8.1	250	17 *	42
17 Dec	7.8	270	13 *	130
19 Dec	—	—	177	262

(continued next page)

TABLE 1 (Continued)

Collection Date	pH	M.O. Alkalinity (ppm)	Turbidity Units	Discharge ◁ (ft^3sec^{-1})
1958				
7 Jan	7.9	202	65 *	184
14 Jan	7.9	270	11 *	128
21 Jan	8.0	244	7 *	163
28 Jan	8.0	216	15 *	111
4 Feb	8.0	220	17 *	92
6 Feb	8.0	280	13 *	100
18 Feb	7.8	272	15 *	68
24 Feb	7.7	264	22 *	81
27 Feb	7.8	214	51 **	111
1 Mar	7.9	134	41 ***	744
3 Mar	8.0	172	23	540
6 Mar	8.0	200	25	400
8 Mar	8.0	190	20	446
13 Mar	8.0	226	9	245
19 Mar	8.1	240	12	209
25 Mar	8.3	236	16	190
30 Mar	8.2	230	14	162
3 Apr	8.1	246	15	145
8 Apr	8.0	244	22	298
11 Apr	8.1	238	12	198
13 Apr	8.1	240	16	238
21 Apr	8.2	236	20	148
30 Apr	8.2	242	20	128
7 May	8.2	262	21	111
12 May	7.9	278	14	86
26 May	8.1	266	10	42
2 June	8.0	224	19	59
5 July	7.7	150	175	560
7 July	7.8	194	78	391

◁ discharge data courtesy of the USGS.
* ice cover.
** bank ice only.
*** ice jam in study area.

turbidity. In other words, high turbidity is dependent upon both the discharge at the time of measurement and the duration of maximal discharge prior to sampling. Turbidities recorded at the onset of a flood are significantly higher than those taken at the latter stages, even though the discharge is approximately the same. This effect is well demonstrated by the data shown in figure 3. This suggests the maximal turbities that intially accompany floods result from the erosion of stream deposits. The sudden drop in turbidity and seston that occurs in spite of continued high discharge can be interperted as an exhaustion of material from this source.

The seston content of water samples collected during the July 1957 flood is shown in table 2. As expected, high seston concentrations were accompanied by high turbidities. However, variations in the limited data were too great to eastablish a quantitative relationship between the two measurements.

Judging from seston and alkalinity measurements, total solids in the Red Cedar vary between approximately 200 and 300 ppm. McNamee (1930) reports the regional differences in the total solids content of Michigan waters. The range in 29 Lower Pennisula river systems was 200 to 500 ppm. Similar measurements for 13 river systems in the Upper Pennisula varied between 100 and 200 ppm.

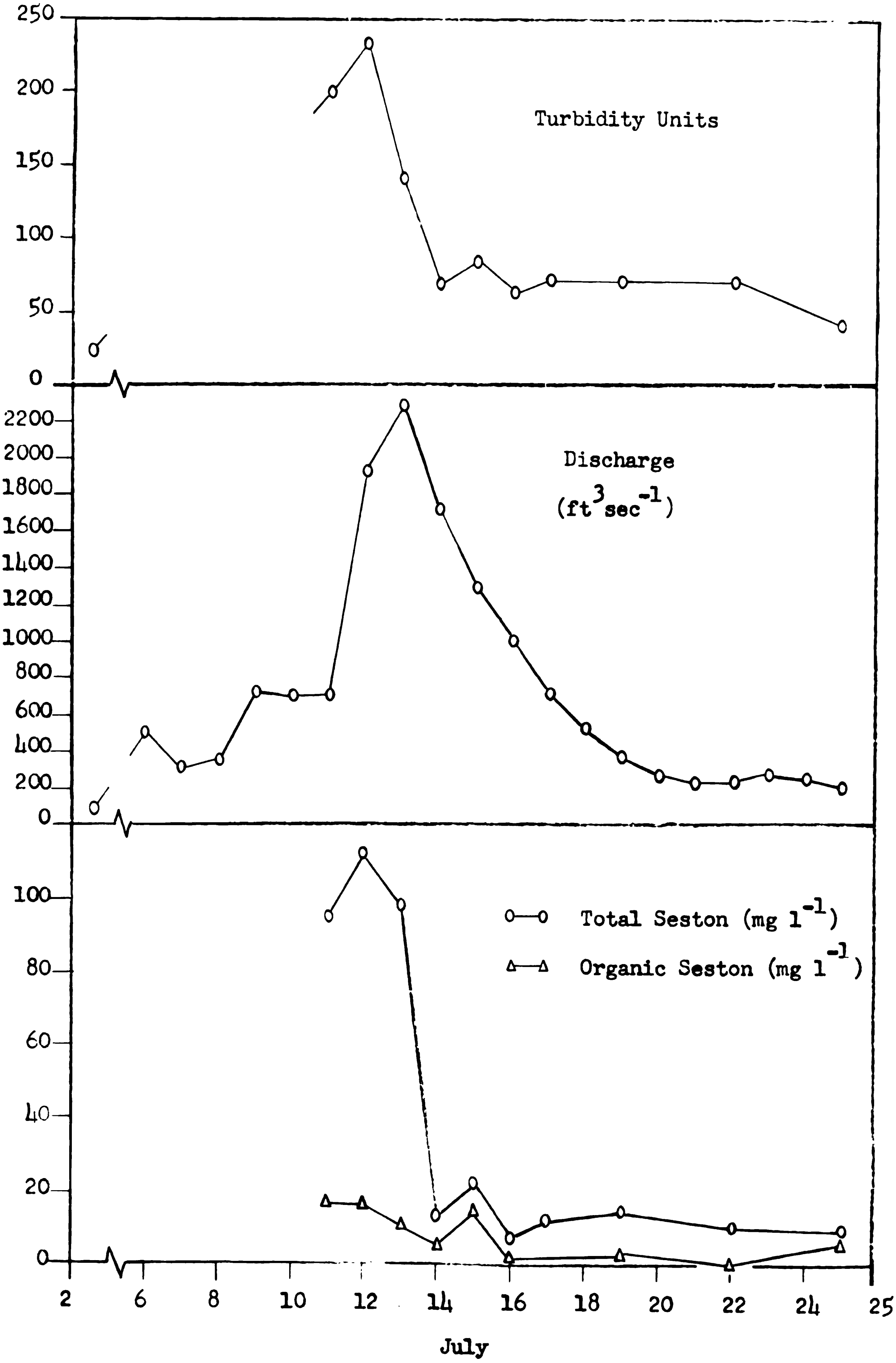
Turbidity and absorbancy. The relationship between turbidity and the absorption of various light fractions is shown in figure 4. These curves demonstrate that suspended materials act as a selective filter favoring the transmission of long-waved radiation. Within the turbidity range of 0 - 20, the absorbancy values for red light (640 - 700 mu) change little. However, after a turbidity of of approximately 25 units is reached, the

TABLE 2

THE SESTON CONTENT OF WATER SAMPLES COLLECTED AT DOBIE ROAD DURING THE 1957 FLOOD

Collection Date	Total Seston ($mg\ l^{-1}$)	Organic Seston ($mg\ l^{-1}$)
11 July	95	18
12 July	114	18
13 July	99	12
14 July	14	6
15 July	23	7
16 July	5	2
17 July	12	2
19 July	15	3
22 July	10	1
25 July	10	5

Figure 3. Changes in turbidity, seston, and discharge during the July 1957 flood.


Turbidity Units
0
50
100
150
200
250
Discharge
(ft^3 sec^{-1})
0
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
Total Seston (mg l^{-1})
Organic Seston (mg l^{-1})
0
20
40
60
80
100
2
6
8
10
12
14
16
18
20
22
24
25
July

red absorption curve breaks into a gentle slope that is roughly linear. In contrast, very slight changes in suspended matter, even at minimal turbidities caused an immediate increase in the absorption of blue light (400 - 450 mu). The absorption curve for green light (500 - 570 mu) is intermediate in position and behavior to red and blue light.

Pietenpol (1918), in a laboratory study of lake water, concluded that suspended matter acts as a non-selective light filter. Similarly, Welch (1952) states that suspended materials in certain turbid rivers non-selectively screen all visible wavelenghts of light. Birge and Juday (1930) showed that heavily stained or very turbid lake water favored the transmission of long-waved radiation. They also reported that increasing transparency resulted in the selective transmission of increasingly shorter waved radiations. Likewise, Ellis (1936) found that very turbid rivers were slightly selective in the transmission of long-waved radiation. In the Red Cedar River, even at maximal transparency, red transmission always exceeded green and blue, and green transmission was always intermediate between red and blue.

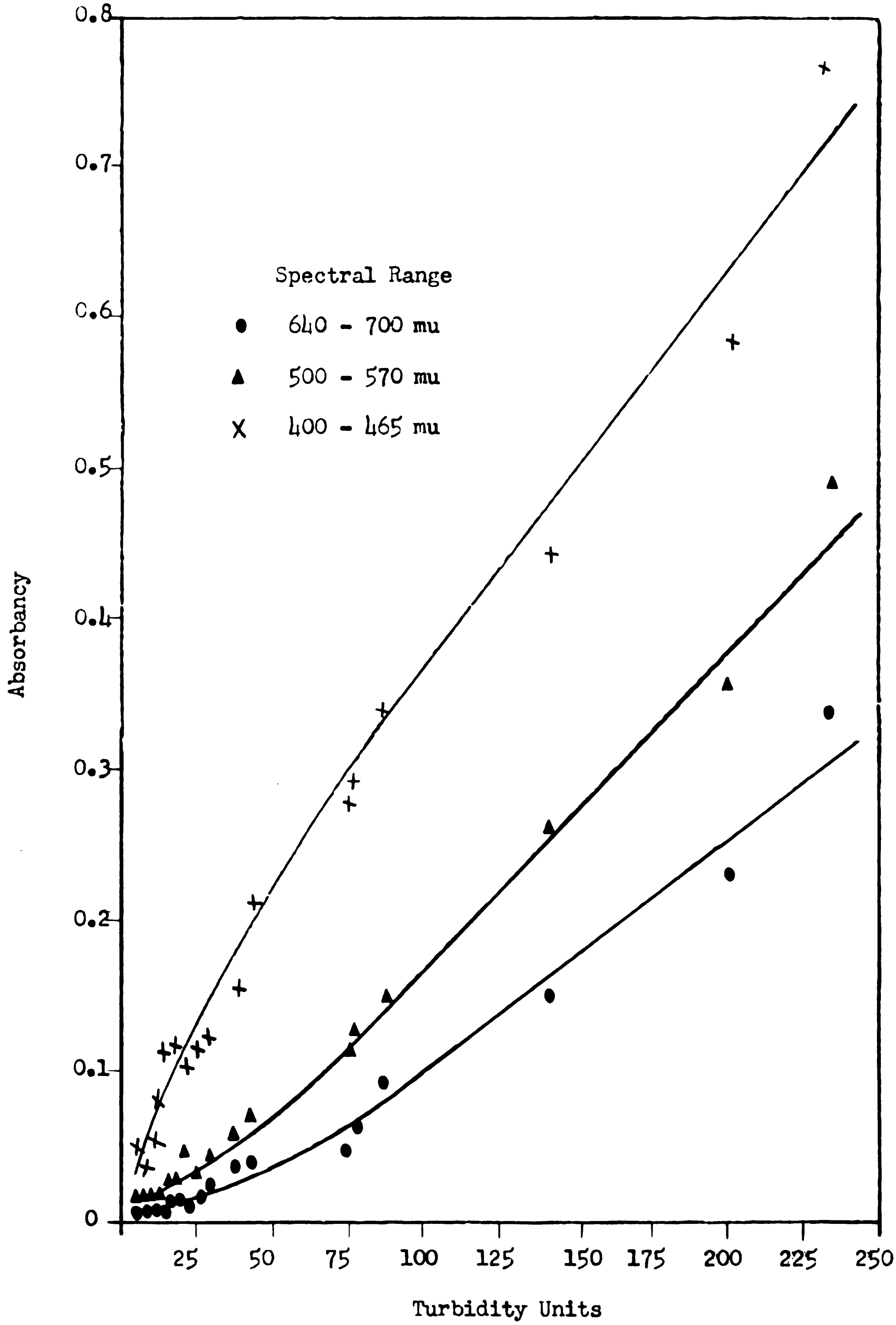
In interperting the data shown in figure 4 it must be remembered that the system contains two factors that contribute to light extinction. They are; the suspended particles, and dissolved color. Water is not considered a factor because the colorimeter was adjusted so that transmission was 100% when it contained a distilled water blank. The absorbancy values for filtered water samples (HA type Millipore membrane, 0.45 u pore size) ranged from nearly zero to about 0.06. However, variations functioned independently of turbidity. Therefore, suspended matter is the controlling extinction factor and dissolved color is an accessory factor that introduces random errors into the experimental data when

TABLE 3

THE ABSORBANCY OF WATER SAMPLES COLLECTED FROM DOBIE ROAD AT VARIOUS SPECTRAL RANGES

Collection Date	Absorbancy		
		Spectral Range	
	400-465 mu	500-570 mu	640-700 mu
1957			
3 July	0.114	0.034	0.014
11 July	0.586	0.356	0.228
12 July	0.777	0.494	0.346
13 July	0.444	0.260	0.150
14 July	0.292	0.126	0.066
15 July	0.338	0.150	0.092
16 July	0.268	0.102	0.046
17 July	0.276	0.108	0.050
19 July	0.276	0.108	0.046
22 July	0.276	0.130	0.060
25 July	0.202	0.070	0.036
29 July	0.154	0.060	0.034
31 July	0.114	0.046	0.024
6 Aug	0.092	0.036	0.012
9 Aug	0.080	0.036	0.018
16 Aug	0.066	0.022	0.010
27 Aug	0.060	0.020	0.006
3 Sept	0.056	0.022	0.010
10 Sept	0.034	0.018	0.010
16 Sept	0.034	0.020	0.010
23 Sept	0.040	0.018	0.008
1 Oct	0.044	0.014	0.006
14 Oct	0.024	0.012	0.006
25 Oct	0.112	0.054	0.028
16 Nov	0.234	0.096	0.048
27 Nov	0.106	0.034	0.012
5 Dec	0.098	0.036	0.014
11 Dec	0.110	0.026	0.010
17 Dec	0.090	0.032	0.004

Figure 4. The relationship between suspended matter and the absorption properties of unfiltered river water to three spectral ranges. Dots represent mean absorbancy values.



0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Absorbancy
Spectral Range
640 - 700 mu
500 - 570 mu
400 - 465 mu
25
50
75
100
125
150
175
200
225
250
Turbidity Units

they are presented as an absorbancy vs. turbidity plot. James and Birge (1938) conducted laboratory experiments where the absorption properties of each component of a three factor extinction system (lake water, dissolved color, and suspended particles) were analyzed.

Primary Production and Energy Transfer

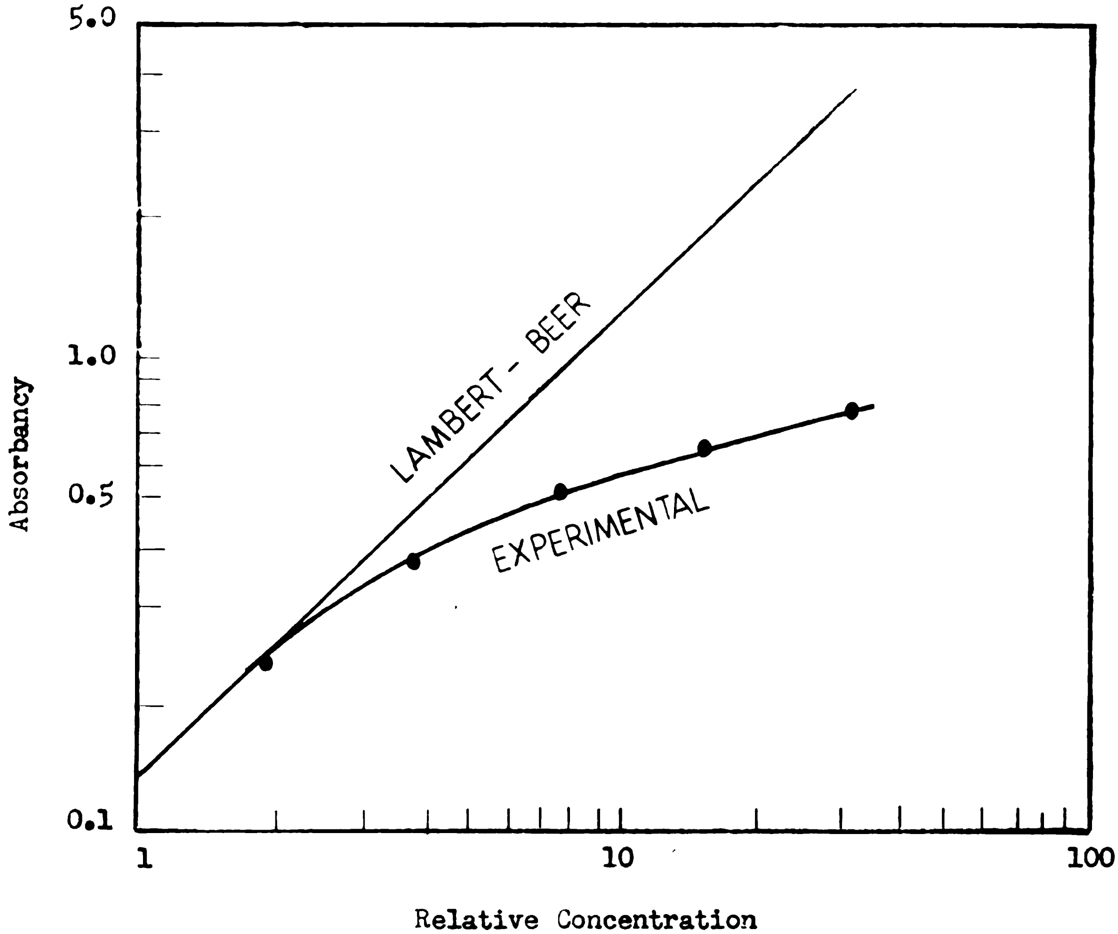
PERIPHYTON

Optical characteristics of pigment extracts. Experiments showed that the absorption of broad spectrum light (600-700 mu) is not linearly related to the concentration of 95% enthanol extracts of phytopigment. The deviation from the Lambert-Beer Law becomes apparent at an absorbancy of 0.20 when read on a Klett-Summerson colorimeter and increases proportionately with higher concentrations. Nonlinearity was also noted for measurements made with monochromatic light at the peak absorption wavelength. Inorganic solutions (Harvey Standards) did not exhibit nonlinearity with either monochromatic or polychromatic light. Therefore, it is believed this effect was due to interaction between the solvent and solute or to changes among the molecules (e.g. polymerization).

The measured absorbancy may be corrected to correspond with the theoretical absorbancy as related to concentration by constructing a correction graph (figure 5). This graph is made by plotting absorbancy against concentration as determined by dilution. This portion of the curve corresponds to the line labled EXPERIMENTAL in figure 5. The line labled LAMBERT-BEER corresponds to the theoretical absorbancy of the solution.

The correction graph is used in the following manner. The measured absorbancy is found on the ordinate and is followed horizontally to intercept with the experimentally determined line; this intercept is then read vertically to intercept the extrapolated LAMBERT-BEER line; the absorbancy unit opposite this intercept represents the corrected absorbancy reading. In order to avoid confusion between measured absorbancy and corrected absorbancy, the corrected absorbancy will henceforth be designated as

Figure 5. A correction graph for converting experimental data into absorbancy values (phytopigment units) related to pigment concentration. The experiments were jointly conducted by Brehmer (1958) and the author.


5.0
1.0
0.5
0.1
Absorbancy
LAMBERT - BEER
EXPERIMENTAL
1
10
100
Relative Concentration

phytopigment units.

Phytopigment-weight relationship. Experiments showed that phytopigment units could be used to make quantitative estimates of organic weight (ash-free dry weight) for phytopigment values less than 1.3. For greater values the variations were too large to be useful as a quantitative technique. However, such values are still valuable for comparative studies.

It is believed that the increasing variation was due to the physical state of the algal colony. More specifically, samples having the greatest variations were those which supported the most luxuriant growth of periphyton. The increased variation is probably a combined effect of the death of some members of the colony and the accumulation of organic detritus on the surface of the substrate. Therefore, for quantitative studies it is important that the exposure period be short enough to avoid this condition.

The data presented in figure 6 were collected from July 1957 to July 1958. The exposure periods ranged from one to three weeks depending upon the accrual rate of periphyton.

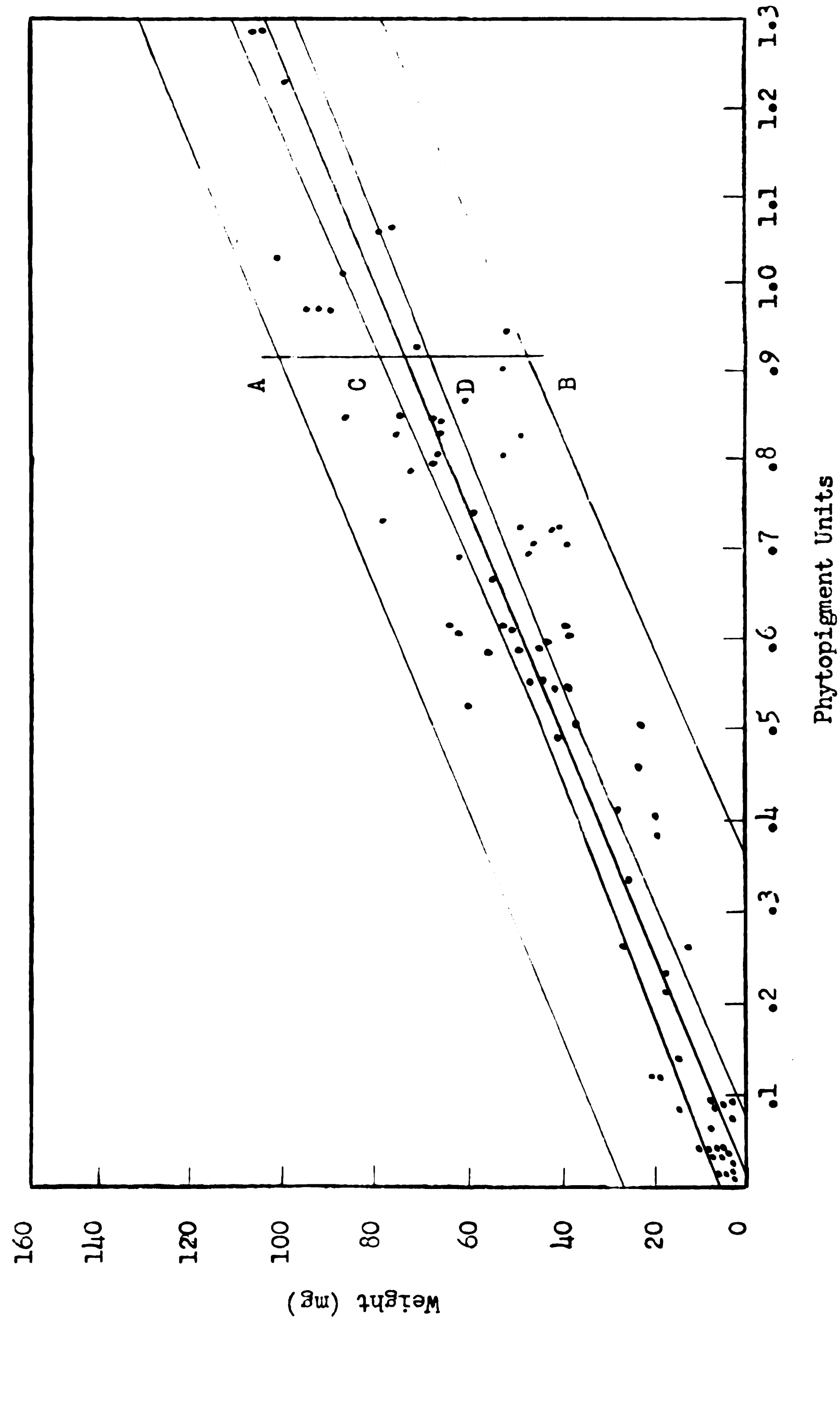
A linear regression was fitted to the phytopigment-weight relation for phytopigment values less than 1.3. The model used was Model I as given by Snedecor (1956). The sample regression for this model is

$$\hat{Y} = a + bX$$

where in this case

$\hat{Y}$ = the mean weight estimate.
a = the intercept of the Y axis.
b = the point estimator of the population slope.
X = the observed phytopigment reading.

Figure 6. The relationship between phytopigment units and the ash-free dry weight of periphyton. The 95% confidence region is shown for mean estimates (CD) and individual estimates (AB).


Weight (mg)
0
20
40
60
80
100
120
140
160
Phytopigment Units
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
1.1
1.2
1.3
A
C
D
B

Using the computed constants the equation for predicting $\hat{Y}$ from X becomes

$$\hat{Y} = -1.72 + 82.37\ X$$

Equations for computing a confidence region on the regression are given by Snedecor (1956). The confidence region appears as curved borders on both sides of the regression. The width of the confidence belt for any prediction made by X is dependent upon how far removed X is from $\bar{X}$ (the mean of the X's). Since all of the values of X in figure 6 are close to $\bar{X}$ (0.52), the confidence region appears as two lines that are nearly parallel. The maximum 95% confidence limit for any estimate of Y (individual estimates) made from phytopigment values between 0 and 1.3 is $\pm$ 29.03 mg and is located at the maximum value of X. The minimum 95% limit is found at $\bar{X}$, and in this case it is $\pm$ 28.42 mg. The same limits for Y (mean estimates) are $\pm$ 3.05 mg and $\pm$ 6.82 mg respectively.

Periphyton production. Net periphyton production was measured, using artificial substrata, from July 1957 to July 1958. The taxonomic composition of the community varied with the season. *Gomphonema*, *Navicula*, *Diatoma*, and *Fragellaria* were the most common genera in spring and summer communities. *Cocconeis* was the dominant genus in the early fall. Late fall and winter communities were composed almost entirely of *Navicula* and *Fragellaria*. Peters (1958) gave a very detailed account of seasonal diatom periodicity in the Red Cedar River. Peters also found that the taxa present on the stream bottom and natural substrata were the same as those colonizing artificial substrata. Similar observations were reported by Butcher (1932) and Patrick, Horn, and Wallace (1954) for periphyton colonizing glass slides.

The seasonal peridicity of net periphyton production is shown in figure 7. The mean rates ranged between 0.11 and 22.78 mg ash-free dry weight dcm^{-2} day^{-1}. The highest rates were observed in June and the lowest when the river was covered with ice. In the latter part of August production dropped very sharply. In less than a week the mean rate fell from 9.54 to 0.52 mg dcm^{-2} day^{-1}. This situation was observed at the same time by Brehmer (1958) for six stations upstream from Dobie Road. There was no great change in the physical (turbidity, temperature, and discharge) or chemical (pH, alkalinity, nitrogen, and phosphorus) character of the stream concurrent with production cessation. As fall progressed there was a gradual increase in production that subsided with the event of ice cover. Prior to the decline, the community was composed of many genera of diatoms. By mid-September the colony was comprised almost entirely of Cocconeis. This suggests the decline was caused by a shift from a strong light - warm water community to a weak light - cold water community (Ruttner 1953). However, the abruptness of production cessation is still very puzzling.

E.P. Odum (1959) has adjusted and corrected primary production estimates obtained by various methods and different authors to make them comparable with one another. Using these conversions he gives annual net production estimates for Silver Springs, Florida (H.T. Odum 1957) and the Sargasso Sea (Riley 1957). They are 7.4 and 0.26 g dry organic weight m^{-2} day^{-1} respectively. Data given by H.T. Odum (op. cit.) and Riley (op. cit.) suggest that in aquatic biotypes gross production is approximately equal to two times net production. On this basis the mean annual gross production rate in the Red Cedar River would be about 1 g m^{-2} day^{-1}. This places the Red Cedar River in the second order of productivity along with grasslands, coastal seas, some shallow

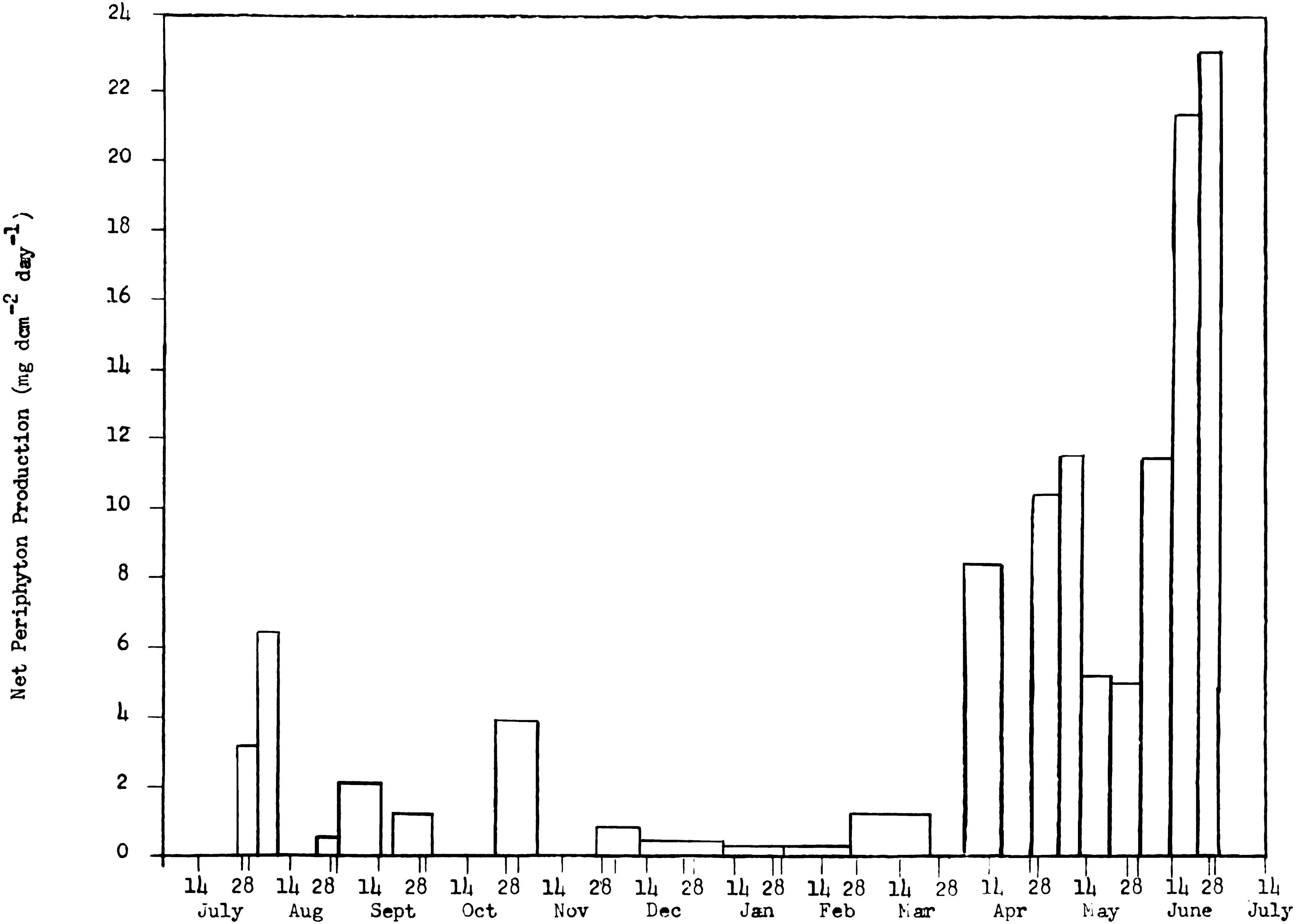
TABLE 4

NET PRIMARY PRODUCTION DETERMINED BY PERIPHYTON ACCRUAL ON ARTIFICIAL SUBSTRATA

Collection Date	Exposure Period (days)	Water Temp. Range for Period °C	Mean Net Production [1] (mg dcm^{-2}day^{-1})	Two Standard Errors (mg dcm^{-2}day^{-1})
1957				(±)
31 July	7	18.0-22.5	3.28	1.13
8 Aug	7	18.0-22.0	6.58	0.84
16 Aug	7	18.0-24.0	9.54	1.53
27 Aug	7	17.5-20.5	0.52	0.16
3 Sept	14	18.5-22.0	2.06	0.17
17 Sept	14	14.0-18.0	1.04	0.12
1 Oct	14	14.0-18.0	1.25	0.20
18 Oct	14	6.0-14.5	2.14	0.89
4 Nov	14	6.0- 8.0	4.08	0.32
5 Dec	14	0.5- 1.0	0.86	0.24
1958				
7 Jan	34	0- 6.5	0.13	0.08
28 Jan	21	0	0.11	0.02
18 Feb	21	0	0.12	0.05
19 Mar	28	0- 6.5	1.01	0.26
17 Apr	14	7.0-17.0	8.33	0.71
5 May	10	8.5-14.0	10.12	1.40
12 May	7	10.0-17.0	11.47	1.22
19 May	7	14.0-21.0	5.11	0.57
29 May	10	12.0-19.0	4.89	1.37
11 June	9	14.0-20.0	11.34	0.71
18 June	7	14.0-20.0	21.21	7.45
25 June	7	14.0-20.0	22.78	14.72

[1] To convert the data to g m^{-2}day^{-1} move the decimal point one place to the left.

Figure 7. The seasonal periodicity of net periphyton production in the Red Cedar River.


Net Periphyton Production (mg dcm^{-2} day^{-1})
0
2
4
6
8
10
12
14
16
18
20
22
24
14 28 14 28 14 28 14 28 14 28 14 28 14 28 14 28 14 28 14 28 14 28 14 28 14
July
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
June
July

lakes, and ordinary agriculture (E.P. Odum 1959).

A comparison of net production rates determined by loss on ignition and phytopigment methods is shown in table 5. The degree of agreement between the two methods is remarkable considering the regression was computed from diatom populations having different taxa living under various light, temperature, and nutrient conditions. These findings are inconsistant with some previous investigations. Ryther (1956) points out that many workers have shown that chlorophyll content per cell varies over a wide range depending upon the physical and chemical environment. However, Tucker (1949) demonstrated a good correlation (0.84) between planktonic diatom counts and pigment absorbancy. Similar findings were reported by Peters (1959) for diatoms in the Red Cedar River.

The use of artificial substrata, like other crop methods of measuring net production, has intrinsic shortcomings which tend to lower the rate estimate. They are: predation by consumer organisms; and in the case of stream periphyton, downstream drift. Both of these sources of error can be held to a minimum by removing the substrate when there is a firm uniform coat of periphyton. Longer exposure results in a flocculent colony that is susceptible to losses by downstream drift and insect predation. As a general rule, this condition can be avoided by removing the substrate before the colony has an ash-free dry weight of 150 mg. It is not likely that drift and predation were significant in this study except in three instances when production was maximal. At this time the substrata were clearly over exposed since they supported a flocculent colony densely populated with aquatic insects. At other times the substrata supported few if any insects and required vigorous scrubbing to remove the algal coating.

TABLE 5

A COMPARISON OF OBSERVED NET PRODUCTION RATES AND NET PRODUCTION RATES CALCULATED FROM THE PHYTOPIGMENT-WEIGHT REGRESSION

Collection Date	Observed Mean Rate ($mg\ dcm^{-2} day^{-1}$)	Calculated Mean Rate ◁1 ($mg\ dcm^{-2} day^{-1}$)
1957		
31 July	3.38	3.43
8 Aug	6.58	6.81
16 Aug	9.54	7.84
27 Aug	0.52	0.51
3 Sept	2.06	2.53
17 Sept	1.04	2.22
1 Oct	1.25	1.65
18 Oct	2.14	1.77
4 Nov	4.08	3.28
5 Dec	0.86	0.30
1958		
7 Jan	0.13	0.30
28 Jan	0.11	- 0.02
18 Feb	0.12	0.05
19 Mar	1.01	1.32
17 Apr	8.33	7.09
5 May	10.12	11.20
12 May	11.47	15.54
19 May	5.11	6.21
29 May	4.89	5.75
18 June	21.21	19.74
25 June	22.78	16.38

◁1 Calculated rates computed from

$$Y = -1.72 + 82.37\ X$$

where Y = mean weight estimate

X = mean phytopigment reading

Diurnal gas curves. Sargent and Austin (1949) used changes in dissolved oxygen to estimate the productivity of a coral reef. Their methodology did not correct for oxygen gains or losses due to diffusion. However, this was not critical because deviations from saturation were small relative to total oxygen production. Odum (1956) gave a more sophisticated version of this technique that provided for diffusion corrections. This method was successfully used by Odum (op. cit., 1957a) in Florida springs and a turtle-grass community; and by Kohn and Helfrich (1957), for a coral reef. However, McConnell and Sigler (1959) found that Odum's method was unsuitable for productivity studies in a shallow rapid river.

Diurnal oxygen curves were found to have only limited value in the Red Cedar River for measuring primary production. One test trial out of four was successful. Two trials were conducted during the winter when production was minimal; both were unsuccessful because no change in dissolved oxygen could be detected between the upstream and downstream stations. Measurements made during a period of high productivity yielded paradoxical data; that is, negative changes occurred at dusk and dawn that exceeded the calculated losses attributed to diffusion and community respiration. This indicates the methods for computing the gas transfer coefficient (K) and respiration were inadequate.

The formation of oxygen bubble by photosynthesis could be responsible for these and other errors inherent to gas curve productivity measurements. Bubble escapement to the surface would result in underestimates if such losses were not considered by the investigator. Odum (1957a) reckoned with this problem and was able to measure the net production of benthic algae by collecting ascending bubbles with a funnel trap. Such a technique assumes that the bubbles are lost to the surface shortly after formation. This was not the case in the Red Cedar River. At times bubble accumulation within the algal mat became so great that walking in the stream gave the water an effervescent appearance. This condition was still present after nightfall and absent by the following morning. Presumably the oxygen went into solution at night when the water was unsaturated. Nocturnal solution of oxygen bubbles would introduce several errors into the production estimate. The gas transfer coefficient (K) is calculated on the basis of nocturnal dissolved oxygen changes assuming such changes are caused solely by diffusion and community respiration. However, if bubble solution takes place (at night) the extent of outward diffusion will be underestimated. This will result in an error in the computation of K. For the same reason the community respiration measurement will also be incorrect. Since no quantitative data are available to illustrate this effect it is impossible to say whether such descrepancies would cause other than minor anomalies in the data. However, it is likely that bubble accumulation during the day could cause a significant underestimate simply because large quantities of oxygen did not go into solution when the productivity measurements were made.

In April 1958 a diurnal gas curve, free from anomalies, was obtained from the Red Cedar River at Dobie Road. The gas transfer coefficient (3.1 g O_2 m^{-2} hr^{-1}) is in general agreement with literature values quoted by Odum (1956). The gross and net production rates were found to be 3.6 and 2.4 g O_2 $m^{-2}day^{-1}$ respectively. Odum (1957a) reports gross production rates from 0.7 to 64 g O_2 m^{-2} day^{-1} in 11 Florida springs. The gross production / community respiration quotient for Dobie Road is 3.0, which according to Odum (1956) classifies it as an oligosaprobic community.

Energy conversion. The energy content of periphyton samples was estimated using chemical analyses and caloric values obtained from the literature. Birge and Juday (1922) report the following analyses for diatoms collected from Lake Mendota: crude protein, 37.81%; fats (ether extract), 22.48%; carbohydrates (crude fiber plus nitrogen free extract), 39.71%. These percentages are in terms of the ash-free dry weight. Standard caloric figures on a dry weight basis are; 5,650 calories[1] per gram protein, 9,450 calories per gram fat, and 4,100 calories per gram carbohydrate (Juday 1940).

Solar radiation data were obtained from a pyrheliometer station maintained by the Soil and Water Conservation Research Division of the U.S. Department of Agriculture. The measurements express the amount of solar energy received by a horizontal plane at the earth's surface and carry the dimensions of g cal cm^{-2}. The pyrheliometer station is located approximately two miles west of the Dobie Road study area.

Lindeman (1942) defines energy intake efficiency as the ratio of energy intake at a given trophic level to the energy intake at the preceding (I_t/I_{t-1}). According to Odum (1959) at the primary level this can be expressed as the ratio of gross production to surface radiation (P_g/L) or as the ratio of gross production to available radiation (P_g/L_a). Juday (1940) in addition to using the efficiency percentage P_g/L_a employed the following efficiencies based on net production (P_n); P_n/L and P_n/L_a.

Seasonal P_n/L efficiencies obtained from the Red Cedar River are shown in table 6. They ranged from 0.003% to 0.245%, with an annual mean

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[1] The calorie or small calorie is a cgs unit of heat defined as the quantity of heat required to raise the temperature of one gram of water from 3.5°C to 4.5°C (Handbook of Chemistry and Physics. Chem. Rubber Pub. Co., Cleveland, Ohio). In pyrheliometry the same unit is called the gram-calorie (Crab 1950).

of 0.07%. Juday (1940) estimates that 1/3 of the total energy fixed by photosynthesis is degraded to heat by plant respiration. On the basis of this figure the annual mean P_g/L efficiency for the Red Cedar is about 0.01%. This value is lower than most similar values reported in the literature. According to Odum (1957) Silver Springs, Florida has a P_g/L efficiency of 1.2%. Using respiration figures given in the same work it was calculated that Silver Springs has a P_n/L efficiency of about 0.7%. Juday (op. cit.) reports annual P_n/L and P_g/L values for Lake Mendota, Wisconsin of 0.27% and 0.35% respectively. Cedar Bog Lake, Minnesota has a P_g/L efficiency of 0.1% (Lindman 1942). Using data given by Lindeman (1941, op. cit.) it was estimated that Cedar Bog Lake has a P_n/L value of 0.07%. Efficiencies reported by Riley (1941) and Clarke (1946) for productive marine areas were roughly the same as those cited for Lake Mendota.

Clarke (op. cit.) points out that efficiency estimates made on the basis of surface radiation are a function of the photosynthetic efficiency of the organism and light transmission within the environment. It should be recalled that the Red Cedar is subject to prolonged ice cover as well as high turbidity caused by periodic floods. Under such conditions lower efficiencies (P_g/L and P_n/L) are expected in comparison to less turbid lacustrine and marine environments because more energy is lost to abiotic absorption. The Red Cedar has a productivity comparable to most temperate lakes and shallow marine areas (page 38) even though the relative utilization of surface radiation is less. This indicates the Red Cedar is more efficient (P_g/L_a and P_n/L_a) in converting available radiation into plant products than other biotypes having the same level of productivity. This idea can be clarified by restating Odum's (1959)

TABLE 6

THE CONVERSION EFFICIENCY OF SURFACE SOLAR RADIATION INTO PERIPHYTON CROP

Collection Date	Exposure Period (days)	Energy Content of Crop (g cal cm^{-2})	Surface Radiation for Period (g cal cm^{-2})	% Efficiency (P_n/L)
1957				
31 July	7	1.4	4,269.9	0.032
8 Aug	7	2.7	3,455.9	0.078
16 Aug	7	3.7	3,609.0	0.101
27 Aug	7	0.2	3,246.4	0.006
3 Sept	14	1.0	5,109.8	0.019
17 Sept	14	0.9	5,518.6	0.016
1 Oct	14	1.0	5,071.7	0.020
18 Oct	14	1.8	3,779.2	0.046
4 Nov	14	3.4	2,326.7	0.145
5 Dec	14	0.7	1,702.9	0.042
1958				
7 Jan	34	0.3	4,302.7	0.006
28 Jan	21	0.1	3,563.3	0.004
18 Feb	21	0.1	4,839.2	0.003
19 Mar	28	1.7	3,841.3	0.043
17 Apr	14	6.8	6,492.9	0.105
5 May	10	6.0	5,170.1	0.115
12 May	7	4.7	4,502.0	0.105
19 May	7	2.2	4,609.7	0.048
29 May	10	2.9	6,713.7	0.043
11 June	9	6.0	4,955.3	0.121
18 June	7	8.6	4,214.8	0.208
25 June	7	9.4	3,838.7	0.245

definition of photosynthetic efficiency based on available radiation.

$$(1) \quad \text{Efficiency} = P_g/L_a$$

or

$$(2) \quad P_g = L_a \times \text{Efficiency}$$

$$(3) \quad L_a = P_g \,/\, \text{Efficiency}$$

From equation (2) it can be seen that a given level of productivity can not be concurrent with a reduction in available radiation unless the photosynthetic efficiency increases.

Odum (1959), on the basis of data given by Rabinowitch (1951), states the overall efficiency of available light fixation by the plant world is about 1%. There is some justification for extrapolating this estimate to aquatic communities. Juday (1940) reports an annual P_g/L_a efficiency of 0.91% for Lake Mendota. A rough estimate of the annual mean available energy input (L_a) for the Red Cedar can be made by substituting this figure (1%) and the annual mean gross production estimate into equation (3). The estimated L_a is 34.4 g cal cm^{-2} day^{-1} or 10.3% of the mean surface energy input.

A summary of primary energetics based on the data and assumptions stated in the text is shown in figure 8. Two categories of abiotic energy loss are recognized in the energy-flow model. The first is the loss of surface energy by reflection and energy degradation caused by the absorption of transmitted light by the aqueous medium and suspended solids. This loss is calculated by subtracting the radiation reaching the stream bottom from the surface radiation ($L - L_a$). The second is the degradation of available light that is not used in photosynthesis. This quantity is estimated by subtracting the radiation reaching the stream

Figure 8. Primary energetics in the Red Cedar River. Data based on annual means and expressed in gram-calories centimeter^{-2} day^{-1}.

L = surface energy.

L_a = energy reaching the stream bottom.

$L - L_a$ = energy lost by reflection and medium absorption during transmission.

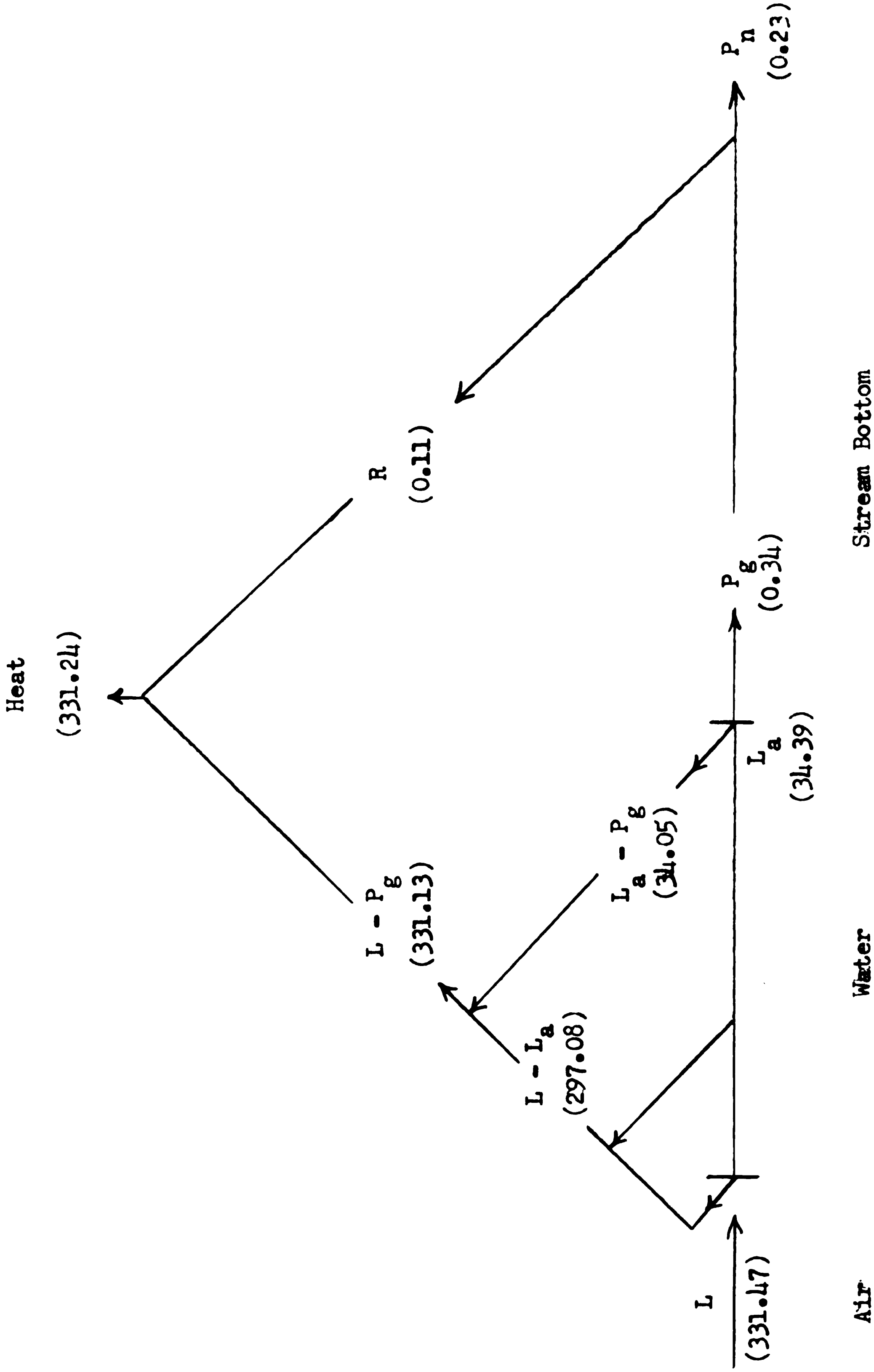
$L_a - P_g$ = energy reaching the stream bottom not utilized in photosynthesis.

$L - P_g$ = total abiotic energy loss.

P_g = gross primary production.

P_n = net primary production.

R = respiration.


Heat
(331.24)
R
(0.11)
P_n
(0.23)
L - P_g
(331.13)
L_a - P_g
(34.05)
P_g
(0.34)
L - L_a
(297.08)
L_a
(34.39)
L
(331.47)
Air
Water
Stream Bottom

bottom (L_a - P_g). The expression ($L - L_a$) + ($L_a - P_g$) may be reduced to ($L - P_g$) and is termed the total abiotic energy loss. Energy lost by evaporation and energy gained by condensation are not considered in the model because they involve energy that has already been converted to heat.

The preceeding computations assume that primary production is limited to periphyton on the stream bottom. This assumption appears to be accurate in that extractions from suspended materials obtained by filtration of water samples showed a virtual absence of phytopigments. Since only primary energentics are considered, periphyton respiration is the only source of biotic energy loss. The annual mean rate of net production (0.23 g cal $cm^{-2}day^{-1}$) is the amount of energy that is available for transfer to consumer organisms. The term consumer as used in the framework of this model includes the reducer organisms which are usually considered separately in the more complex energy-flow models.

Nutrient Supply and Utilization

PHOSPHORUS

The phosphorus concentration in water samples collected from July 1957 to July 1958 is shown in figure 9. The sampling frequency was dictated by existing stream conditions; that is, periods of change such as floods were sampled daily and static periods were sampled two or three times a week.

The concentration data were converted into load estimates. A load is defined as the absolute quantity of detrital and dissolved phosphorus transported into the study area by suspension in a given period of time. A soluble load refers to materials carried in solution. The following terms are used synonymously throughout the text: load with import; and downstream drift with export. Traction and saltation transport are not considered in this study. Investigations on the Red Cedar River by Kevern (ms) indicate that phosphorus transport by traction and saltation is negligible. Krumbein and Sloss (1956) discuss the classification and characteristics of various modes of stream transport.

Load estimates were made in the following way. The observed phosphorus concentration for the day was multiplied by the total discharge for the same day. This product was then plotted against the sampling date. A curve was constructed by repeating this process for all samples taken during the month. The area under the curve was then measured and taken to be the quantity of phosphorus transported into the study area for that period of time.

The accuracy of this method is dependent upon two assumptions: first, that the increase or decrease of phosphorus between the observed points is uniform; second, that all major changes in phosphorus

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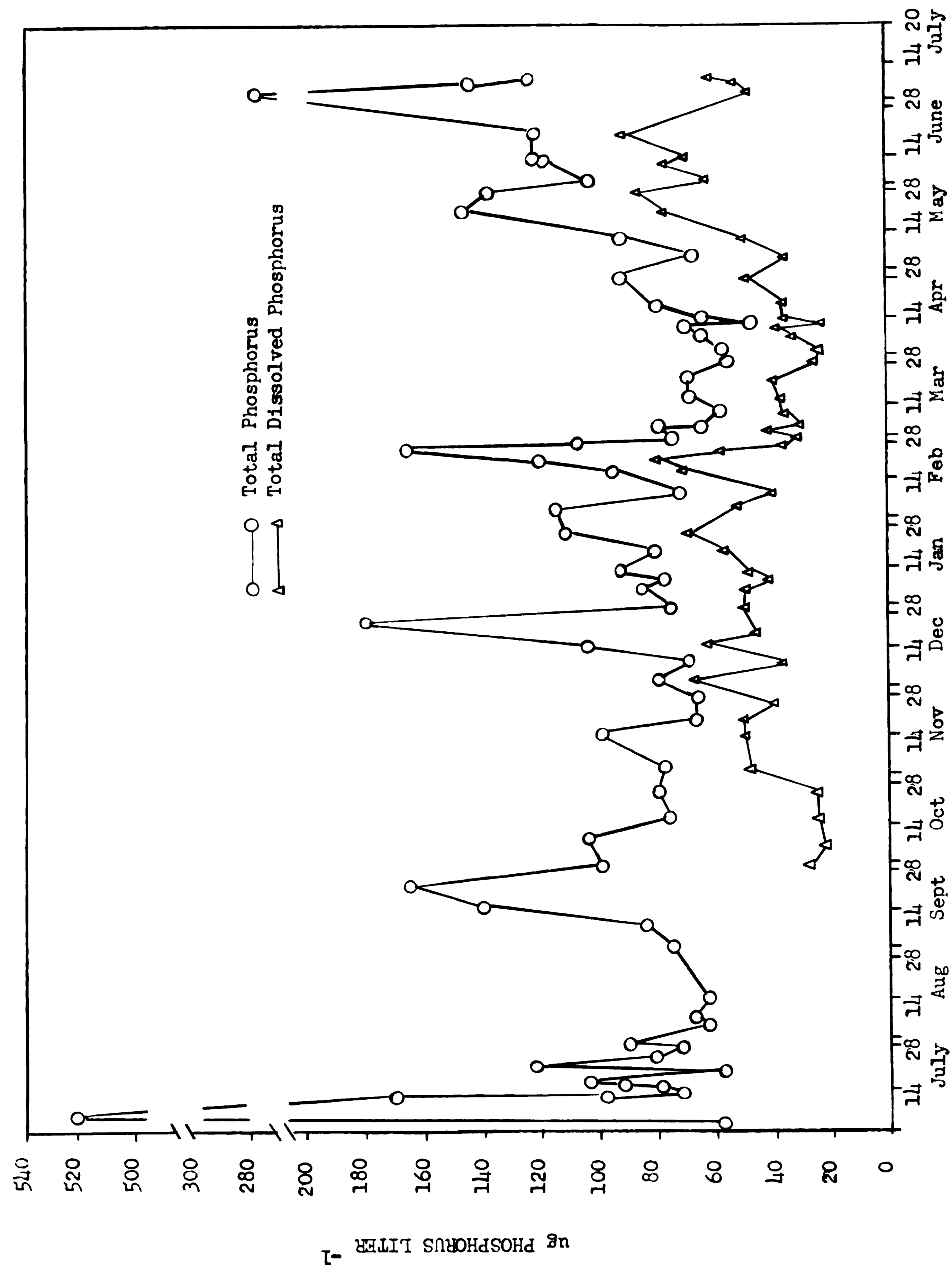
1 Master's thesis in preparation, Dept. Fisheries and Wildlife, M.S.U.

Figure 9. Phosphorus concentrations of water samples collected at Dobie Road


Total Phosphorus
Total Dissolved Phosphorus
ug PHOSPHORUS LITER -1
540
520
500
300
280
200
180
160
140
120
100
80
60
40
20
0
14 July 28
14 Aug 28
14 Sept 28
14 Oct 28
14 Nov 28
14 Dec 28
14 Jan 28
14 Feb 28
14 Mar 28
14 Apr 28
14 May 28
14 June 28
14 20 July

concentration were recorded by the investigator. The chief advantage of this method is that an estimate of phosphorus import can be made for any time period simply by measuring the area of the curve over the desired dates.

Total phosphorus. The monthly distribution of phosphorus is dependent upon the discharge trends of the river. The months of July, December, February, and March accounted for 59.62% of the total discharge and for 65.39% of the phosphorus load for the year. The maximum monthly import was observed in July 1957 when 5,992 kg P were transported into the study area. Similarly, a minimum load of 299 kg P was recorded in August 1957. The peak phosphorus loads that accompanied individual floods are shown in table 8 . These data show that 45% of the annual phosphorus import was carried into the study area by three floods having a combined duration of 31 days. Therefore, floods function to make nutrients most available when the conditions for their utilization are least favorable.

The phosphorus yield of the watershed area is estimated to be 50 kg P mile^{-2} year^{-1}. Sawyer (1947) reports a figure of 72 kg P mile^{-2} year^{-1} for agricultural drainage and runoff in the Madison, Wisconsin, lake region. Brehmer (1958) estimated the annual phosphorus output of a sewage disposal plant located 9.9 miles upstream from the study area as 2.5 metric tons. This quantity of phosphorus is 15.5% of the yearly import at Dobie Road.

Soluble phosphorus. The soluble phosphorus loads were more uniform than total loads even during periods of high discharge (table 7). A maximum value of 726 kg P was recorded for the month of March 1958. Similarly, a minimum value of 162 kg P was observed in November 1957.

TABLE 7

COMPUTED MONTHLY PHOSPHORUS LOADS FOR THE DOBIE ROAD STUDY AREA
DATA ARE GIVEN IN KILOGRAMS OF ELEMENTAL PHOSPHORUS

Month	Total P	Percent of Total	Soluble P	Percent of Total	Discharge (m^3 sec^{-1})
1957					
July [1]	5,992.0	37.34	—	—	461.83
August	299.2	1.86	—	—	53.03
September	362.2	2.26	—	—	41.91
October	531.8	3.31	161.8	3.51	67.89
November	1,259.6	7.85	726.0	15.74	138.44
December	1,860.8	11.59	673.6	14.61	254.19
1958					
January	749.8	4.67	472.6	10.25	120.67
February	1,164.0	7.25	556.8	12.07	108.64
March	1,477.6	9.21	726.4	15.75	262.20
April	850.0	5.30	426.8	9.26	147.64
May	660.6	4.12	418.0	9.06	75.87
June	540.8	3.37	365.4	7.92	52.81
July [2]	300.0	1.87	84.0	1.82	37.92
Totals	16,048.4		4,611.4		1,823.04

[1] Data computed for 3-31 July only.

[2] Data computed for 1-3 July only.

TABLE 8

PEAK PHOSPHORUS LOADS FOR THE DOBIE ROAD STUDY AREA DURING FLOOD PERIODS. DATA ARE GIVEN IN KILOGRAMS OF ELEMENTAL PHOSPHORUS

Date	Total P	Percent of Total P for the Year	Discharge (m^3 sec^{-1})
1957			
5-15 July	4,524	28.19	304.56
18-31 Dec	1,528	9.52	174.87
1958			
24 Feb-4 Mar	1,160	7.23	122.31
Totals	7,212	44.94	601.74

From 1 October 1957 to 3 July 1958, 48.1% of the load was composed of soluble phosphorus. Perhaps this figure would be somewhat lower if the July 1957 flood was sampled for soluble phosphorus.

Biotic Utilization of phosphorus. It was found that the rate of phosphorus fixation by periphyton is closely related to the growth rate of the community. The two rates somewhat resemble an exponential relationship where the rate of phosphorus fixation would be equal to the growth rate of the periphyton colony raised to some power. If this was the case a semilog plot of the data would result in a straight line. As can be seen in figure 10 this is far from being the case; however, the plot is still suggestive of such a relationship.

The degree of scatter shown in figure 10 is not surprising considering the data were collected over a period of a year from diatom communities which had different dominant genera. Since each group has its own characteristic growth rate range it was not possible to determine if the scatter would be reduced if the same taxa were present throughout the entire growth rate range.

A maximum fixation rate of 383.2 ug P dcm^{-2} day^{-1} was noted in June 1958. The minimum fixation rate of 0.7 ug P dcm^{-2} day^{-1} was observed in January 1958.

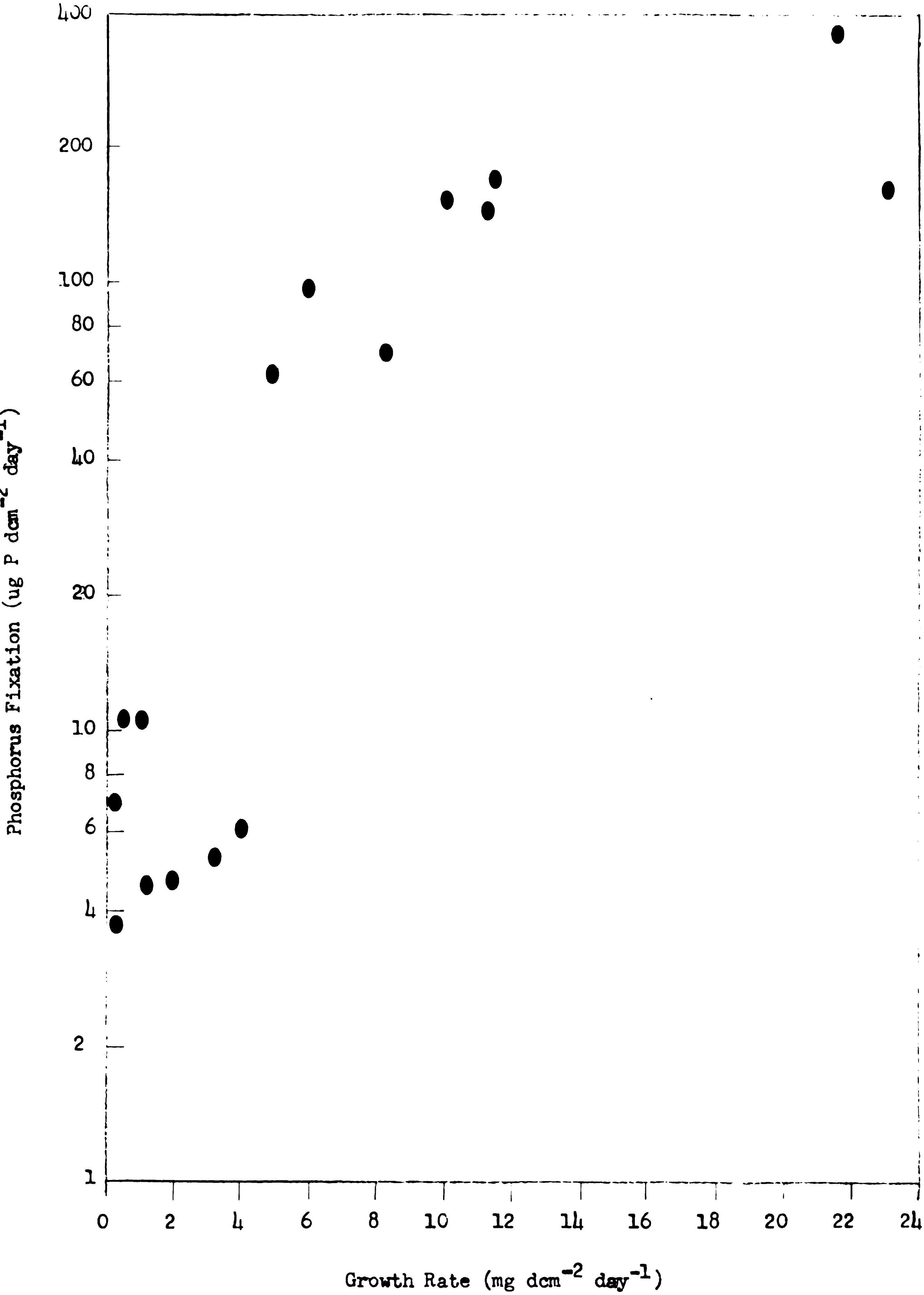
The phosphorus fixation rates of periphyton colonizing artificial substrata were used to estimate the phosphorus anabolism of the river bottom. Before making such estimates the surface area available for periphyton growth had to be determined. This was accomplished by taking profile measurements of the stream bottom at the time of base flow. A graphic profile of these data was made and the surface area determined with a planimeter. In a strict sense this figure does not represent the

TABLE 9

A COMPARISON OF PHOSPHORUS UPTAKE BY PERIPHYTON AND NET PERIPHYTON PRODUCTION.

Collection Date	Mean Phosphorus Uptake (ug P $dcm^{-2}day^{-1}$)	Mean Periphyton Production (mg $dcm^{-2}day^{-1}$)
1957		
31 July	5.7	3.38
8 Aug	13.3	6.58
27 Aug	10.9	0.52
3 Sept	6.0	2.06
1 Oct	4.8	1.25
4 Nov	6.3	4.08
5 Dec	10.5	0.86
1958		
7 Jan	0.7	0.13
28 Jan	7.0	0.11
18 Feb	3.8	0.12
19 Mar	11.0	1.01
17 Apr	75.5	8.33
5 May	151.6	10.12
12 May	175.0	11.47
19 May	99.0	5.11
29 May	62.9	4.89
11 June	147.6	11.34
18 June	383.7	21.21
25 June	173.5	22.78

Figure 10. The relationship between phosphorus fixation by periphyton and periphyton growth.


400
200
100
80
60
40
20
10
8
6
4
2
1
Phosphorus Fixation (ug P dcm^{-2} day^{-1})
0
2
4
6
8
10
12
14
16
18
20
22
24
Growth Rate (mg dcm^{-2} day^{-1})

actual surface area of the stream bottom since it makes no allowances for fluctuations in stream depth or the surface area of the sand particles composing the stream bottom. Therefore, this value is taken to be the average effective surface area available for periphyton growth throughout the year. This interpretation is based on the following assumptions: first, the surface created by the sand particles is too finely divided to provide additional space for periphyton growth; second, fluctuations in stream depth would have only a negligible effect on the total amount of nutrient utilized by the community. There is some empirical justification for the former. It was found that increasing the surface area of a substrate by scoring it with a file failed to stimulate increased growth. The latter assumption is also somewhat justified since there is a two foot bank on the stream and minor fluctuations in depth would only increase the surface area by two vertical distances on both sides of the stream. Furthermore, such increases in surface area are ephemeral and occur when conditions for periphyton colonization and phosphorus utilization are unfavorable. Therefore, it is felt that the concept of an effective surface area is not only convenient, but desirable.

In extrapolating data from artificial substrata to stream bottom it is also necessary to make the following assumptions; the taxonomic components of the artificial community are the same as the natural community, and both communities are growing at the same rate. The first assumption has been shown to be valid in the Red Cedar River by Peters (1958), the latter has not been investigated. If it is assumed that the bulk of the standing crop of periphyton is actively utilizing phosphorus, then fixation values computed from artificial substrata represent only the quantity of nutrient fixed by new growth. However, if it is assumed that a major part of the plant biomass on the stream bottom is not actively utilizing phosphorus, then the data become actual estimates of the total phosphorus intake of the area. Data from the Red Cedar showed that a saturation concentration is reached within a colony of periphyton growing on an artificial substrate. Therefore, the amount of phosphorus fixed by the "old" standing crop is probably negligible compared to the quantity fixed by new growth. On this basis it is felt that the data that follow are most closely related to the total phosphorus intake of the area under consideration.

The difference between the previously cited maximum and minimum fixation rates can be vividly illustrated by considering what length of river morphometrically the same as the study area would be required to autotrophically fix the daily phosphorus output of the Williamston sewage treatment plant. The daily output was estimated to be 6,790 g P day^{-1}. (Brehmer 1958). Using the maximum fixation rate it was computed that 7.9 km (4.97 miles) would be required to deplete the daily phosphorus load. During the winter, when the minimal rate occurred, 4,380.7 km (2,722.6 miles) would be required to fix the same quantity of phosphorus.

Obviously, in nature, this length of stream is not required to deplete the daily sewage output. Initially there is a severe depletion of nutrients in the first 50 meters downstream from the sewage outfall due to heterotrophic utilization. Further downstream the system becomes morphologically adjusted to increasing nutrient loads. That is, a river will broaden and develop depositional features such as flood plains and bars which increase the effective surface area available for periphyton growth and nutrient fixation.

The seasonal efficiency of nutrient fixation will be discussed in terms of gross and net efficiency quotients. The area under consideration is a 100 meter length of stream at Dobie Road. This zone is a relatively uniform sand bottomed run having an effective surface area of 2,213 m^2. This figure was obtained by the previously cited method.

The above mentioned quotients are defined as:

$$\text{Gross efficiency quotient (\%)} = \frac{P_f}{L_t} \times 100$$

$$\text{Net efficiency quotient (\%)} = \frac{P_f}{L_t} \times 100$$

where

P_f = the total quantity of phosphorus fixed by periphyton during the study period.

L_t = the total phosphorus import for the study period.

L_s = the soluble phosphorus import for the study period.

From these equations it can be seen that the gross efficiency quotient takes into account both the utilizable and non-utilizable fractions of the nutrient load while the net efficiency deals only with the utilizable fraction.

The seasonal efficiency quotients and the percentages of the annual phosphorus load carried into the experimental area during the study periods are shown in table 10. The lowest efficiencies were noted during the winter months when periphyton production was minimal. The large supply of nutrients available for periphyton growth during the winter tend to minimize these values. Similar values were observed during floods when nutrient import was maximal and periphyton production minimal.

TABLE 10

SEASONAL PHOSPHORUS EFFICIENCY QUOTIENTS CALCULATED FOR 100 METERS OF RIVER

Collection Date ①	% of Annual Total P Import	% of Annual Soluble P Import ②	Gross Efficiency Quotient (%)	Net Efficiency Quotient (%)
1957				
31 July (7)	1.65	———	0.0033	———
8 Aug (7)	0.59	———	0.0219	———
27 Aug (7)	0.38	———	0.0274	———
3 Sept (14)	0.86	———	0.0135	———
1 Oct (14)	1.20	———	0.0077	———
4 Nov (14)	5.00	3.29	0.0024	0.0128
5 Dec (14)	2.20	5.31	0.0092	0.0132
1958				
7 Jan (34)	13.15	18.08	0.0003	0.0007
28 Jan (21)	3.31	7.40	0.0030	0.0047
18 Feb (21)	2.18	4.34	0.0005	0.0009
19 Mar (28)	11.24	17.31	0.0038	0.0085
17 Apr (14)	11.37	20.20	0.0128	0.0253
5 May (10)	1.55	2.73	0.1349	0.2663
12 May (7)	0.84	1.27	0.2011	0.4610
19 May (7)	0.95	2.07	0.1006	0.1604
29 May (10)	1.28	3.23	0.0675	0.0932
11 June (9)	1.21	2.84	0.1512	0.2248
18 June (7)	0.89	2.09	0.4139	0.6140
25 June (7)	0.67	1.66	0.2516	0.3517

① the number in parenthesis indicates the exposure period in days.

② total annual soluble phosporus import computed from 1 Oct 57 to 3 July 58.

In January 1958 the gross and net efficiency quotients were 0.003% and 0.0007% respectively. In the same period 13.1% of the total annual phosphorus load and 18.1% of the annual soluble phosphorus load were imported into the study area. In contrast, during a study period in June 1958 only 0.89% of the total annual phosphorus import and 2.09% of the annual soluble import were available. The gross and net efficiency quotients were 0.42% and 0.61% respectively.

Seasonal changes in the phosphorus concentration within the periphyton colony were studied by means of phosphorus/weight quotients obtained from artificial substrata. The ash-free dry weight measurements were determined by the methodology described on page 11. The P/W quotients are shown in table 11. Each quotient represents the mean weight value obtained from four to five substrata and the mean phosphorus value obtained from two to three substrata. The quotient obtained from the means was multiplied by 1,000 as a notational convenience.

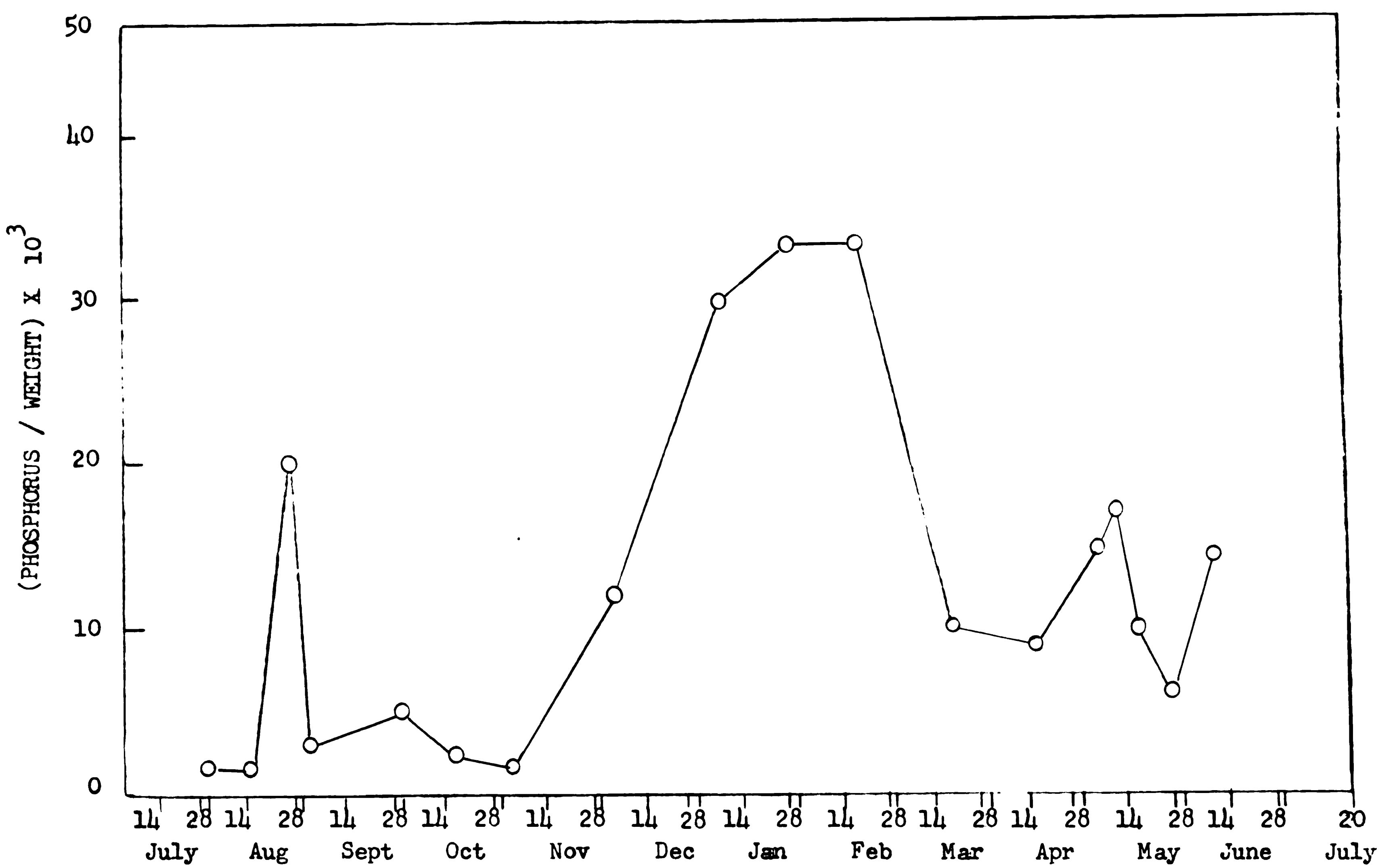
The P/W x 10^3 values for the year ranged between 1.49 and 33.63. Some of the variation can be attributed to the seasonal differences in taxa. However, some striking differences were noted in communities having essentially the same taxonomic composition. For example, in late July and early August the quotients ranged between 1.49 and 1.66; later in August a quotient of 20.98 was observed. The increase in the relative phosphorus content of the colony was accompanied by a decrease in growth rate. The late July and early August growth rates ranged between 3.38 and 9.54 mg $dcm^{-2}day^{-1}$; in late August the rate dropped to 0.52 mg dcm^{-2} day^{-1}. When midwinter periphyton growth was less than 0.20 mg $dcm^{-2}day^{-1}$, P/W quotients were as high as 33.5 in two out of three observations. Therefore, in some cases when dealing with the same taxa, the phosphorus content of the colony appeared to be inversely related to the growth rate.

TABLE 11

SEASONAL PHOSPHORUS/WEIGHT QUOTIENTS OF PERIPHYTON COLLECTED FROM ARTIFICIAL SUBSTRATA

Collection Date	Mean P (mg)	Mean W (mg)	$\frac{\text{Mean P}}{\text{Mean W}} \times 10^3$	Standard Error P (mg)	Standard Error W (mg)
1957				(±)	(±)
31 July	0.055	33.20	1.66	0.0028	5.56
16 Aug	0.130	87.37	1.49	0.0540	7.51
27 Aug	0.107	5.10	20.98	0.0035	0.77
3 Sept	0.117	23.86	4.90	0.0073	1.61
1 Oct	0.095	24.48	3.88	0.0010	1.10
4 Nov	0.123	80.02	1.54	0.0010	3.13
5 Dec	0.205	16.86	12.16	0.0301	3.37
1958					
7 Jan	0.034	6.44	5.28	0.0006	2.00
28 Jan	0.103	3.07	33.55	0	0.36
18 Feb	0.113	3.36	33.63	0	0.68
19 Mar	0.431	39.66	10.86	0.0451	10.25
17 Apr	1.480	162.00	9.13	0.2793	6.96
5 May	2.123	141.60	14.99	0.1633	7.01
12 May	1.715	112.40	15.26	0.1354	6.01
19 May	0.970	53.07	18.27	0.0997	2.82
29 May	0.880	68.35	12.87	0.1003	6.85
11 June	1.860	142.87	13.02	0	4.45
18 June	3.760	207.90	18.09	0.0204	36.51
25 June	1.700	223.17	7.62	0.2507	72.15

Figure 11. Seasonal variations in phosphorus/weight quotients obtained from artificial substrata.


50
40
30
20
10
0
(PHOSPHORUS / WEIGHT) X 10^3
14 28 14 28 14 28 14 28 14 28 14 28 14 28 14 28 14 28 14 28 14 28 14 28 20
July Aug Sept Oct Nov Dec Jan Feb Mar Apr May June July

Other times this relation was not so well defined. Perhaps the high quotients (13.02 - 18.27) observed in May and June when production was maximal resulted from over exposing the substrata. It must be remembered that the mean production rates were computed on an arithmetic basis. Therefore, it is quite possible that production at the time of collection was minimal and hence the phosphorus concentration maximal. Such a situation was described by Lund (1949) in his studies of annual spring blooms of Asterionella formosa. In this case it was observed that the phosphorus concentration within the cell was much greater near or at the peak of a bloom.

Nihei (1955) reports a mechanism that explains the increase in phosphorus concentration accompanying growth cessation. Working with Chlorella he found that prior to mitosis there is an accumulation of polyphosphates which are used as an energy source in processes connected with cell division. As division occurs the phosphorus is dissipated by being redistributed to the new cells. However, if mitosis is inhibited there is an accumulation of polyphosphates within the cell.

In January 1958 two sets of substrata were exposed for periods of 21 and 34 days respectively. At the time of collection both sets had P/W x 10^3 quotients that were practically indentical (33.55 and 33.63). There are two factors which indicate a P/W quotient of this magnitude represents the community saturation concentration. It is to be noted that an additional 13 days of exposure failed to cause an increase in phosphorus concentration; furthermore, production was minimal and hence polyphosphate accumulation maximal. The periphyton colony was predominantly composed of two genera of diatoms; Navicula, and Fragellaria.

Phosphorus as a limiting factor. Soluble phosphorus concentrations found in the Red Cedar River ranged between 21 and 108 ug P l^{-1}; with an annual mean concentration of 50.1 ug P l^{-1}. Chu (1943) working with laboratory cultures gave values for minimal concentrations of phosphorus just permitting optimal growth in six species of phytoplankton. These values ranged from 6 to 29 ug P l^{-1}.

More recent studies, by Rhode (1948), indicate that Chu's minimal concentrations are too high when dealing with natural populations. Rhode found that Asterionella formosa could thrive in a lake having phosphorus concentrations that were inadequate for growth in artificial media. Fogg and Westlake (1955) suggest that some compound, possibly a peptide, is present in lake water which facilitates the ease of phosphorus utilization. Thus, on the basis of experiments by Lund (op. cit.), Rhode (op. cit.), and Chu (op. cit., 1945) it seems very unlikely that the phosphorus concentrations found in the Red Cedar are low enough to limit periphyton production.

It is more probable that the high level of phosphorus present in the Red Cedar would tend to limit or exclude certain taxa of periphyton. Rhode (op. cit.) studied the chrysophycids Dinobryon divergens and Uroglena americana and found they were able to reproduce at a maximal rate when the phosphorus concentration of the water was bearly detectable. Both species became inhibited after the phosphorus concentration was raised to 1.6 ug P l^{-1}.

NITROGEN

The inorganic nitrogen concentration in water samples collected from 26 November 1957 to 7 July 1958 is shown in figure 12 . The nitrogen sampling schedule, like the one described for phosphorus, was determined determined by the discharge trends of the river. Similarly, nitrogen loads were computed by the area under the curve method.

The method of analysis did not provide for the differentiation between nitrate and nitrite. Therefore, the total inorganic nitrogen concentration was accounted for in the following way; nitrate plus nitrite, and ammonia nitrogen. Nitrite occurs in natural waters as an oxidation-reduction intermediate between ammonia and nitrate and is seldom present in appreciable amounts except in cases of extreme organic pollution.

Ammonia nitrogen. Ammonia in natural water is present in the form of NH_4^+ and NH_4OH. For the usual pH values found in the river the ratio of NH_4^+ to NH_4OH would be approximately 30 to 1. Under normal winter and fall conditions the ammonia concentration never exceeded 0.30 mg $N.NH_3$ l^{-1}. During the summer and spring months ammonia is usually present only as a trace (Brehmer 1958). However, an exception to this general rule was noted following an industrial accident which occurred 35 miles upstream from the experimental area.

On 21 May 1958 a fire destroyed a portion of a metal plating plant located in Fowlerville, Michigan. In the course of extinguishing the fire water flooded the cyanide tanks and toxic chemicals were diverted into a waste lagoon . The lagoon outlet was closed and its contents treated with sodium hypochlorite to oxidize the cyanide to the relatively non-toxic cyanate (Eldrige 1933, Dobson 1947). Cyanate is hydrolized to ammonia compounds at a rate which is a function of pH. When the reaction was complete the contents of the lagoon were feed into the river. It is thought this incident was responsible for the extraordinarily high ammonia concentrations (between 0.25 and 0.73 mg $N.NH_3$ l^{-1}) observed during the first 14 days of June.

The maximum monthly ammonia load was noted in February 1958, when 2,144 kg $N.HH_3$ were transported into the study area. A minimum monthly value of 54 kg $N.NH_3$ was recorded for the months of April and May 1958.

In June following the industrial accident, nearly half of the total inorganic nitrogen import (2,765 kg $N.NH_3+NO_2+NO_3$) consisted of ammonia nitrogen. Ammonia nitrogen comprised 9.83% of the total inorganic nitrogen load for the entire study. This value is not a fair estimate of the per annum percentage of ammonia for two reasons. First, the study was weighted in favor of those months characterized by the presence of ammonia (Brehmer 1958); second, because of the high concentrations of ammonia attributed to the accident at Fowlerville. In any case, it is safe to say that ammonia comprises only a small fraction of the total inorganic nitrogen that is available for biotic utilization in the Red Cedar River.

Nitrite and nitrate. The monthly nitrite plus nitrate loads are given in table 12. These values were computed for a study period ranging from 26 November 1957 to 7 July 1958. The total import for this period was 75.7 metric tons $N.NO_2+NO_3$ or 91.2% of the total inorganic nitrogen load. A maximum monthly value of 20.9 metric tons $N.NO_2+NO_3$ was noted in December 1957. A minimum monthly value of 1.4 metric tons $N.NO_2+NO_3$ was recorded in May 1958.

The nitrite plus nitrate yield of the watershed is estimated to be 34.7 kg $N.NO_2+NO_3$ $mile^{-2}$ $month^{-1}$. The total phosphorus yield for the same period was 4.1 kg P $mile^{-2}$ $month^{-1}$.

The magnitude of these loads, as was the case with phosphorus, was found to be dependent upon the discharge trends of the river. That is, periods of high discharge were accompanied by high nutrient import. However, one essential difference between phosphorus and nitrogen is

Figure 12. Nitrogen concentrations of water samples collected at Dobie Road.

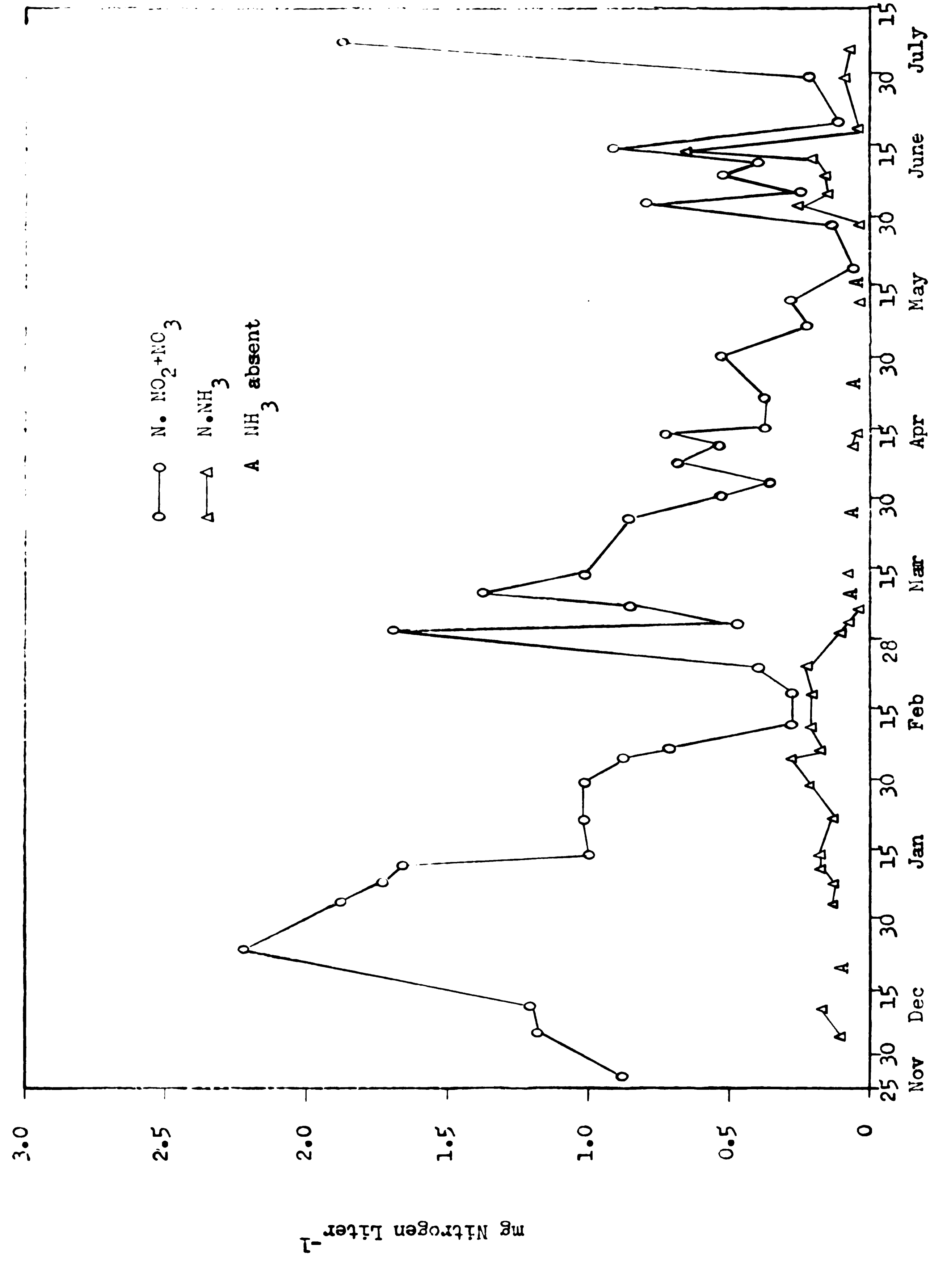

N• NO2+NO3
N•NH3
A NH3 absent
mg Nitrogen Liter-1
0
0.5
1.0
1.5
2.0
2.5
3.0
Nov
Dec
Jan
Feb
Mar
Apr
May
June
July
25 30 15 30 15 30 15 28 15 30 15 30 15 30 15 30 15

TABLE 12

COMPUTED MONTHLY INORGANIC NITROGEN LOADS FOR THE DOBIE ROAD STUDY AREA
DATA ARE GIVEN IN KILOGRAMS OF ELEMENTAL NITROGEN

Month	NO_2+NO_3	NH_3	Total Inorganic Nitrogen	Percent of Total
1957				
November [1]	1,142	132	1,274	1.52
December	20,850	1,848	22,698	27.02
1958				
January	13,028	1,448	14,476	17.23
February	5,316	2,144	7,460	8.88
March	20,592	1,008	21,600	25.71
April	6,098	54	6,152	7.32
May	1,384	54	1,438	1.71
June	1,751	1,014	2,765	3.29
July [2]	5,580	556	6,136	7.30
Totals	75,741	8,258	83,999	

[1] Data computed for 26-31 November only.
[2] Data computed for 1-7 July only.

quite clear. A peak load of phosphorus during a flood is characterized by both a sudden rise and fall. Peak nitrogen loads are characterized by a sudden rise followed by a period of sustained nitrogen enrichment. For example, during the February-March flood in 1958 the daily phosphorus loads dropped to their pre-flood levels in four days. However, the daily nitrite plus nitrate loads were sustained at a level eight times greater than the pre-flood values for a period of three and a half weeks.

The data indicate that agricultural runoff is the major source of inorganic nitrogen while sanitary drains are the major source of phosphorus. For example, during an extended freeze in the winter of 1957-1958 the inorganic nitrogen values dropped uniformly over a period of a from 2.21 to 0.45 mg $N.NO_2 + NO_3 + NH_3$ l^{-1}. This low level of inorganic nitrogen was maintained until a thaw occurred. It is believed this decrease was caused by the gradual elimination of agricultural runoff by freezing.

During the thaw no depression was noted in the phosphorus concentration. This adds strength to the notion that the origin of phosphorus is sanitary drains rather than agricultural runoff since the former are not subject to freezing. Such an interpertation explains the difference between the nature of the phosphorus and nitrogen loads during and following floods. The rapid and striking rise of both phosphorus and nitrogen would represent the "flushing out" of stream deposits. The rapid recovery of phosphorus to pre-flood levels signifies and exhaustion of phosphorus from this source. On the other hand, the sustained high level of nitrogen would be interperted as originating from the increased runoff which is maintained for a considerable period after the flood crest has been reached and the stream bed flushed.

Prior to the freeze over 90% of the inorganic nitrogen was in the nitrite plus nitrate form with the remainder being ammonia nitrogen. During the freeze when minimal nitrogen concentrations were present nearly half of the total inorganic nitrogen was ammonia nitrogen. Following the thaw normal winter ratios of ammonia nitrogen to other forms of inorganic nitrogen were restored.

Biotic utilization of inorganic nitrogen. The nitrogen content of periphyton colonizing artificial substrata was studied using the previously cited methods. The N/W x 10^3 quotients from 5 May to 25 June 1958 are shown in table 13. The quotients ranged between 9.32 and 22.42.

The percentage of nitrogen in the ash-free dry weight of diatomaceous communities in the Red Cedar River varied between 0.93 and 2.24%; with a mean of 1.49%. These values are somewhat lower than those given by Ketchum and Redfield (1949) for laboratory cultures. They found that the diatom, Nitzschia closterium, had a mean nitrogen content of 6.67%. Similar values for members of the Chlorophyceae averaged between 6.62 and 8.65%. Ketchum and Redfield (op. cit.) also noted that the percentage of nitrogen in Chlorella pyrenoidosa was approximately halved when grown in media deficient in nitrogen, or nitrogen and phosphorus. Algae cultured in phosphorus deficient media had nitrogen concentrations slightly higher than those grown in phosphorus rich media.

The net efficiency quotients calculated for 100 meters of stream are shown in table 14. These values varied from 0.029 to 0.187%. Six out of seven of the net nitrogen quotients were lower than the net phosphorus quotients for the same time periods by factors ranging from two to twenty. The absolute quantities of nitrogen and phosphorus fixed by the community were nearly the same (table 15). Therefore, the difference in the net

TABLE 13

NITROGEN/WEIGHT QUOTIENTS OF PERIPHYTON COLLECTED FROM ARTIFICIAL SUBSTRATA

Collection Date	Mean N (mg)	Mean W (mg)	$\frac{\text{Mean N}}{\text{Mean W}} \times 10^3$	Standard Error N (mg)	Standard Error W (mg)
1958				(±)	(±)
5 May	2.18	141.60	15.40	0.283	7.01
12 May	1.09	112.40	9.70	0.071	6.01
19 May	1.19	53.07	22.42	0.191	2.82
29 May	1.29	68.35	18.87	0.099	6.85
11 June	2.40	142.87	16.80	0.141	4.45
18 June	2.41	207.90	11.59	0.141	36.51
25 June	2.08	223.17	9.32	0.233	72.15

TABLE 14

NITROGEN EFFICIENCY QUOTIENTS CALCULATED FOR 100 METERS OF RIVER

Collection Date	Exposure Period (Days)	% of Total Inorganic N Import ◁1	Net Efficiency Quotient (%)
1958			
5 May	10	1.51	0.027
12 May	7	0.84	0.024
19 May	7	0.28	0.080
29 May	10	0.18	0.131
11 June	9	0.73	0.062
18 June	7	1.43	0.032
25 June	7	0.21	0.187

◁1 total inorganic N import computed from 27 November 1957 to 7 July 1958.

TABLE 15

NITROGEN/PHOSPHORUS QUOTIENTS OF PERIPHYTON COLLECTED FROM ARTIFICIAL SUBSTRATA

Collection Date	Mean N (mg)	Mean P (mg)	Mean N / Mean P	Standard Error N (mg)	Standard Error P (mg)
1958				(±)	(±)
5 May	2.18	2.12	1.03	0.283	0.1633
12 May	1.09	1.72	0.63	0.071	0.1354
19 May	1.19	0.97	1.23	0.191	0.0997
29 May	1.29	0.88	1.47	0.099	0.1003
11 June	2.40	1.86	1.29	0.141	0
18 June	2.41	3.76	0.64	0.141	0.0204
25 June	2.08	1.70	1.22	0.233	0.2507

efficiencies were due to the greater availablity of inorganic nitrogen. During the study period the ratio of inorganic nitrogen to soluble phos- was approximately five to one.

The relation between the phosphorus and nitrogen content of periphyton was studied from 5 May to 25 June 1958. Nitrogen/phosphorus quotients for this period varied from 0.63 to 1.47 with a grand mean of 1.04 (table 15).

Working with laboratory cultures of several species of green algae and diatoms, Ketchum and Redfield (1949) noted N/P values ranging from 1.6 to 5.3. Correll (1958) found that diatoms growing in an oligotrophic stream had N/P ratios of about 10. These data and information from the Red Cedar seem to indicate that N/P values are dependent upon the availability of phosphorus and the growth rate of the algae. That is, algae grown in phosphorus rich media tend to have lower ratios of N to P because of phosphorus storage. In addition, growth inhibition favors even lower N/P quotients because of the associated accumulation of polyphosphates.

Pollution

The biological evaluation of stream pollution is based primarily on taxonomic changes in the biota. The presence or absence of certain indicator species along with their relative abundance has long been used as a criterion of pollution (Turner 1927, Gaufin and Tarzwell 1952). Such methods are, at best, semi-quantitative and often deal with organisms whose identification is difficult and uncertain. Patrick (1949) gave a quantified system for evaluating pollution based on the taxonomic composition of the biomass. Patrick's work is significant because it extends the concept of indicator species to indicator communities and shows the inadequacy of chemical analyses for pollution detection. However, this method cannot be seriously regarded as a field technique by pollution biologists because of the time and taxonomic knowledge required.

A functional rather than a taxonomic approach to pollution evaluation has been suggested by Odum (1956). Odum classified lotic communities as being oligosaprobic, mesosaprobic, or polysaprobic on the basis of the ratio of community oxygen production to community respiration. This is essentially a quantified version of earlier attempts to categorize pollution by the extent of oxygen depletion. However, unlike previous methods it provides a continuum of index figures (production/respiration quotients) ranging from oligosaprobic to polysaprobic communities. These figures are easily obtained from standard D.O. determinations made in the field. Unfortunately, such a classification is applicable only in cases of organic pollution. Data from the Red Cedar River indicate that the functional composition and physiology of periphyton colonizing artificial substrata might be useful indices of pollution.

C/W and P/W quotients. The floral components of a periphyton colony can be placed into two functional groups; the producers, and the reducers.

In a clean-water zone the community is composed primarily of autotrophic organisms. In constrast, extreme organic pollution is characterized by a large proportion of heterotrophic plants. Therefore, in the transition from oligosaprobe to polysaprobe there should be a continuum of index figures, based on changes in the proportion of producers to reducers, which reflect the degree of organic pollution.

The relative proportion of producers to reducers in periphyton colonizing artificial substrata was studied using the following quotient.

$$C/W \times 1{,}000$$

where

C = the corrected absorbancy of phytopigments extracted from the colony.

W = the ash-free dry weight (mg) of the colony.

This quotient makes use of the fact that a quantitative estimate of the weight of a diatom population can be made from the extracted phytopigments (page 34). Therefore, C is proportional to the weight of the producer fraction of the colony. As the proportion of reducers in the colony becomes greater W will increase and the ratio of C to W becomes smaller.

C/W ratios obtained from a clean-water zone, a polluted zone, and a recovery zone are shown in table 16. The polluted zone was sampled at a point 25 meters downstream from the sewage outfall of the Williamston treatment plant. The clean-water site was located at Dobie Road and the recovery zone 50 meters downstream from the sewage outfall.

The difference in quotients between the polluted zone and the clean-water zone are quite distinct. Mean C/W ratios from the non-polluted zone varied from 10.02 to 16.91. Mean values obtained from samples 25 meters downstream from the sewage outfall were 2.84 and 1.84. A mean

C/W quotient obtained 50 meters downstream from the sewage outfall was essentially the same as one obtained from the clean-water zone on the same day (16.91 vs. 18.89). This dramatically demonstrates the rapid recovery of the stream to an oligosaprobic state.

Brehmer (1956) found that a septic zone was never formed, even in the immediate vicinity of the sewage treatment plant. On the basis of Odum's classification (1956) the intensity of pollution was, at worst, mesosaprobic. Therefore, it was not possible to obtain C/W quotients from the full gamut of saprobe states. Nevertheless, it was demonstrated that C/W ratios can be used to differentiate between oligosaprobe and mild mesosaprobe. It seems logical to assume that polysaprobic communities would have their own characteristic C/W value. When considering extreme polysaprobic conditions, such as described by Bartsch (1948), where extensive stands of "sewage fungus" exist, one can be reasonably certain that the ratio of producers to reducers will be very small.

Thus far only the evaluation of pollution from sanitary wastes has been considered. Data from the Red Cedar indicate that periphyton techniques might have some limited value in detecting sublethal doses of industrial pollution. Since the degree of industrial pollution present in the Red Cedar is unknown the following discussion is more speculative than factual.

It has been demonstrated that algal growth inhibition results in internal polyphosphate accumulation (Nihei 1955). Therefore, any compound which inhibits algal growth would cause an increase of phosphorus within the periphyton colony. Such a state would be reflected in the quotient of the phosphorus content to colony weight, or in the analogous ratio of phosphorus content to the absorbancy of phytopigments extracted

TABLE 16

A COMPARISON OF C/W QUOTIENTS OBTAINED FROM A CLEAN-WATER ZONE, A RECOVERY ZONE AND A POLLUTED ZONE

Collection Date	Clean-Water	C/W Quotient Recovery	Polluted
1957			
1 Oct	16.91	18.89	____
18 Oct	10.56	____	1.84
4 Nov	10.02	____	2.84

from the colony. It has been shown by Procter (1958) and Lawrence (1958) that a wide variety of compounds, both inorganic and organic, can inhibit algal growth.

Such an index of pollution is subject to severe limitations. Data from the Red Cedar (page 72) and elsewhere (Lund 1949) have shown that growth inhibition and subsequent polyphosphate accumulation is a natural occurence in non-polluted waters. It is also unlikely that P/W or P/C quotients occur in a quantitative continuum because of the many factors (i.e. species composition, nutrient supply, growth rate) that contribute to their magnitude. Therefore, the use of such quotients would have to be on a comparative basis (clean-water vs. suspected pollution) and be limited to detecting rather than evaluating pollution. Besides its simplicity, the only advantage this technique might have is the capability of detecting extremely low levels of pollution.

SUMMARY

1. At base flow the Red Cedar River has a methyl orange alkalinity of 250 ppm and a pH of 8.1. The amount of normal carbonate present throughout the year is negligible. The total solids content of the stream varies between approximately 200 and 300 ppm.

2. Suspended solids act as a selective filter favoring the transmission of long-waved radiation. At all levels of turbidity red transmission exceeds green, and green transmission exceeds blue. Dissolved color fluctuates independently of turbidity and plays only a minor role in influencing the total quantity of light transmitted to the stream bottom.

3. The absorbancy of extracted phytopigments can be used to make quantitative estimates of periphyton weight if corrected to conform with the Lambert-Beer Law. Productivity measurements based on phytopigment units showed excellent agreement with gravimetric productivity estimates. Successful measurement of primary production by diurnal oxygen curves appears to be limited to periods of intermediate productivity.

4. The seasonal range in net primary production as measured by artificial substrata is 0.01 to 2.28 g m^{-2} day^{-1} with an annual mean of 0.56 g m^{-2} day^{-1}. The annual gross rate of periphyton production is estimated to about 1 g m^{-2} day^{-1}. The preceeding rates are given in terms of ash-free dry weight.

5. Photosynthetic efficiencies based on net production and surface radiation vary from 0.003% to 0.245% with an annual mean of 0.07%. The annual mean efficiency based on gross primary production and surface radiation is estimated to be about 0.1%. The annual mean rate of energy fixation by periphyton is 0.23 g cal·cm^{-2} day^{-1}. This figure represents the amount of energy available for transfer to consumer organisms.

6. The annual import of phosphorus into the study area is 16 metric tons. During three flood periods collectively representing a time lapse of 30 days about 45% of the total phosphorus import for the yeat was carried into the study area.

7. Phosphorus fixation by periphyton is closely related to periphyton growth. When the two rates are plotted, the relationship resembles an exponential curve. The ratio of phosphorus content to the ash-free dry weight of the periphyton colony (x 1000) varies from 1.54 to 33.63. In general the slowest growing colonies have the highest phosphorus content. Seasonal phosphorus efficiency quotients based on total phosphorus import and calculated for a 100 meter length of stream vary from 0.0003 to 0.41%. Similar efficiency quotients based on soluble phosphorus range from 0.0007 to 0.61%.

8. The total inorganic nitrogen import for a nine month period was 84 metric tons. The effect of floods on the seasonal distribution of inorganic nitrogen was less pronounced than in the case of phosphorus. The data appear to indicate that runoff is the primary source of inorganic nitrogen.

9. The nitrogen content of periphyton samples was 1.49% of the ash-free dry weight. The ratio of nitrogen to phosphorus in periphyton samples collected during periods of maximal growth is approximately 1. Inorganic nitrogen efficiency quotients calculated for a 100 meter length of stream range from 0.03 to 0.19%.

10. The ratio of phytopigment absorbancy to periphyton colony weight can be used to differentiate between oligosaprobic and mesosaprobic communities. Such ratios obtained from a clean-water zone fall between 10.0 and 16.9. Similar values obtained from a polluted zone vary from 1.84

to 2.9. Ratios based on the phosphorus content of the colony are less reliable indices of pollution and appear to be limited to pollution detection rather than evaluation.

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