PRIMARY PRODUCTION IN A MICHIGAN STREAM

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ABSTRACT

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MICHIGAN STREAM

By

Frank J. Tesar

This thesis is part of a pre-impoundment ecological study of a section of a central Michigan stream (Pine River). During summer, 1968, primary production rates of periphyton and aquatic vascular plants were measured and compared at four stations. Measurements in the Pine are compared with similar values in the literature.

Periphyton biomass and production rates were determined gravimetrically from accrual on Plexiglas substrates exposed from 2 to 14 weeks. Diatoms and Cladophora glomerata were the dominant algae in the periphyton. Population turnover times for the four stations were: station 1, 28; 2, 30; 4, 25; and 5, 14 days (stations 1 and 2 were 14.4 and 9.2 km upstream, and 4 and 5, 2.1 and 5.5 km downstream from the proposed dam). Growth curves from May to July were sigmoid with a carrying capacity of 5 to 8 (station 1) and 10 to 20

(stations 2, 4, and 5) g organic matter m^{-2} being reached after 6 to 7 weeks of exposure.

Periphyton production rates were lowest during May and highest in June and July except at station 1 where rates were highest in August. Average summer production rates were: station 1, 0.208; 2, 0.268; 4, 0.272; and 5, 0.374 g organic matter m^{-2} day^{-1}. When rainfall was over 2 cm in a 24 hour period production rates were low because of overcast skies, high turbidity, and scouring of the stream bottom. Substrates in riffles were usually highest in production rates compared to rates in pools and shaded areas. Lowest rates were found in shaded areas. Production rates in the Pine were moderate to high compared with rates measured by other investigators in lakes and streams. Percentage organic matter was low when production rates were high, and compared to values from other investigations, percentages in the Pine were low to average.

Macrophyte biomass and production rates were gravimetrically determined after harvesting plants from weed beds at one and two week intervals. Growth curves of the dominant aquatic vascular plants (three species of Potamogeton) were sigmoid. Maximum standing crop was greatest at station 2 and lowest at station 1. Standing crops in the Pine were similar to crops in other rivers, but lower than emergent plant standing crops.

Average summer macrophyte production rates in plant beds were: station 1, 0.65; 2, 2.83; 4, 1.57; and 5, 1.28 g organic matter m^{-2} day^{-1}. Rates were greatest before maximum standing crop occurred, except at station 1, where the highest production rate occurred at the time of maximum standing crop. Compared to other rivers and lakes, production rates in the Pine were average.

Percentage organic matter of Potamogeton decreased from May to September, apparently due to increased carbonate encrustation later in summer. Values in the Pine were low compared to percentage organic matter of Potamogeton in other streams and lakes.

Summer net production rates at each station were: 1, 0.23; 2, 0.95; 4, 0.53; and 5, 0.56 g organic matter m^{-2} of stream bottom day^{-1}. Stream cover (bankside trees and shrubs), limiting available light, was evidently the major parameter causing low primary production at station 1. Average annual rate of net primary production was estimated at 0.33 g organic matter m^{-2} day^{-1}.

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INTRODUCTION

Primary production rate of an ecological system is defined by Odum (1959) as the rate at which energy is stored by photosynthetic and chemosynthetic activity of producer organisms in the form of organic substances which can be used as food materials. Because secondary consumers, including man, are dependent upon energy fixed by producer organisms, primary production and its measurement are of considerable importance. Biologists are still developing accurate methods for measuring primary production. Great differences and complexities in types of ecosystems have caused ecologists to develop various methods for individual systems. This study was an attempt to measure with existing methods two components of primary production in a natural ecosystem and compare these values with values determined by other workers for similar natural systems.

Most primary production measurements have been made in the past 20 years. The majority of the work has been on marine and lake phytoplankton. In the last decade the significant role that periphyton and aquatic macrophyte production plays in stream and shallow-lake ecosystems

has been emphasized with lakes receiving the most attention. Periphyton and macrophytes are being increasingly studied today because they perform an important function in streams.

Periphyton and aquatic macrophytes serve an important role in streams as food and shelter for higher life forms. In many small streams (e.g., northern trout streams) periphyton and macrophytes are the predominant primary producer serving as a basic food source for primary consumers. Higher trophic levels in the stream ecosystem are ultimately dependent to a considerable extent on this primary production if allochthonous matter input is low. Periphyton and macrophytes, besides being a food source, provide dense habitats which supply food and shelter to small organisms living among the plants. Besides serving an important function in the stream ecosystem, aquatic plants and periphyton are becoming important from man's viewpoint.

With increased usage of streams and rivers as a water source for man, the need for understanding the total stream ecosystem and its components becomes obvious. Presence or absence of aquatic macrophyte and (especially) periphytic algal species is being increasingly used as an indicator of stream purity. As pollution of streams increases this role becomes important in determining the extent and intensity of pollution. Of more importance to man is the part periphyton and aquatic plants perform in

the purification of sewage and water supplies. If nutrients removed by macrophytes and periphyton can be recycled back to man by cropping the biomass directly, this purification role assumes even greater economic importance. Even without considering direct economic values, the complex and important role of periphyton and aquatic macrophytes as primary producers has to be discerned if we are to manage effectively and beneficially the stream ecosystem.

The present work is part of an ecological study being conducted through the Institute of Water Research and Department of Fisheries and Wildlife, Michigan State University. The study was initiated to evaluate ecological effects of impoundment on the Pine River, Michigan. This thesis, one on invertebrate populations (Barber, 1970) and another on fish populations (Mense, 1970) are part of the pre-impoundment investigation. It is hoped that these theses will supply a firm basis for the post-impoundment study.

Objectives of this study were to: (1) identify primary producers in the proposed impoundment area of the Pine River, (2) measure and analyze primary production rates there, (3) compare measured production rates with production estimates of other ecosystems, and (4) provide a basis of comparison for the post-impoundment study.

STUDY AREA

The Pine River, a major tributary of the Tittabawassee River basin, drains the center of the lower peninsula of Michigan. Arising from Pine Lake (T.14 N., R.8 W., Secs. 22, 27) in Mecosta County, the stream flows southeasterly for approximately 71 river km, then northeasterly for approximately 100 river km before joining the Chippewa River, 4.8 river km before the Chippewa enters the Tittabawassee River near Midland. Total drainage area is 1023 km^2. Edaphic, climatological, and hydrological features along with human influence and use of the watershed have been summarized by the Michigan Water Resources Commission (1960).

Climate varies from modified maritime, when wind is from the Great Lakes east or west, to continental when the wind is southerly or northerly. Average monthly temperatures for March and April 1968 were considerably above the 30 year normal (Figure 1). During the rest of the study period from May to September, average monthly temperatures were near the 30 year normal. High precipitation in 1968 compared to the 30 year normal for months of May, September, and December offset low precipitation in February,

Figure 1. Average monthly air temperature and precipitation for 1968 and the 30 year normal at Mt. Pleasant, nearest weather station to the study area (data from Environmental Science Services Administration).

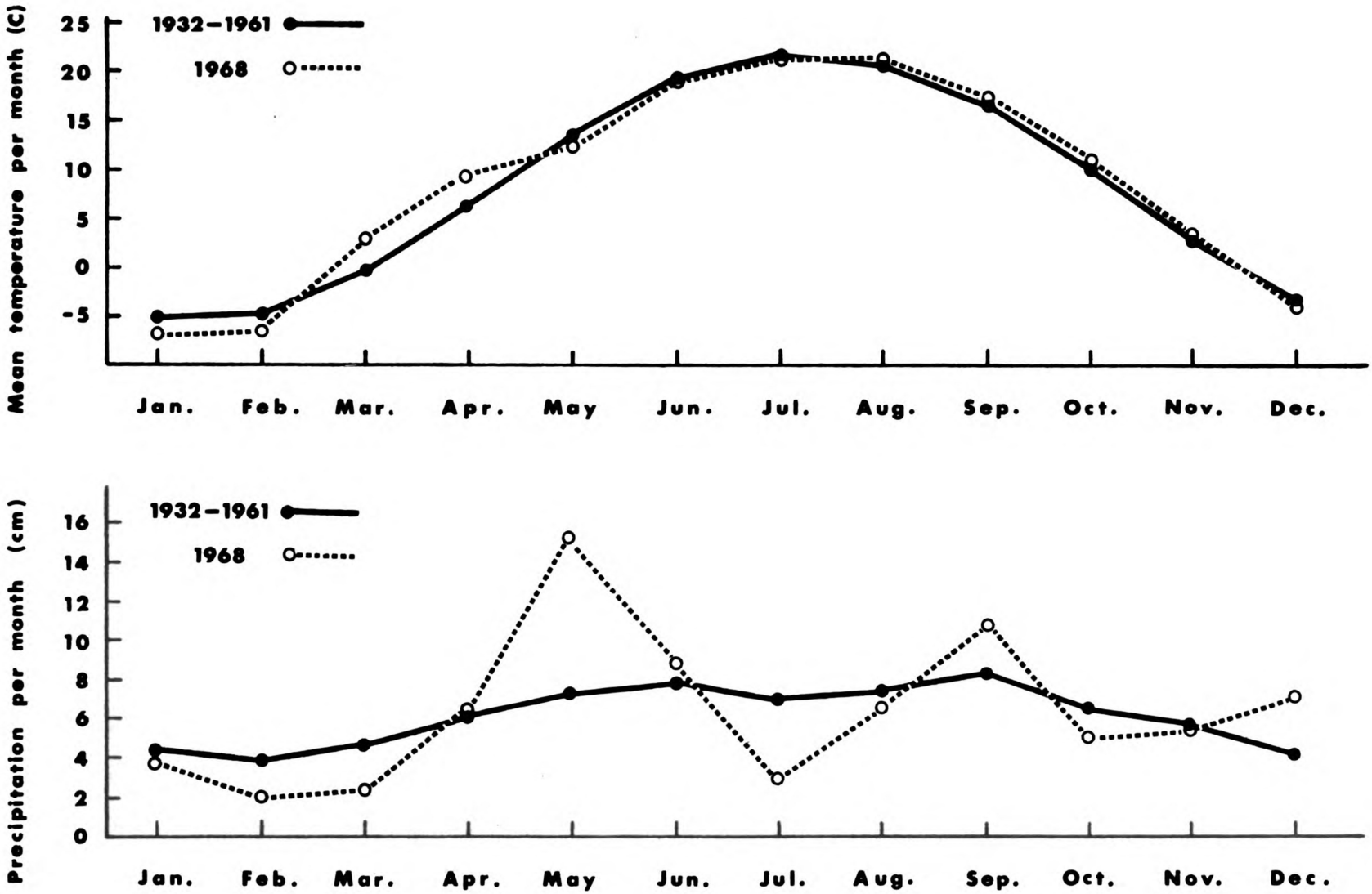
Mean temperature per month (C)
25
20
15
10
5
0
-5
1932–1961
1968
Jan.
Feb.
Mar.
Apr.
May
Jun.
Jul.
Aug.
Sep.
Oct.
Nov.
Dec.
Precipitation per month (cm)
16
14
12
10
8
6
4
2
0
1932–1961
1968
Jan.
Feb.
Mar.
Apr.
May
Jun.
Jul.
Aug.
Sep.
Oct.
Nov.
Dec.

Figure 1

March, October, and especially July to give slightly less than 5 cm over the 30 year normal of 73.99 cm (Figure 1). Rainfall was very high in May, 1968, compared to the 30 year normal.

The study area was chosen between 16.9 and 36.7 river km from Pine Lake. Sampling stations were established near bridge crossings for convenience (Figure 2). Distances in river kilometers between stations were: (1-2) 5.2, (2-3) 8.2, (3-4) 3.1, and (4-5) 3.4 km as determined from U.S.G.S. topographic maps. Average stream widths at stations 1-5 were respectively 8, 11, 12, 14, and 17 m. Chemical and physical data (Appendix A) were determined at stations 1 through 5, while production measurements were determined at all except station 3. Site of the proposed dam is between stations 3 and 4 (Figure 2), leaving stations 4 and 5 below the impoundment, 2 and 3 in the reservoir, and station 1 in the headwaters or in the reservoir depending on the amount of water impounded.

Drainage area above station 5 was estimated to be 332 km^2. Mean annual discharge for 1968 at station 5 was calculated as approximately 2.94 m^3 sec^{-1} ranging from a low of 0.57 m^3 sec^{-1} in August to a high of 21.20 m^3 sec^{-1} in February. Measurements of discharge at station 5 indicated it was 50% of the discharge at Alma (Figure 3). Gradient (estimated from U.S.G.S. topographic maps) in the study area was 0.79 m km^{-1} (Figure 4). Stream width

Figure 2. Map of the upper portion (near the headwaters) of the Pine River, showing the five stations of the study.

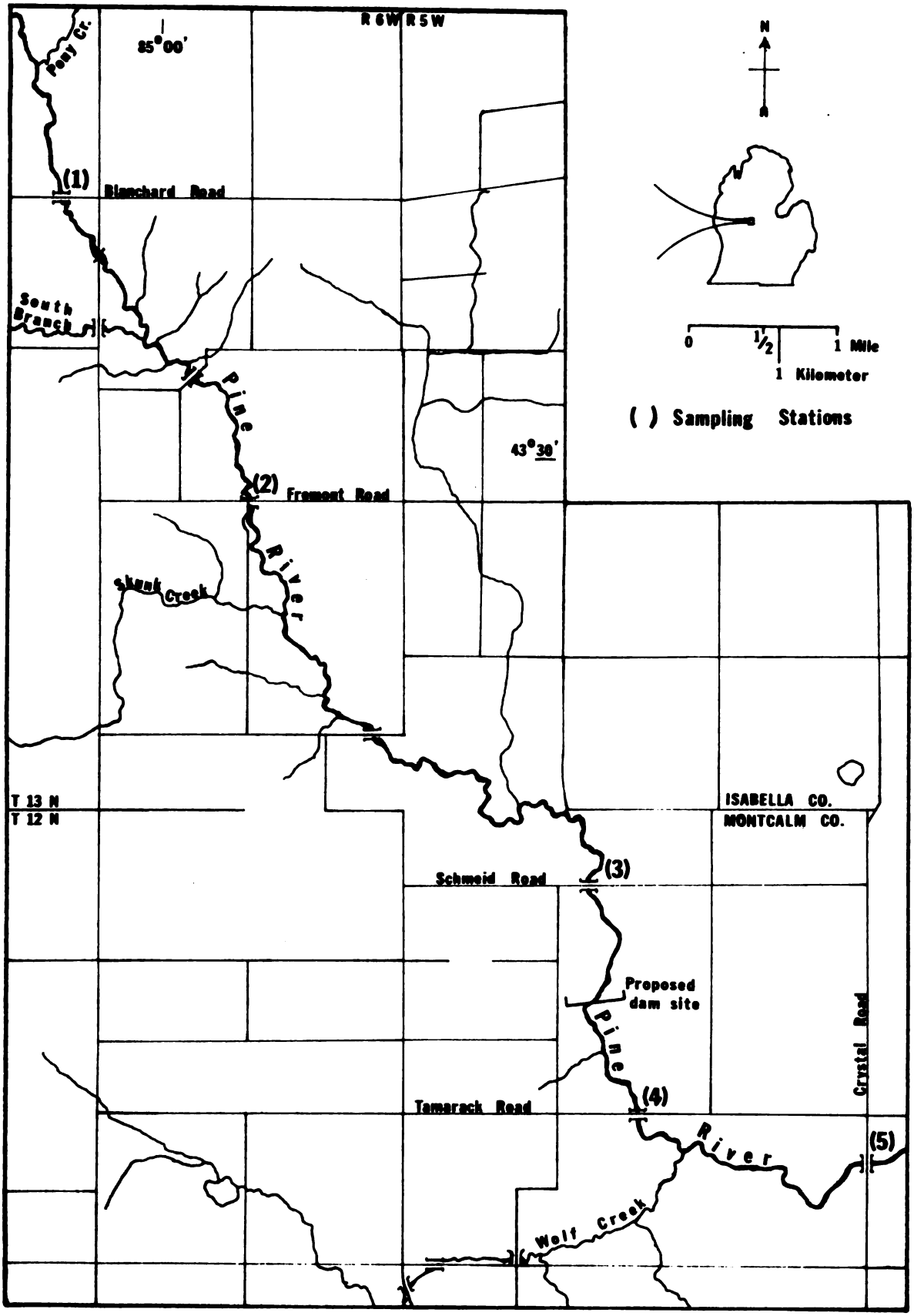
R 6W R 5W
85°00'
Pony Cr.
(1)
Blanchard Road
South Branch
Pine
River
43°30'
(2)
Fremont Road
Skunk Creek
T 13 N
T 12 N
ISABELLA CO.
MONTCALM CO.
Schmeid Road
(3)
Proposed dam site
Pine
River
Crystal Road
Tamarack Road
(4)
(5)
Wolf Creek
N
0
1/2
1 Mile
1 Kilometer
( ) Sampling Stations

Figure 2

Figure 3. Average monthly discharge in m^3 sec^{-1} for the Pine River during 1968 and for the 28 year average (1931-1958). Data from U.S.G.S. gauging station at Alma, Michigan (drainage area 746 km^2, 60 river km downstream from station 5).

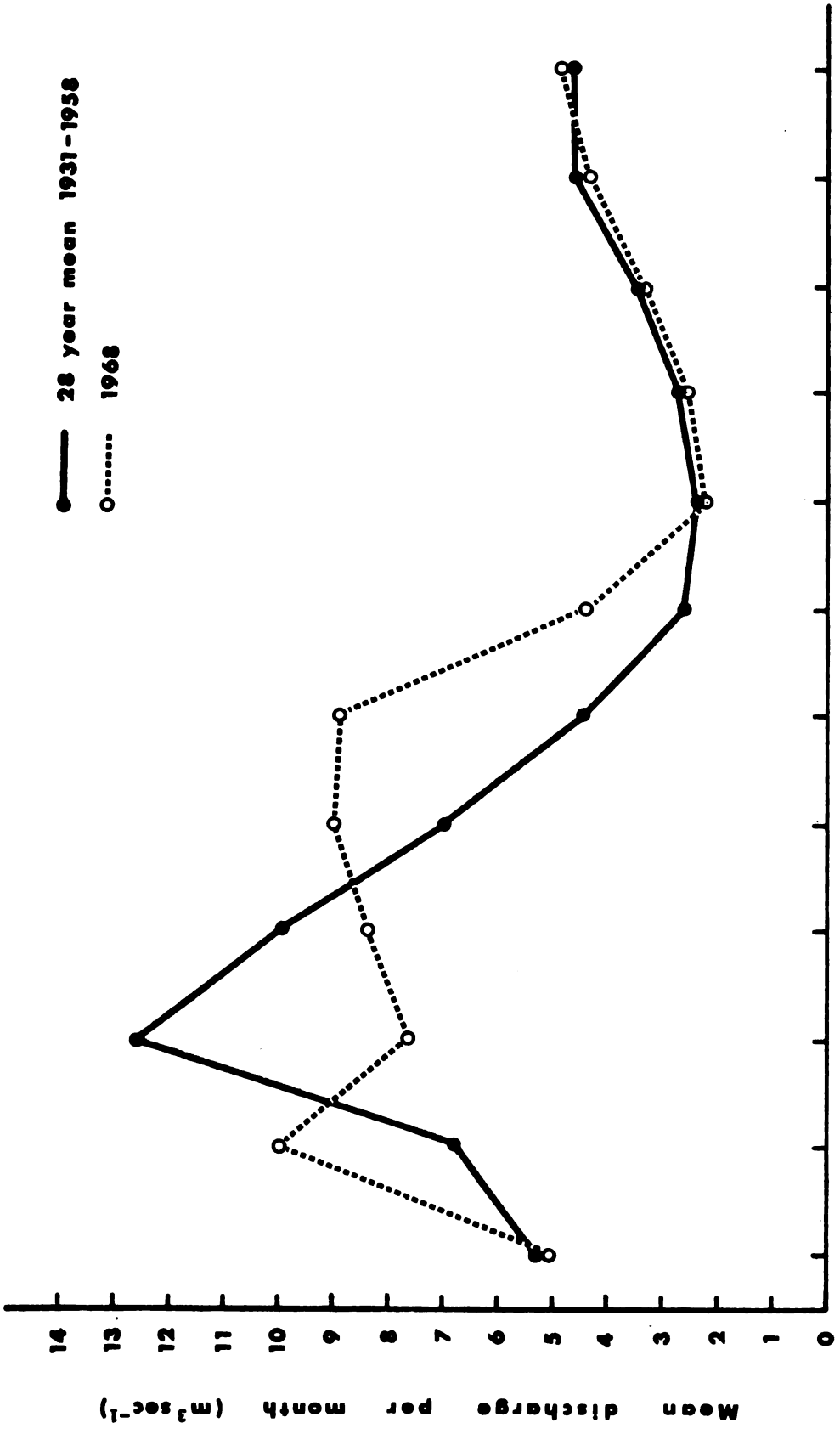
28 year mean 1931-1958
1968
Mean discharge per month ($m^3 sec^{-1}$)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Jan.
Feb.
Mar.
Apr.
May
Jun.
Jul.
Aug.
Sep.
Oct.
Nov.
Dec.

Figure 3

Figure 4. Stream gradient from the source of the Pine River (Pine Lake) to station 5. Data from U.S.G.S. topographic maps.

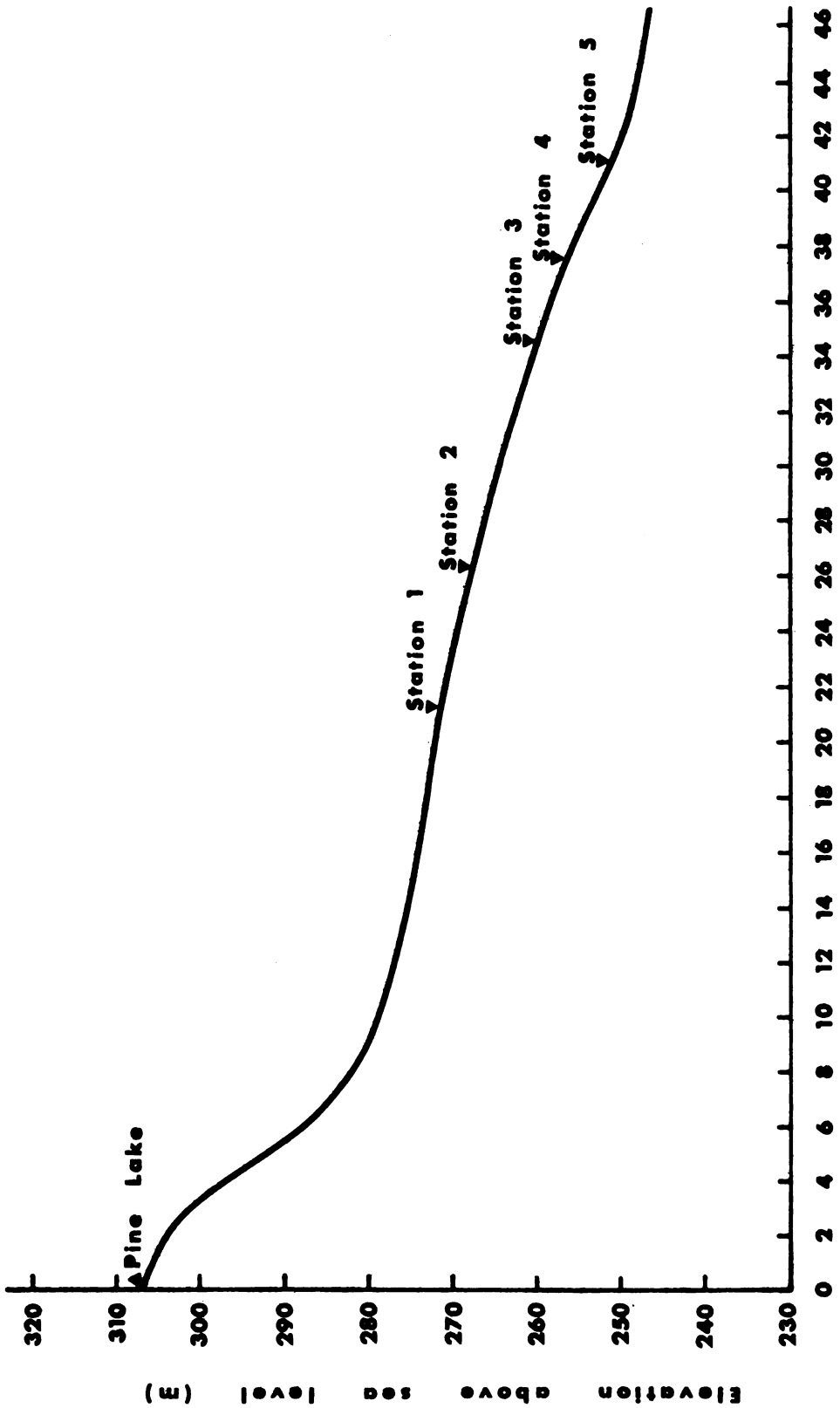
Elevation above sea level (m)
320
310
300
290
280
270
260
250
240
230
Pine Lake
Station 1
Station 2
Station 3
Station 4
Station 5
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42 44 46
River length (km)

Figure 4

varied between 5 and 23 m. Depth varied between riffles of 15 cm to deep pools up to 1.5 m. Major tributaries in the study area are Pony, Skunk and Wolf Creeks, and the South Branch of the Pine River.

Podzol soils in the study area are derived from parent material of glacial origin with major groups being Sims, Kawkawlin, Capac, and Iosco at stations 1, 2, and 3, and Montcalm, Kalkaska, and Emmet at stations 4 and 5. These soils are light textured and mostly well drained. Farming in the area consists of small grains, potatoes, beans, hay, and cucumbers. A few farmers draw water from the Pine for irrigation purposes. Part of the area is under agricultural drainage; an artificial drain enters the river above station 3. Approximately 70% of the area is in agricultural use, the rest being Aspen and Oak hardwood forests. Appendix B contains a list of the more common streambank shrubs and trees in the study area.

The river in the study area is regarded as a marginal trout stream (Mense, 1970). Recreational uses of the river are limited to light trout and sucker fishing pressure (trout fishing is heavy during opening week of the season) and occasional canoists during the summer.

No known human pollution sources exist in the study area, but the community of Remus and Remus Creamery discharge raw or semitreated sewage into a storm drain which eventually enters Pine Lake at the headwaters

(Seeburger, 1969). High chloride concentrations in Wolf Creek (Appendix A) which enters between stations 4 and 5, indicated that the community of Cedar Lake may be discharging wastes into the creek.

METHODS

Periphyton

Periphyton production was gravimetrically measured after its accrual on Plexiglas artificial substrates placed in the stream. Rectangular Plexiglas plates (13 x 5 x 0.6 cm) with an exposed area of 1.5 dcm^2 were attached horizontally to a wood cross piece. Ten substrates were held to the cross piece by metal paper clamps. The cross piece was bolted to a vertical wood support which was forced into a concrete building block. This method of substrate support was similar to that used by Grzenda (1960) and King (1964). With blocks on the stream bottom the artificial substrates were all approximately 23 cm from the bottom. Placing three blocks at each station gave a total of 30 substrates for analysis per station.

Blocks were positioned to give an average value of production at each station. One block was placed in a pool, another in a riffle, and the third near the bank where there was more shading. Average water depths above the substrates in these areas were respectively 75, 30, and 45 cm.

Artificial substrates were exposed for periods from 1 to 19 weeks. At each sampling date a substrate

was removed from each block giving three substrates per station. After a substrate was removed, a new clean substrate was put in its place for later sampling dates. Therefore at all times during the study period 10 substrates were on each block. Throughout the summer predominantly two, three, and four week samples were collected to give an estimation of the monthly change in production. Earlier studies have shown that two, three, and four week exposures gave a good growth of periphyton for estimating production rates (Grzenda, 1960; Castenholz, 1961; King, 1964; and Szczepański and Szczepańska, 1966). Longer exposure periods (5 to 14 weeks) were collected to estimate standing crop.

Substrates were placed in plastic bags after removal from the blocks and frozen in the laboratory. Stored substrates were thawed and macroinvertebrates removed with tweezers. Using a rubber scraper, periphyton was scraped into porcelain evaporating dishes. All periphyton was rinsed from the plastic bag, plate, and scraper with distilled water.

Tare weights (± 0.5 mg) of acid washed dishes were made after firings at 600 C in a muffle furnace (to remove organic matter) and cooling in a dessicator. Samples were oven dried at 105 C ± 2 C and constant weights ± 0.5 mg determined on an analytical balance. At least four periods (6 hr each) of drying in the oven were needed to reach a

constant weight. Ash-free dry weight, assumed to be organic weight, was then determined by ashing at 550 C ± 10 C in a muffle furnace. Care was taken in ashing to prevent flaming or flashing (rapid combustion, causing discharge of material from the containers). Samples were put in at 100 C and then temperature was raised 100 C every half hour until 550 C was reached. Before weighing, all samples were allowed to cool in a dessicator approximately 12 hr after drying or firing.

Randomly selected samples of periphyton from a 1 cm^2 area of the substrate were removed before scraping and stored in 90% ethyl alcohol. After centrifuging for 1 min., the alcohol was poured off and a drop of the remaining residue examined microscopically (430 x). Genera of the first 100 cells counted were determined. Approximately 10-20 fields were viewed before 100 cells were counted. Genera from 66 substrates were determined. This method was used because only a general picture of dominant genera present was desired.

To determine if current velocity was different between stations and block locations, readings were taken four times during the study period. Current velocity was measured with a "Price" type Gurley Pigmy current meter held at substrate depth, 5 cm in front of each block.

Macrophytes

Macrophyte production was gravimetrically measured after cropping whole plants including roots. During April when aquatic plants first appeared, a bed was chosen near each station for study and an area of 10 x 30 m marked and staked off. A plant bed did not emerge at station 1 until mid-May when an area of 3 x 33 m was staked off. The river was narrow at station 1 (6 to 10 m) and aquatic plants were sparse.

Weed beds were sampled every one or two weeks during the summer to estimate increase in standing crop. At each sampling date three plots of 1 m^2 were chosen by using a table of random numbers. Each area was then marked by means of a chain that enclosed an area of 1 m^2. All plants in the plot were removed by hand, field washed, put in plastic bags, and frozen in the laboratory. After thawing, samples were washed again in an enamel pan to remove as much algae and invertebrates as possible.

Samples were oven dryed to a constant weight $\pm$ 0.1 g at 105 C in 500 ml beakers. A subsample of the oven dryed material (approximately 100 g) was then ashed at 550 C in large porcelain containers. As previously mentioned under periphyton methods, caution was exercised during ashing to prevent flaming. Before weighing all samples were cooled in a dessicator for 6 to 8 hr after drying or 10 to 14 hr after firing. A percentage of ash

weight to dry weight was calculated to determine ash-free dry weight (organic weight).

After calculating ash-free dry weight m^{-2}, standing crop was estimated by averaging the values from the three samples collected at each station. Production rate for a plant bed was estimated by dividing standing crop by number of days in the growth period. By observing when plants first appeared at each station, start of the growth period was determined.

Values for calculation of macrophyte production for an entire station were determined by walking the stream and visually noting percentage bottom area covered by plants in 20 m long sections. Average width of each 20 m section was measured to give an estimation of stream bottom area in m^2. Aquatic plant cover was measured 1.5 km upstream and downstream at each station. Using these values, percentage bottom area covered by macrophytes was calculated for an entire station. Production rates of the plant bed at each station were multiplied by the percentage bottom area covered by plants to give total macrophyte production.

RESULTS AND DISCUSSION

Periphyton

Biologists have made numerous qualitative studies of algae in water. In the past 70 years the plankton of oceans and lakes have received much attention by oceanographers and limnologists. Recently the role benthic algae plays in freshwater environments has come under scrutiny. Currently, plankton and benthic algae are usually studied collectively in production studies of lakes. Not until the past 20 years was benthic algae in lotic ecosystems studied to any extent qualitatively and quantitatively.

Before preceding a clarification of the term periphyton as used in this study is needed. The heterogeneous assemblage of bacteria, plants, and animals on substrates in aquatic environments has been given various names. English and American limnologists have referred to this assemblage as periphyton, generally meaning sessile or attached organisms on any substrate. The German term "Aufwuchs" has a broader connotation and comprises all organisms that are firmly attached to a substrate but do not penetrate into it (Ruttner, 1963). Following the definition used by Wetzel (1964a), periphyton in the present work will connotate all sessile benthic

producers exclusive of macrophytes, primarily epilithic, epipelic, and epiphytic algae. This definition (when used in quantitative results) must be qualified further because weight of biomass was measured rather than carbon-14 uptake as in Wetzel's study. Biomass measured, besides periphytic algae, included microinvertebrates and organic debris which constituted a small amount of the total weight.

Qualitative

Methods of collecting benthic algae from streams have utilized scrapings from rocks, sediments, and macrophytes and examination of exposed artificial substrates. The widely used method for lotic waters has been scrapings from natural substrates. There are extensive reviews of literature on collecting periphyton for qualitative purposes from natural substrates (e.g., Patrick, 1948; Cooke, 1956; Blum, 1956; Lund and Talling, 1957; and Sládecková, 1962). Artificial substrates are being used increasingly for collecting benthic algae, particularly since estimates of production can also be made.

Historical development of artificial substrates.--European investigators are credited with being first to use artificial substrates for qualitative collecting. Cooke (1956) reported that Naumann (1915) was first to use glass microscope slides for collecting periphyton.

Naumann was followed by Hentschel (1916) who suspended glass slides vertically from pontoons at 1 and 2 m in Hamburg Harbor. A later development of Naumann (1919), described by Butcher (1932), was glass slides fixed in a photographic frame for the study of iron bacteria. Geitler (1927), also referred to by Butcher, collected algae from mountain streams on glass slides fixed between two pieces of wood. Butcher also described the apparatus used by Bachmann (1920) and Hurter (1928) which was an anchored, floating rectangular frame of cement and asbestos board from which glass slides and other materials were suspended vertically to various depths by hooks.

Godward (1937) used glass slides to identify algae in Lake Windermere. Comparing algae collected from stones, mud, plants, and slides, he found slides collected mostly diatoms. Slides placed on the bottom acquired a growth more like that on natural substrates than those at mid-depth. In addition Lund and Talling (1957) list the following as using glass slides for qualitative investigation of periphyton: Thomasson (1925), Godward (1934), Abdin (1949), Brook (1955), and Smyth (1955).

Besides glass slides other artificial materials have been used as artificial substrates to collect periphyton qualitatively. These studies and the historical development of Plexiglas usage will be discussed under quantitative results.

Results and discussion.--All diatom genera found in the Pine (Table 1) have been reported previously in other stream and river studies (Blum, 1954, 1956, 1960; Round, 1957, 1965; Patrick, 1948, Gumtow, 1955; Margalef, 1960; Chudyba, 1965; and McFarland and Weber, 1970). The Pine is a calcareous stream (see Appendix A for hardness) and genera of algae reported are similar to those found in other calcareous streams (McFarland and Weber, 1970, and Round, 1957). Except for Stephanodiscus, genera found were typical of epiphytic, epilithic and epipelic algae communities.

Stephanodiscus, a planktonic diatom, was collected from two artificial substrates (Table 1). Other workers have reported collecting planktonic forms in periphyton. McFarland and Weber (1970) observed S. invisitatus and Cyclotella Meneghiniana in small numbers on glass slides in an Ohio stream. Patrick et al. (1954) reported collecting typically planktonic forms such as Asterionella formosa on glass slides in Pennsylvania streams. Using large glass plates exposed for 1 and 2 weeks, Albin (1965) collected species of Stephanodiscus and Asterionella on about 10% of the plates in a South Dakota lake. Peters (1959) collected Cyclotella Meneghiniana abundantly in late summer on Plexiglas substrates (similar to those in this study) in the Red Cedar River, Michigan. Evidently planktonic forms are trapped or caught in the periphyton.

Table 1. Numbers of diatoms per genera from the first 100 cells counted per substrate for exposure periods of 1-14 weeks during summer (July to September) 1968 in the Pine River

Station	Number of substrates examined	Navicula	Cocconeis	Diatoma	Melosira	Gomphonema	Rhoicosphenia	Amphora	Achnanthes	Nitzschia	Synedra	Stephanodiscus	Cymbella
1	15	576	577	82	36	59	105	11	29	23	1	1	0
2	15	268	533	309	281	23	12	20	23	1	29	0	1
4	15	492	394	254	22	86	25	72	81	64	0	10	0
5	15	675	389	125	15	115	66	51	17	46	0	0	1
Total	60	2011	1893	770	354	283	208	154	150	134	30	11	2
Percent of Total		34	32	13	6	5	3	2	2	2	1	Tr.[a]	Tr.

[a]Tr. = trace (less than 1%)

However, the sample from the substrate at station 4, which contained 10 cells of Stephanodiscus out of 100 diatom cells counted, indicates that possibly more than just an occasional cell was being trapped in the periphyton. Planktonic forms may not be necessarily truly open water plankters in streams. This may point to the need for a better classification of stream algae.

Besides diatoms the filamentous alga Cladophora glomerata was present on 31 of 66 artificial substrates examined. Massive growths of this species were observed in mid to late summer on any available submerged substrate. Some growths on fallen trees reached lengths up to 7 m at station 1. According to Blum (1956) C. glomerata appears to be the most abundant filamentous alga in streams throughout the world. Chudyba (1965) describes the species as a settled benthonic alga, mostly inhabiting well aerated waters in all rivers of the northern hemisphere. The C. glomerata association is a widely distributed epilithic group which occurs attached to stones and rocks in slow flowing rivers and streams with moderately base-rich waters (Round, 1965). This association of C. glomerata and diatoms was found to be the dominate group of algae in the Pine River study area.

Navicula and Cocconeis were the dominant genera of diatoms in the periphyton on artificial substrates in the Pine River (Table 1). Butcher (1946) found that

C. placentula was a dominant species in the periphyton collected on microscope slides from three highly calcareous streams in England. Samples from the Pine were taken during July, August, and September. A Cocconeis-Navicula community dominates periphyton on artificial substrates during the summer. Peters (1959) reported a Navicula cryptocephala-Cocconeis placentula community during the summer in the Red Cedar River, Michigan. Gumtow (1955) mentions that Navicula was the most abundant diatom during August and September on natural substrates in the West Gallatin River, Montana. Cocconeis was abundant from May to August on glass slides in English rivers (Butcher, 1932). Species of Cocconeis and Navicula among other species were dominate diatoms collected on glass slides in a small calcareous stream in Ohio (McFarland and Weber, 1970). Evidently Navicula and Cocconeis are common genera of diatoms found in the periphyton of rivers and streams of the north temperate regions of Europe and America.

Navicula as stated before was a dominant genus of diatoms in the Pine River, but has not been reported as a typical genus in the Cladophora glomerata association by other workers (Round, 1965). Either the algae association in the Pine is different from previously reported associations or a mixture of "typical" algae associations or communities exists. Peters (1959) reported seven diatom

communities each with a dominate diatom species in the Red Cedar River. Identification in this study was not carried to species level so dominant species communities could not be categorized. Although dominate groups have been characterized in this study and previous studies, rigorous year-round sampling from all types of substrates would have to be performed before a true picture of all algae associations in one section of a stream could be delineated. To characterize a whole river by algae associations would be difficult and to categorize accurately different streams by algae associations would be extremely difficult at this time.

No differences in numbers of diatoms per genera between months were observed. Other studies, e.g., Patrick et al. (1954), Douglas (1958), Peters (1959), Whitford and Schumacher (1963), and McFarland and Weber (1970) have shown seasonal differences or periodicity in types of diatoms in rivers and streams, but this could not be verified in the present study. If this study had been performed over a full year, evidently seasonal differences would have been found.

Some differences were observed in numbers of diatoms per genera at different stations. Relatively large numbers of Melosira were found at station 2 (Table 1). This filamentous diatom has been reported as planktonic (Patrick, 1948, and Prescott, 1964) and epiphytic or

epipelic in streams (Round, 1957). The stream at station 2 can be characterized as relatively wide with little cover and luxuriant macrophyte growth. Which of these factors or other unknown ones caused the abundance of Melosira remains obscure. Other differences in numbers of diatoms between stations were observed (Table 1), but reasons for them were undetermined. Obviously more work is needed on the life history, physiology, and ecology of species of stream diatoms before the above differences can be explained.

Differences in numbers of diatoms on substrates exposed for different periods were observed. Navicula and Cocconeis numbers (Table 2) depended on length of substrate exposure. Cocconeis dominated substrates exposed for short periods (2 weeks). Substrates exposed longer (11 weeks) tended to be dominated by Navicula. Whitford (1956) noted that Cocconeis was a pioneer on most bare surfaces such as young plant leaves in springs and spring streams of Florida. Whitford and Schumacher (1963) also observed that Cocconeis placentula was a pioneer species in North Carolina streams with a pH above 7. Similar results were also found in the Pine River. Cocconeis attaches like a postage stamp which apparently permits colonization of bare areas. Navicula, usually a motile diatom, is not a pioneer species, but it abundantly colonizes surfaces that have a pioneer growth.

Table 2. Comparison between numbers of diatoms per genera on artificial substrates exposed for 2 and 11 weeks in the Pine River during summer 1968. Data are counts of the first 100 cells counted per substrate

Station	Month	Weeks exposed	Number of substrates	Navicula	Cocconeis	Diatoma	Melosira	Gomphonema	Rhoicosphenia	Amphora	Achnanthes	Nitzschia	Synedra
1	July	2	1	16	79	1	0	1	0	1	1	1	0
	July-Sept.	11	1	65	17	6	0	2	5	2	1	2	0
2	July	2	1	6	81	3	9	0	0	0	1	0	0
	July-Sept.	11	1	16	21	42	16	0	3	0	0	0	2
4	July	2	1	12	54	21	2	6	2	1	2	0	0
	July-Sept.	11	1	49	10	22	9	1	3	1	1	4	0
5	July	2	1	37	41	4	3	8	0	2	0	5	0
	July-Sept.	11	1	46	19	4	0	4	26	0	0	1	0

Large differences in numbers of other genera over various exposure periods were not observed.

Evaluation of artificial substrates.--Whether algae collected from artificial substrates represents a true picture of naturally occurring algae has been questioned. Results from the literature generally indicate that the species composition of periphyton on artificial substrates is usually similar (but not necessarily identical) to that on natural substrates (Wetzel and Westlake, 1969).

Young (1945) stated that growths on non-living natural substrates (particularly dead bulrush stems) were different from growths on living substrates in Douglas Lake, Michigan. Other workers comparing artificial substrates to natural substrates found no differences in types of algae. Comparing stream algae on glass slides with that on stones, Reese (1937) found that the variety of species at any particular time was similar on both substrates. Castenholz (1960) also found that diatom species on large glass plates were similar to those occurring on shallow rocks and macrophytes in Washington lakes. Patrick et al. (1954) reported that glass slides probably collect a truly representative sample of the species of diatoms living in a given region of a river. In Silver Springs, Florida, the complex of algae attached to glass slides was very similar to the algae attached to Sagittaria blades (Odum, 1957). In North Carolina streams, Whitford and

Schumacher (1963) found that detailed examination of rock and wood surfaces indicated that algae attached to smooth glass as regularly and abundantly as to these natural surfaces. Glass plates placed in Polish lakes were colonized by periphyton similar (qualitatively and quantitatively) to periphyton on natural substrates (Pieczyńska and Spodniewska, 1963). Using Plexiglas substrates similar to those used in this study, Peters (1959) found that in the Red Cedar River artificial substrates were not selective, but had the same dominant organisms attached as did rocks, wood, and other naturally occurring substances.

Round (1965) criticizes the use of artificial substrates in that information on actual flora is biased by growth of species that tend to grow in dense patches on slides. He also mentions that most data from these methods are on small attached forms and only rarely are large filamentous or motile species recorded. Species of algae on artificial substrates from the Pine were mostly small, but larger forms, e.g., Diatoma and Melosira, were collected abundantly as was Cladophora glomerata a large filamentous green alga. Also motile forms (i.e., Navicula, Amphora, Nitzschia, and Cymbella) were collected. McFarland and Weber (1970) also collected filamentous (Stigeoclonium, Schizothrix, and Microcoleus) and motile forms (Navicula, Nitzschia, and Amphora). Albin (1965) collected filamentous green and blue-green algae on glass plates (although

not as abundantly as on natural substrates of rocks) in Swan Lake, South Dakota. It is believed that artificial substrates in the Pine were representative of natural accrual of periphyton.

In a study comparing artificial to natural substrates in a lake, Albin (1965) found the glass plate method (a method similar to Castenholz, 1960) was qualitatively valuable for most species of algae except filamentous algae. He also concluded that glass substrate was selective for some diatoms and selective against some filamentous algae. The majority of Albin's plates were exposed for only 1 week. I believe that he would have had a better comparison if the exposure period had been longer (2-4 weeks) since he observed that relative abundance of Cladophora was 7.0% on 1 week exposed glass, 19.3% on 2 week exposed, and 19.8% on natural substrates. Other workers have found 2 to 4 week exposure periods gave growth similar to natural substrates (Peters, 1959; Castenholz, 1961; Pieczyńska and Spodniewska, 1963; Szczepański and Szczepańska, 1966).

It appears from these observations and works of others that artificial substrates give a representative sample of periphyton present in aquatic ecosystems. Whether production rates on artificial substrates are comparable to that on natural substrates remains an unanswered question. Primary production has been measured from

natural substrates, but I have not found a study where production rates in a lotic ecosystem on artificial and natural substrates have been compared directly. It is assumed in this study that rate of production on Plexiglas substrates is similar to that on natural substrates.

Quantitative

Quantitative estimates of algae production in aquatic ecosystems have been made for many years. Because of the importance of phytoplankton in ocean and lake food chains, standard quantitative methods for measuring phytoplankton production have been developed. Periphyton can be a major contributor to the primary production of some lakes (Wetzel, 1964a) and may be the only primary producer in some flowing waters (Grzenda and Brehmer, 1960). Some methods for measuring phytoplankton production have been adapted (to some success) to measure periphyton production in lentic systems (Mann, 1969). The lotic environment presents a set of dynamic conditions which have not lent themselves readily to established measurement techniques. Ecologists are still at a stage of developing accurate standard measurements of periphyton production in streams and rivers. Much of the choice of methodology must be made by the investigator in view of individual habitats and questions under investigation (Wetzel and Westlake, 1969).

Historical development.--Numerous quantitative numerical estimates of periphyton on natural substrates have been made (for a review of the literature see Sládečková, 1962). Numerical estimates add to descriptive studies of periphyton, but do not lend themselves readily to comparable production estimates.

Quantitative (numerical) studies of periphyton in lakes and rivers have been made from a variety of artificial substrates. Most common material in river studies has been glass. Sládečková (1962) credits Hentschel (1916) with being the first to use glass slides quantitatively. Butcher (1932, 1940), like Hentschel, made numerical counts of algae from glass slides in a series of ecological studies of British rivers. Patrick et al. (1954) used glass slides mounted in a "Diatometer" to study diversity of diatoms in polluted and unpolluted rivers. Other workers have made numerical counts from glass slides in the lentic environment and are reviewed by Sládečková (1962).

Besides glass a variety of other materials have been tried as artificial substrates for descriptive and numerical studies in lakes and rivers. More common materials have been wood, slate, clay, concrete, asbestos, asbestos-cement (eternite), various sheet metals, celluloid, and many organic plastics (Sládečková, 1962). Sládečková (1966) found that the best materials for collecting

periphyton growth were plastics, then wood, glass, and metals. Another method has been coating concrete or rocks with "collodium film" (Margalef, 1949) or paraffin (Baers and Neuhold, 1968) then counting or analyzing for chorophyll or attached algae. A recent technique developed by Neal et al. (1967) is suspending polyethylene tape vertically in a lake and obtaining a depth profile of growth of attached algae. With advent of new synthetic materials, undoubtedly more materials will be tried as artificial substrates.

I believe that use of artificial substrates for descriptive studies and numerical counts of periphyton is not advantageous. Methods are available for collecting algae from natural substrates (e.g., Douglas, 1958) which can be used for diversity studies of periphyton in lakes and streams. The real value of artificial substrates lies with their advantage in making biomass measurements which lead to estimates of production rates in aquatic environments. Lakes have received the most attention from the first workers making biomass measurements.

Newcombe (1949) was first to make quantitative organic matter measurements from glass slides. In Sodon Lake, Michigan, he experimented with different numbers, sizes, positions, and exposure periods of glass slides. He also compared production rates in Sodon Lake with Walnut Lake, Michigan (Newcombe, 1950). Noting the

limitations of the method he concluded that advantages outweigh disadvantages in determining lake production. Nielson (1953) used glass slides for measuring organic matter accrual in four lakes in California. Suspending slides with clothespins at different depths he obtained estimates of lake production rates. Using Newcombe's techniques, Castenholz (1960) studied seasonal changes in production rates of specific attached diatoms and total littoral production in freshwater and saline lakes of the Lower Grand Coulee, Washington. In evaluating the glass plate method in lakes and marine littoral regions Castenholz (1961) concluded that its greatest usefulness was demonstrating major seasonal changes in production, although values obtained were more relative than absolute.

Others have measured production rates in the lentic environment using organic matter accrual on artificial substrates. Knight et al. (1962) measured and compared periphyton production rates on Plexiglas plates in four Michigan ponds. They indicated that rates of accrual were only indices of intensity of production in ponds because information on average area of substrate suitable for colonization was lacking. Maciolek and Kennedy (1964) used glass slides to measure periphyton production in Laurel Lake, California. Using the wet oxidation method (rather than ash weights) to measure organic matter, they found one area in the lake had

greater production than other parts of the lake. They concluded that a complex illumination regimen arose from modification of direct sunlight by various morphological factors. Sládeček and Sládečková (1964) determined periphyton production on vertically held glass slides at different depths in Sedlice Reservoir, Czechoslovakia. Pieczńyska (1965) also used glass slides (and reed plants) to measure variations in periphyton production in the littoral zone of lakes in Poland. She indicated the need to take numerous samples to reduce variability in production estimates. Recently, a quantitative method for obtaining a survey of the developmental stages of periphyton growth was published by Dumont (1969). He stressed that orientation of substrates in relation to wind-driven currents is important in evaluating total periphyton production in lakes.

The only study I found on comparing periphyton accrual qualitatively and quantitatively on artificial and natural substrates was Albin (1965). Using glass plates in the littoral zone of Swan Lake, South Dakota, he concluded that the glass plate method was not quantitatively comparable to the natural population for many species of algae. One week exposure periods led him to the above conclusion. His data on biomass showed that two week exposed substrates were more comparable to natural substrates. As stated previously, I believe he

would have concluded that artificial substrates were comparable quantitatively and qualitatively had he used a longer exposure period as previous workers have done.

From the above works on lakes, it is apparent that periphyton production rate measurements from artificial substrates have been made with some success in the lentic environment. Whether this method is more accurate than methods of enclosing periphytic algae in bottle or chambers and measuring oxygen production or ^{14}C uptake (see Wetzel, 1963, or Mann, 1969) remains unanswered. Both methods can give useful results in ecological and comparative studies of periphyton production in lakes (Wetzel, 1969c). Because metabolism of lotic periphyton is greatly affected by restriction of water movements (Whitford, 1960; Whitford and Schumacher, 1961) attempts at estimating periphyton production in flowing situations by oxygen and ^{14}C methods in closed containers must be viewed with reservation (Wetzel, 1969b). To date, gravimetric measurement of organic matter on artificial substrates has been the only method to yield a reasonable estimate of periphyton production in streams.

Grzenda (1960) was first to measure the rate of periphyton production gravimetrically from accrual on artificial substrates in the lotic environment. Brehmer (1958) and Grzenda were the first to use Plexiglas plates to collect stream periphyton for production measurements.

They also used phytopigment density as an index of periphyton production (Grzenda and Brehmer, 1960). Earlier experiments (Grzenda, 1955; Alexander, 1956) combined the phytopigment technique with artificial substrates made from cedar shingles and bricks. Other workers also have used Plexiglas plates to estimate the rate of periphyton production (Peters, 1959; Rawstron, 1961; King, 1964; and Gehring, 1969). Except for Gehring, the above works (including Brehmer, 1958, and Grzenda, 1960) have been done on the Red Cedar River, Michigan; parts on periphyton production are summarized by Ball et al. (1969). Plexiglas plates have also been used (by other students in the Fisheries and Wildlife Department at M.S.U.) for responses of periphyton to herbicides (Sohacki, 1965, 1968) and phosphorus uptake (Clifford, 1959).

Kevern et al. (1966) and Cushing (1967) have used artificial substrates to determine periphyton production rates in other streams. Nelson et al. (1967) used glass slides to collect periphyton for measuring ^{32}P uptake in estimating periphyton mass and stream bottom area. Besides their use in natural stream ecosystems, artificial substrates have been used in artificial streams to measure periphyton production rates (Stokes, 1960; Kevern and Ball, 1965; Kevern et al., 1966; McIntire and Phinney, 1965; and McIntire, 1966).

Evaluation of the artificial substrate method.-- With any measurement technique there are sources of error. Besides inherent errors of weighing biomass, the artificial substrate method has sources of error associated with substrate placement in the environment. Castenholz (1961) has evaluated the method and its limitations. Wetzel (1965) has also discussed some problems of the method. Serious sources of error will be discussed in the following paragraphs.

1. Selectivity of attached algae: This problem has been discussed in the preceding section on Evaluation of artificial substrates.

2. Mechanical losses: When removing a substrate from its holding apparatus and from the water some loss of material occurs, particularly in lentic waters where algae are not firmly attached. In the Pine, algae were firmly attached because of mechanical action of the current. Great care was taken when removing the substrates by hand. No losses of material were observed when sampling.

3. Sedimentation: Suspended organic matter settling on artificial substrates will increase measurements of standing crop and raise production rate estimates. This sedimentation can be significant in lentic waters with little current. Substrates in the Pine were suspended in the current and it is assumed that water movement prevented organic sedimentation. Little turbidity was observed

during most of the study period. Late in the summer turbidity increased, but it was assumed to be too low to produce a significant amount of organic sedimentation (against the current).

4. Predation losses: Micro and macroinvertebrates that feed on diatoms can cause biomass loss. Brook (1955) observed mayfly and stonefly nymphs and chironomid larvae feeding on diatoms on microscope slides in filter beds of water works. He found from gut analyses that many insects were selectively feeding on diatoms. Douglas (1958), studying diatoms on natural substrates in a small stream, showed a numerical relationship between Achnanthes population and numbers of the caddis Agapetus fuscipes. She found a negative correlation that suggested a high population of Achnanthes only developed where there were few Agapetus, and with many, Achnanthes populations remained low.

Mayfly and caddis nymphs and dipteran larvae were observed on some artificial substrates in the Pine. On substrates exposed for short periods (1-4 weeks), Simulium and chironomid larvae were sometimes observed. Some substrates exposed for more than 4 weeks held a few mayfly and caddis nymphs and dipteran larvae. No protozoans were noticed when identifying diatoms, but two rotifers were observed. Extent to which these invertebrates were feeding on diatoms was not determined. Undoubtedly some

loss of biomass from predation occurred which would result in an underestimate of production rates.

5. Substrate placement: Differences in organic matter accrual between horizontal and vertical artificial substrates have been observed in lentic studies. Newcombe (1949) found that organic weight of material collected from vertically and horizontally placed substrates was in a ratio of 1:6.6 during the summer in Sodon Lake, Michigan. In Falls Lake, Washington, Castenholz (1960) found the ratio to be 1:6.2 in the summer. Organic sedementation evidently increased the weight on horizontal substrates in lakes. Newcombe and Castenholz believed that horizontal placement was better than vertical to estimate organic matter production in lakes.

King (1964) found the ratio to be 1:1.15 during the summer in the Red Cedar River, Michigan. His results indicated no significant difference between organic weight accrual on vertical and horizontal substrates. Substrates were placed horizontally in the Pine River. This position was assumed to be similar to a flat-rock surface. No differences in amount of periphyton on upper and lower surfaces were observed. Seemingly periphyton growing on the upper surface would eventually extinguish light reaching the lower surface as biomass accumulated during long exposure periods. Evidently enough reflected light reaches the lower surface for growth.

One of the major criticisms of the artificial substrate method is that the substrates are placed in an unrealistic position ecologically (Wetzel, 1965). He states that

> in a great majority of the studies on periphyton the substrates are suspended in the pelagic regions of standing bodies of water or the main flow areas in lotic situations. Natural substrates are primarily benthic and macrophytic in nature. Any substrates that occur for any length of time in the open water are strictly fortuitous and completely insignificant to the productivity of an ecosystem. Therefore, many of the estimates of periphyton production represent only colonization rates of certain of the phytoplankton and may be, and I suspect usually are, entirely unrelated to true productivity by sessile producers.

His criticism is valid for some of the previous studies on periphyton production. However, meaningful studies have been made and can be performed if care is taken in positioning substrates.

Substrates in the Pine were placed close (23 cm) to the stream bottom. If placed any closer or on the bottom, movement of sand, debris and rubble in the current would have scraped periphyton from the substrates. This placement is equivalent to a rock projecting from the stream bottom or a macrophyte growing in the current. The three holding blocks at each station were placed according to three representative habitat types of a stream bottom. One block was placed in a pool, another in a shallow riffle, and the third near the stream bank where shading was predominant. Production values at

each station therefore represent an average of the three areas and are assumed to be an average estimate for a typical stream section. Collections of algae on artificial substrates in the Pine were almost totally, epiphytic, epipelic, and epilithic periphyton (see Qualitative results). Although criticisms of Wetzel (1965) are valid for some previous lake studies, I believe they are invalid for this and many previous stream studies. Artificial substrates, if placed in ecological realistic positions, should give a practical estimation of the rate of periphytic, organic matter production in the aquatic environment.

6. Turnover rate: Population turnover is the time needed for renewal of individual periphyton species or the whole community as an average (Sládeček and Sládečková, 1964). In most field studies on production, population turnover rate represents an average of individual species rates.

Kevern (1962) pointed out that the exposure period should be long enough to allow accrued periphyton to approach a growth phase similar to that of periphyton on the stream bottom. It would appear that for a realistic estimate of production rate by the substrate method, the exposure period should be near or at the turnover time. Theoretically, if sampled at the turnover time, biomass on the substrate will be near the carrying capacity of

the substrate. The production rate will therefore be measured in the exponential phase of growth and the rate will be similar to that of the natural periphyton community. However, this is difficult to accomplish for several reasons.

First of all there is an initial period, when the substrate is first exposed, that is required for establishment of periphyton on the substrate (Kevern, 1962). Kevern (1962) finding no measurable periphyton biomass during the first three days on his exposed substrates, subtracted this period from total exposure time for calculating production rates. In the Pine a measurable quantity of periphyton on the substrates was found after one day. Therefore no initial period was subtracted from total exposure time.

Although the initial colonization period may be short there must be some colonization throughout the exposure period. Therefore the estimate of production on the substrate is a combination of daily increments of attachment and daily increments of growth. As Newcombe (1949) indicates these two weight increments are difficult to separate quantitatively. I assumed that after the initial colonization period, biomass accumulation on substrates is primarily due to daily increments of growth.

Using a recently published technique of Bott and Brock (1970) it may be possible to differentiate increments

of attachment and growth. They have used germicidal, ultroviolet radiation successfully to distinguish between in situ growth and passive attachment of aquatic bacteria on slides. As they point out the technique could be used for microalgae.

The second drawback to sampling at the turnover time is population turnover is not easily determined (Sládeček and Sládečková, 1964). Sládeček and Sládečková using their own calculation method have estimated turnover rates from their data and data of other authors. Using their calculation method, the turnover rate of periphyton in the Pine was also calculated (Table 3). Turnover times tend to indicate more rapid turnover of periphyton in streams (Silver Springs, Pine River) than in lakes. Turnover rates in the Pine also increased somewhat in a downstream direction for reasons unknown. It is doubtful that a comparison can be made between values from different authors because of differences in methods. As Wetzel (1965) points out, rates of turnover vary markedly with season, extent of colonization of substrate, and type and position of the substrate and environmental parameters. Variation in turnover rates is quite evident from Pine River data (Table 3). Causes for variation in turnover rates may be differences in numbers of algae per genera between stations (see Table 1) or unknown environmental parameters. Clearly turnover rate estimation of periphyton

Table 3. Comparison of turnover rates of periphyton between literature values (taken from Sládeček and Sládečková, 1964 Table XIII) and the Pine River[a]

Reference	Locality	Turnover	
		Coefficient	Days
Newcombe, 1949	Sodon Lake, Mich.	4.194 x	32
Newcombe, 1950	Sodon Lake, Mich.	2.983 x	33
Assman, 1953	Lake Glubokoye, USSR	6.888 x	22
Odum, 1957	Silver Springs, Fla.	25.4 x	14
Castenholz, 1960	Falls Lake, Wash.	16.67 x	22
	Alkali Lake, Wash.	8.42 x	22
Sládeček and Sládečková, 1964	Sedlice Reservoir, Czech. mean of all depths	5.249 x	60
	depth 1 m	4.496 x	70
	depth 3 m	5.837 x	54
	depth 6 m	6.917 x	45
	depth 9 m	3.439 x	91
Present study	Pine River mean of all stations	6.63 x	24
	station 1	5.30 x	28
	station 2	4.96 x	30
	station 4	5.98 x	25
	station 5	10.28 x	14

[a]Method of calculation is that of Sládeček and Sládečková (1964)

on artificial substrates is at an unrefined stage. Sládeček and Sládečková (1964) also indicate that there are subjective errors dependent on frequency of sampling and estimation of the degree of colonization that represents a climax stage of the community.

While predation losses, colonization versus growth, and turnover rate determination are sources of error, I believe this method is still the best procedure for measuring periphyton production rates in the lotic environment. Until an improved method is found the artificial substrate method will be used to measure the rate of primary production of periphyton.

Growth and standing crop.--To determine the growth curve of the stream periphyton community, substrates were exposed up to 14 weeks. A sigmoid growth curve with a leveling of biomass after about six or seven weeks was found at the four stations (Figure 5). Whether growth curves in Figure 5 are typical of periphyton growth throughout the summer is questionable. Weather conditions during May were poor for plant growth, rainfall was heavy, and temperatures were below normal (see Figure 1). Heavy rains at the end of May evidently caused low biomass measurements for the first four weeks (the effect of heavy rains on periphyton biomass and production rates will be discussed in detail under Discussion of variation in production rates). Heavy rains on June 25, 26, and 27

Figure 5. Average accumulation of periphyton biomass for different time periods on artificial substrates with initial exposure on May 4, 1968, at four stations in the Pine River. Each point is the mean of three substrates in g organic matter m^{-2} except at station 4 (because of vandalism only one substrate could be used at station 4). Vertical lines represent one standard error on each side of the mean.

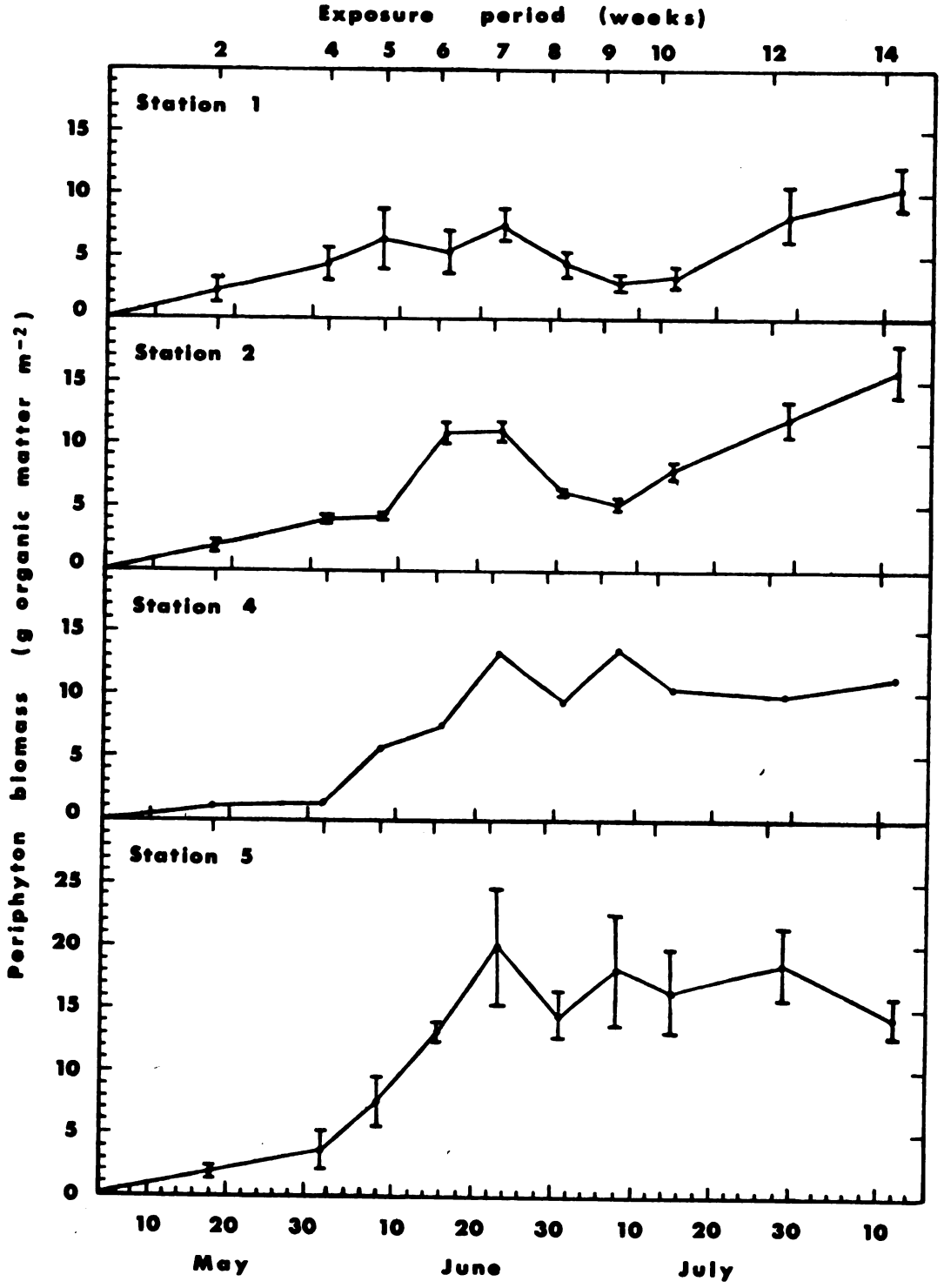
Exposure period (weeks)
2
4
5
6
7
8
9
10
12
14
Station 1
Station 2
Station 4
Station 5
Periphyton biomass (g organic matter m-2)
0
5
10
15
20
25
10
20
30
May
June
July

Figure 5

caused high discharge at the end of June and the first week of July. Scouring action of the high water decreased biomass at eight and nine week exposure periods.

After nine weeks exposure another increase in biomass at stations 1 and 2 was observed (Figure 5). Unfortunately, the experiment was only carried to 14 weeks so it could not be determined if the increase would have continued after 14 weeks. No increase after nine weeks was observed at stations 4 and 5. Biomass leveled off between 9 and 13 g m^{-2} at station 4 and between 14 and 19 g m^{-2} at station 5.

Earlier workers have found shorter exposure periods gave a leveling off of biomass at the asymptote. King (1964) found growth of periphyton in the Red Cedar River during summer occurred at a nearly constant arithmetic rate for exposure periods up to 15 days. At 15 days the colony stabilized at 4 to 5 g organic matter m^{-2} and new growth was equal to organic matter which died and was sloughed from the substrates. Gehring (1969) found that declines in total biomass of periphyton on artificial substrates in ponds in Michigan usually began on the 16th or 20th day of exposure. Accumulated biomass was about 3 to 4 g organic matter m^{-2}. The question whether accumulated biomass on substrates of King and Gehring reached a standing crop similar to that on natural substrates remains unanswered. Although they did not expose artificial

substrates longer than three weeks, apparently the carrying capacity of biomass on the substrates was reached between two and three weeks.

As stated previously biomass did not level off until after six or seven weeks in the Pine, at which time the amount of biomass was approximately 10 to 20 g m^{-2} at stations 2, 4, and 5 and 5 to 8 g m^{-2} at station 1 (see Figure 5). Evidently the biomass carrying capacity on substrates in the Pine was higher and took longer to attain than the carrying capacity of substrates in the Red Cedar River and Michigan ponds. Because of poor growth conditions in May and early June the periphyton growth was slow and carrying capacity was not reached until the exposure period reached six or seven weeks. Later in the summer growth conditions were better and carrying capacity was probably reached on substrates exposed between four and five weeks.

Variation in rate of production.--Although the carrying capacity was not reached on two, three, or four week exposed substrates, they nevertheless were used to estimate an average value for the summer (May to September) rate of periphyton production. Two, three, and four week exposure periods yield a uniform coat of periphyton and are near the estimated turnover rate. Growth up to these exposure periods will be in the exponential phase and the rate of production will be at a maximum. I

believe production rate measurements from substrates exposed near the turnover time approach the actual net rate of periphyton production on natural substrates.

Generally poor growth conditions (heavy rainfall, overcast skies) plus scouring action of high discharge caused a low rate of production during May compared with the other months at all four stations (Figure 6). After heavy rainfall on May 26, 27, and 28 (Figure 7) production rates increased in June and reached a High of 0.864 g m^{-2} day^{-1} at station 5. Production rates then declined at the end of June because of heavy rains on June 24, 25, and 26 (Figure 7). At the beginning of July production rates again increased and reached a high of 0.755 g m^{-2} day^{-1} at station 5. Rates declined appreciably at stations 4 and 5 during the third and fourth weeks of July. This decline could not be explained by weather conditions. It may be that nutrients became limiting, but the exact reason remains obscure.

After July 29 and for the first five days of August, production rates increased at all stations except station 4. This sudden increase cannot be explained. After the sudden increase at the end of July, rates decreased at all stations during the first three weeks of August. Evidently rainfall on August 7 and 17 (Figure 7) caused the decrease. Highest summer production rates at station 1 occurred at the end of August. Between August 26 and

Figure 6. Periphyton production rates on two week exposed (three and four week exposure periods are in parentheses) artificial substrates at four stations in the Pine River during summer 1968. Values are the mean of three substrates. Vertical lines represent one standard error on each side of the mean.

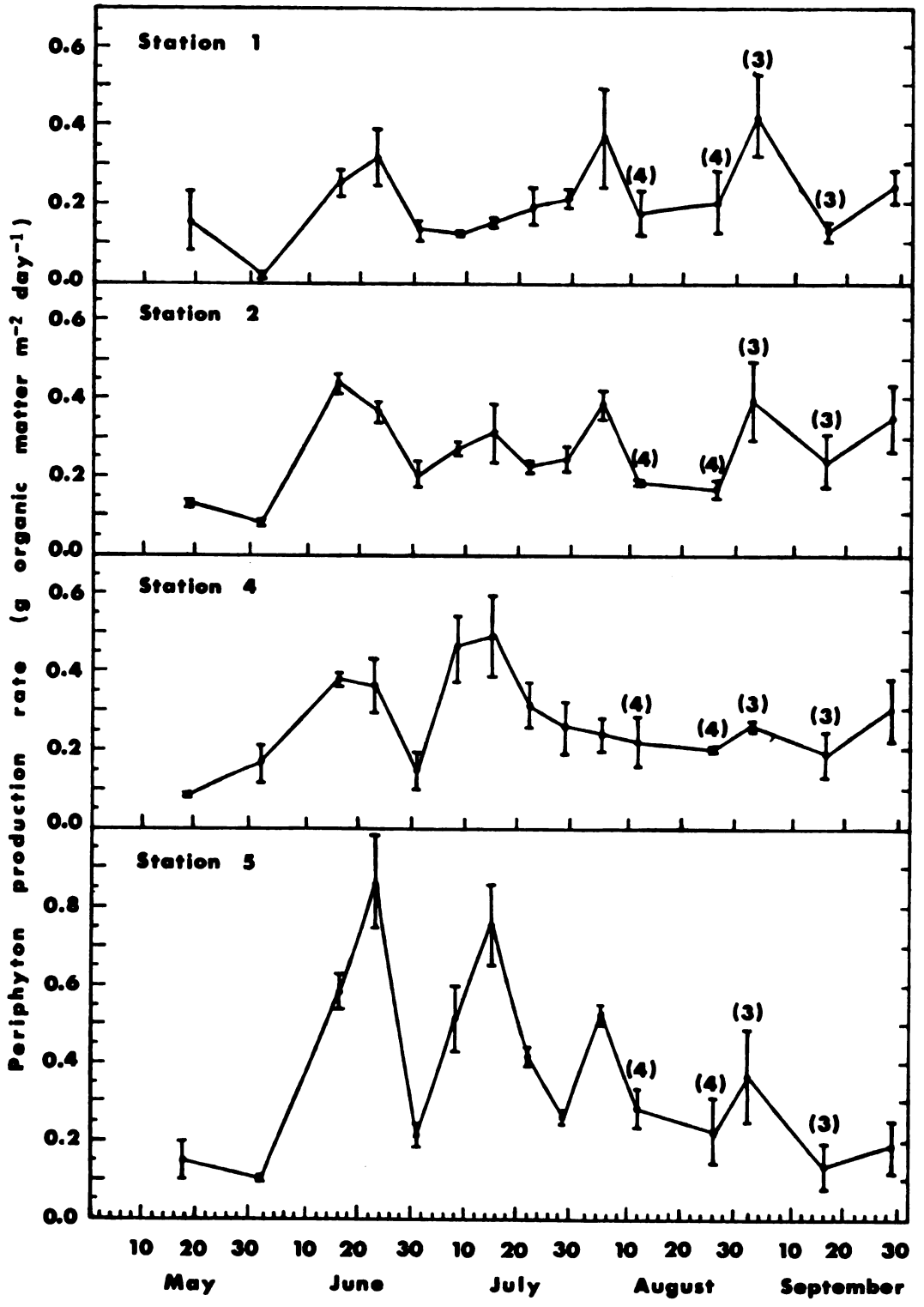
Station 1
Station 2
Station 4
Station 5
Periphyton production rate (g organic matter m⁻² day⁻¹)
0.0
0.2
0.4
0.6
0.8
(3)
(4)
10 20 30 10 20 30 10 20 30 10 20 30 10 20 30
May
June
July
August
September

Figure 6

Figure 7. Discharge of the Pine River during April to September, 1968 (data from U.S.G.S. gauging station at Alma) and precipitation at Mt. Pleasant, nearest weather station (data from Environmental Science Services Administration).

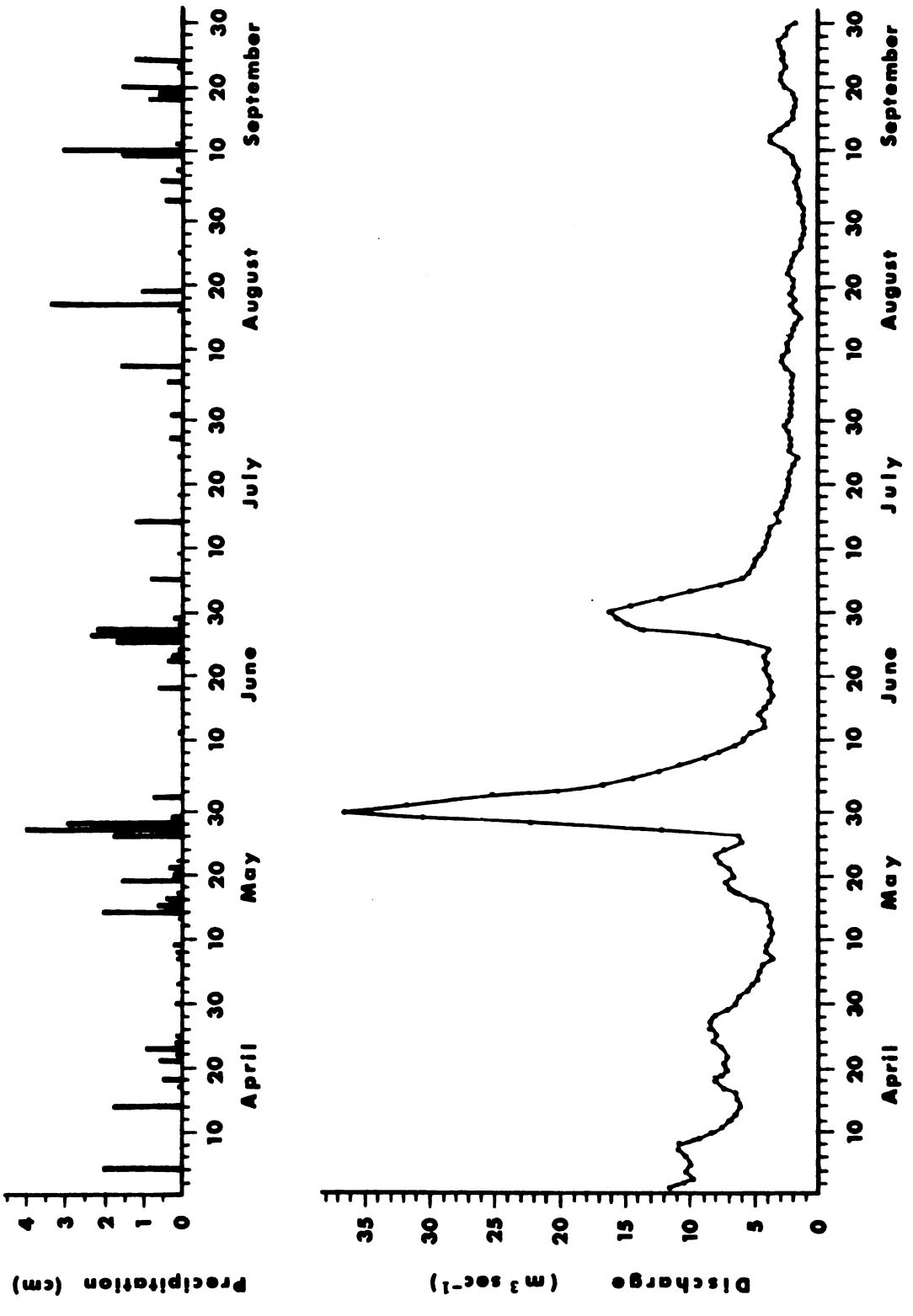
Precipitation (cm)
0
1
2
3
4
Discharge ($m^3 sec^{-1}$)
0
5
10
15
20
25
30
35
10
20
30
April
10
20
30
May
10
20
30
June
10
20
30
July
10
20
30
August
10
20
30
September

Figure 7

September 2 rates increased at all stations. During the rest of September, the rate of production was near the summer average at all stations except 5. Evidently low production rates at station 5 were caused by increased turbidity and macrophyte abrasion during September. A large macrophyte bed was growing upstream from station 5. During September plants began to break loose from the bottom and float downstream. Their abrasive action on the substrates at station 5 would cause low biomass accumulation and therefore low periphyton production rate estimates.

Fluctuations of production rates during the summer at station 5 were greatest among the four stations. Evidently periphyton growth is less stable at station 5 compared to the other stations. Causes for this lack of stability are obscure. No obvious differences in types of algae at station 5 compared to the other stations were observed (Table 1). Part of the reasons for great fluctuations in production rates may be related to high discharge since current velocity was high at station 5. Round (1965) found that streams with rapidly flowing water have greater fluctuations in numbers of diatoms than slow flowing streams.

In summary, overall monthly periphyton production rates during the summer of 1968 in the Pine River varied somewhat between stations (Figure 6). Production rates

were low at all stations during May. During the greater part of June, rates were high at all stations. In July, rates were high at stations 4 and 5, but near the summer average at stations 1 and 2. Rates were near average at stations 2, 4, and 5 in August and high at station 1. During September rates of production were average at stations 1, 2, and 4, but low at station 5.

Discussion of variation in production rates.--As expected, variations about the mean (Figure 6) were high especially at higher production values because each value was the mean of three substrates each from a different habitat type (pool, riffle, and shaded area). Obviously, variation was high, but major trends in production rates throughout the summer were easily identified.

A sharp production rate increase in June to a summer high after low production in May was also found by Brehmer (1958) on artificial substrates in the Red Cedar River. Brehmer found that an extraneous available nitrogen source produced the rate increase. In the Pine, the increase was evidently due to a combination of factors brought about by heavy rains in May. High discharge reduced standing crop to low amounts, therefore, subsequent new growth after peak discharge had adequate growing space. The new growth on scoured substrates will be in the exponential phase of growth and therefore production rates will be high. Great influx of nutrients (phosphorus and

nitrogen) in rivers shortly after rainstorms (Brehmer, 1958) are available to periphyton. Although the influx decreases rapidly after the storm, nutrients still may be available to algae for some time. Light conditions during June were also favorable for plant growth. This combination of good growth conditions evidently caused the increase in periphyton production rates during June in the Pine.

Peak summer periphyton production in June was measured in another study of the Red Cedar River by Grzenda and Ball (1968). Castenholz (1960) and Wetzel (1964a) also found peak periphyton production during May and June in lakes. Evidently growth conditions during early summer (May and June) in north temperate regions are optimal for periphyton production.

In the Red Cedar River, Brehmer (1958) and Grzenda (1960) found a sharp decline in production in the latter part of August. Brehmer gave no explanation for the decline that occurred in late August. Grzenda suggested the decline was caused by a shift from a strong light, warm-water community to a weak light, cold-water community. He found prior to the decline that the community was composed of many genera of diatoms, and by mid-September the community was composed almost entirely of Cocconeis. Although production was low near the end of August at all stations in the Pine, a decline in number

of genera was not observed. Water temperatures were decreasing significantly during September in the Pine, but no change in diatom genera was observed. Evidently if a change exists in number of genera in the Pine it is more gradual than in the Red Cedar or else occurs later in the fall.

Effect of rainfall on periphyton production rate estimates in the Pine is threefold. First, overcast skies during rainstorms reduce sunlight reaching the periphyton and a low rate of production results. Secondly, scouring of periphyton results from high discharges. Scouring was very appreciable when rainfall was over 2 cm in a 24 hour period. Thirdly, because of turbidity, light reaching the stream bottom is reduced when the water level is high.

Effect of high discharge and rainfall on periphyton production rates and numbers of periphytic algae has been documented in previous studies. During flooding in two English rivers, diatom numbers on glass slides were greatly reduced because of scouring (Reese, 1937). Diatom populations on stones were sharply reduced by floods in another stream in England (Douglas, 1958). Brehmer (1958) concluded "that adverse physical conditions in the form of high stream flows and accompanying high turbidities, even though they may last for only a short period of time, can completely destroy the standing crop of periphyton in a river." Hargraves and Wood (1967) working on the Usquepaug

River, Rhode Island found that all periphyton (numbers on macrophyte leaves) was washed away by swift currents following a torrential rain during July, 1964. Hardgrove (1970) found that during high water stages in the Red Cedar River, periphyton drift increased greatly. He also indicated that increased turbidity during high water reduced the rate of periphyton primary production. Undoubtedly floods in the Pine were not great enough to completely destroy the total standing crop on artificial substrates, but were enough to reduce the rate of production.

Average summer production rate.--Average summer production rates of periphyton were estimated by averaging means in Figure 6 for each station. The values for production rates in mg organic matter m^{-2} day^{-1} from the four stations were analyzed via a one-way analysis of variance. The rates between stations were significantly different at the 5% level (Table 4). Duncan's multiple range test revealed the production rate of station 1 to be significantly different from station 5. Stations 1, 2, and 4 were not significantly different from each other and stations 2, 4, and 5 were not significantly different from one another.

Evidently variations in production rates throughout the summer and low values due to floodings caused considerable variation in the means for each station. In

Table 4. Summary of one-way analysis of variance testing means of production rates in mg m^{-2} day^{-1} on artificial substrates at stations 1, 2, 4, and 5 in the Pine River during summer, 1968

Source of Variation	Sum of Squares	df	Mean Square	F Ratio
Stations	211,920.32	3	70,640.10	$F = \frac{70,640.10}{22,263.06} = 3.17$
Within	1,246,731.62	56	22,263.06	$F_{0.05}$ (3,56) = 2.78
Total	1,458,651.94	59		

$F_{exp} = 3.17$ $F_{0.05}$ (3,56) = 2.78 Therefore, there is a significant difference at the 0.05 level among the production values in mg m^{-2} day^{-1} on artificial substrates from the four stations.

Station means in mg organic matter m^{-2} day^{-1}

1	2	4	5
208	268	272	374

Duncan's multiple range test reveals station 1 to be significantly different (0.05 level) from station 5, but not from stations 2 and 4.

1	2	4	5

spite of this variation, rate of production at station 5 was considerably greater than at station 1. Station 1 can be characterized physically as having considerable stream cover, narrow average width, and low discharge compared to station 5. Clearly conditions at station 5 were more favorable for periphyton growth than conditions at station 1. Nitrate and total phosphate (Appendix A) were usually higher during summer at station 1 than 5. Evidently these nutrients were not limiting growth at station 1. Seemingly the shading effect of extensive stream cover at station 1 was limiting periphyton growth.

To determine if position on a substrate holding block affected accrual of periphyton biomass, two substrates from each block were exposed twice during the summer for the same period. Statistical analysis of the values in Table 5, using a paired t test, indicated no significant difference (5% level, 4 df) between positions on the supporting rack at all four stations.

As discussed earlier one-way analysis of variance and multiple range test of all production rate means (Table 4) revealed only a significant difference between stations 1 and 5. Because of variation in production rates throughout the summer at the four stations, average biomass accumulation was statistically tested to determine amount of variation between stations for one exposure period. A one-way analysis of variance (Table 6) of

Table 5. Weight in mg of accrued organic matter from two substrates located at different positions in each of three habitat types at four stations. Exposure period was 2 weeks during the summer 1968 in the Pine River

Collection Date	Station	Position on holding rack	Weights (mg/150cm^2) from three habitats		
			Shaded	Pool	Riffle
June 16	1	1	472	611	543
		2	430	647	741
	2	1	737	891	943
		2	869	929	1140
	4	1	787	805	846
		2	783	834	1030
	5	1	1230	1294	1347
		2	1032	1258	1722
September 29	1	1	353	464	632
		2	189	578	657
	2	1	200	622	1067
		2	284	680	1238
	4	1	467	789	1183
		2	259	523	306
	5	1	59	730	787
		2	72	217	370

Table 6. Summary of one-way analysis of variance testing means of biomass (mg 150cm^{-2}) collected from artificial substrates exposed for two weeks at four stations in the Pine River during June, 1968

Source of Variation[a]	Sum of Squares	df	Mean Square	F Ratio
Stations	1,682,524.832	3	560,841.610	$F = \frac{560,841.610}{22,789.550} = 24.61$
Within	455,791.002	20	22,789.550	$F_{0.05}$ (3,20) = 3.10
Total	2,138,315.834	23		

$F_{exp} = 24.61$ $F_{0.05}$ (3,20) = 3.10 Therefore, there is a significant difference at the 0.05 level among the biomass accumulated on substrates from the four stations.

Station means in mg organic matter 150 cm^{-2}.

1	2	4	5
574	844	918	1314

Duncan's multiple range test reveals all stations to be significantly different (0.05 level) except stations 4 and 2.

1 <u>4 2</u> 5

[a]Values in table 5.

weights from Table 5 for June 16, 1968, revealed a significant difference between stations. Duncan's multiple range test showed all stations to be significantly different from each other except stations 2 and 4. Although other exposure periods were not tested statistically the general trend in significant differences between means of a majority of the stations was assumed to be similar for all exposure periods.

It is hypothesized that stream cover was the greatest single factor limiting the rate of periphyton production at station 1. Nitrate and phosphate concentrations (Appendix A) were generally higher at station 1 compared to station 2, but production rates were generally higher at station 2. Obviously nitrate and phosphate were not limiting growth at station 1. The possibility of some other nutrient limiting growth at station 1 seems very unlikely, although the South Branch entering below station 1 may be adding some trace element which is limiting growth at station 1. Extensive stream cover (streambank trees and shrubs) exists at station 1. After the South Branch enters, the river widens considerably due to added discharge. Because of increased stream width, cover did not shade the stream at station 2 as effectively as at station 1. More sunlight reaching the stream for a greater portion of the day resulted in greater periphyton production rates at station 2. The importance of sunlight

on the rate of periphyton production has been emphasized by Kobayasi (1961) who concluded that among the habitat factors determining the rate of periphyton production, the light condition on the river bed is the most important.

Effects of current.--Although current effects lotic periphyton production rates significantly (Whitford, 1960; Whitford and Schumacher, 1961) differences in current velocity between stations 1 and 2 did not appear to be large enough to affect production. Average current velocities near the substrates at station 1 were similar to velocities at station 2 (Table 7). Current velocities at stations 4 and 5 were also similar, but higher than at stations 1 and 2. Although current velocity at station 4 was greater than at station 2, rates of production for the same exposure period at the two stations were similar. Evidently the increased current at station 4 did not contribute to increased production rates. Production rate during the same exposure period at station 5 was significantly higher than at station 4, but current velocities at both stations were similar. Differences in current velocities between the four stations appear not to be large enough to affect production rates significantly.

Considering the three habitat types, riffle areas were usually greatest in periphyton biomass accumulation and therefore greatest in production rates (Table 5). Shaded habitat was always least productive. Production

Table 7. Average current velocity (m sec^{-1}) measured on four dates near substrates at four stations in the Pine River, 1968

Station	Average current velocity in m sec^{-1} of three habitats		
	Shaded	Pool	Riffle
1	0.18	0.27	0.30
2	0.25	0.28	0.32
4	0.36	0.42	0.48
5	0.43	0.44	0.47

rates in pools were usually less than riffle areas, but always greater than rates in shaded areas. Results are similar to what Rawstron (1961) found in the Red Cedar River. Comparing periphyton production in riffles and pools, he found riffles in general had a faster growth rate and attained higher standing crops than pools. Rawstron attributed differences to effects of increased current in the riffles. Kevern (1962) found production rates on artificial substrates in artificial streams were significantly higher in a fast current riffle compared with a slow current pool. McIntire (1966) also found that accumulation of biomass on gravel and rubble in an artificial stream was more rapid in fast current than slow current.

Although current was slightly higher in riffle areas compared to pools (Table 7) the increase does not seem to be large enough to have caused the increase in production rates in the riffle areas (Table 5). Evidently light reaching substrates was the primary factor increasing rates in riffle areas. Water depth above pool substrates was approximately 76 cm at all stations, while depth above riffle substrates was 30 cm. Effect of available light can also be seen from data on shaded substrates, which received least light through the day and had lowest production rates. Whitford and Schumacher (1963) also found that in shaded areas of streams the standing crop of periphyton was greatly reduced.

Comparison of production rates.--Summer periphyton production rates measured from artificial substrates in the Pine River and in other ecosystems are given in Table 8. The Pine River study area is moderate in production when compared to a small spring (Kevern et al., 1966) and another river (King and Ball, 1966), but high in rate of production when compared to lakes. The Red Cedar River generally considered an enriched, polluted, warm-water stream (Ball et al.,1968; Ball et al., 1969) is high in periphyton production but not considerably higher than production rates in the Pine. Parts of the Red Cedar approach very high periphyton production rates (Grzenda, 1960). Apparently the Pine study area is average in the rate of periphyton production compared with other streams.

As expected most primary production in lakes without an extensive littoral zone is phytoplankton production; whereas, periphyton production rates in lakes (Table 8) are low. The Pacific Ocean was also low in rate of periphyton production, evidently because of the predominance of phytoplankton production. Where the littoral zone was very extensive e.g., ponds studied by Knight et al. (1962), the rate of periphyton production was high. Evidently because of shallow water depths in the littoral zone of ponds, more light is available to periphyton and production rates are high.

Table 8. Comparison of summer net periphyton production rates in g organic matter m^{-2} day^{-1} measured by the artificial substrate method

Reference	Locality	Summer[a] mean production rate (g m^{-2} day^{-1})
Nielson, 1953	Genevieve Lake, Calif.	0.0060
	Edith Lake, Calif.	0.0063
Sládeček and Sládečková, 1964	Sedlice Reservoir, Czech.	0.021
Newcombe, 1950	Sodon Lake, Mich.	0.039
Nielson, 1953	Cloverleaf Lake, Calif.	0.065
Castenholz, 1961	Pacific Ocean, coast of Oregon	0.075
Newcombe, 1950	Walnut Lake, Mich.	0.106
Stokes, 1960	Artificial stream	0.118
Kevern, 1962	Artificial stream	0.143
Castenholz, 1960	Falls Lake, Wash.	0.144
Kevern et al., 1966	Small spring, Tenn.	0.20
Castenholz, 1960	Alkali Lake, Wash.	0.252
Present study	Pine River, Mich.	
	Average	0.281
	Station 1	0.208
	2	0.268
	4	0.272
	5	0.374
Kevern et al., 1966	Artificial stream	0.31
King and Ball, 1966	Red Cedar River, Mich.	0.327
Knight et al., 1962	Small ponds, Mich.	0.364
Grzenda, 1960	Red Cedar River (one station)	0.777

[a]For studies conducted for the whole year, summer values were estimated from the reference data for May to September.

Some comparisons can be made with artificial stream studies in Table 8. Production rates in artificial streams depend on experimental conditions imposed by the investigators. It is interesting that artificial streams, although somewhat lower than natural river systems in production rates, are near production estimates for natural systems. Because artificial streams are "seeded" from natural ecosystems, they do have growth rates similar to natural populations.

Percentage organic matter.--Percentage organic matter (ash-free dry weight divided by dry weight) varied somewhat between months (Table 9). During May percentage organic matter was high, but production rates were low at all stations (Figure 6). Station 1 had lowest production rates and highest percentage organic matter. Part of the reason for high percentage organic matter with low production is carbonate encrustation. As the standing crop biomass on the substrates increased the amount of carbonate encrustation increased. High carbonate encrustation with high standing crop of epiphytic lake periphyton has been reported previously (Szczepański, 1968). With high carbonate deposits on substrates with dense growths of periphyton the percentage organic matter will decrease. Also it may be that with high production more inorganic materials (e.g., silt) accumulate on artificial substrates. The thick growth of periphyton on artificial substrates

Table 9. Variation in percentage organic matter (ash-free dry weight divided by dry weight) of periphyton between months and stations in the Pine River, 1968

Station	Percentage Organic Matter						
Month	May	June	July	August	September	Monthly Mean	Total Mean[a]
Sample size[b]	3	4	5	5	4	21	34
1	38.76[c]	31.79	44.16	39.94	34.18	37.77	37.36
2	41.35	30.14	30.34	23.71	27.75	30.66	30.20
4	44.01	30.84	35.53	36.57	30.21	35.43	31.18
5	46.69	34.34	31.41	30.78	32.89	35.22	30.05
Mean	42.70	31.68	35.36	32.75	31.25	34.77	32.20

[a]Mean of all exposure periods (1-19 weeks).

[b]Number of sampling periods (3 substrates per period).

[c]Monthly values from 2, 3, and 4 week exposed substrates.

exposed during periods of high production rates, may filter or collect suspended inorganic matter, thereby decreasing percentage organic matter.

High percentage organic matter during May may have been caused by a change in the periphyton community. Cushing (1967) found a low correlation between ash and ash-free dry weight for different time periods was due to changes in diatom species composition of the periphyton community in the Columbia River, Washington. This could not be verified in the Pine because qualitative samples were not collected in May.

When all exposure periods (1-19 weeks) were averaged for percentage organic matter, the percentages are lower than those from monthly averages (Table 9). Undoubtedly the longer exposed substrates with high carbonate encrustations decreased the percentage organic matter in the total mean values. Part of the reason for this decrease may be that high standing crop on substrates from long exposure periods (5-19 weeks) collect inorganic suspended matter and decrease percentage organic matter.

A comparison of percentage organic matter of periphyton on artificial substrates from different ecosystems (Table 10) shows lakes to generally have a higher percentage organic matter than rivers. Seemingly the cause for this is high sedimentation rate of organic matter on artificial substrates in lakes. Comparing

Table 10. Comparison of percentage organic matter or periphyton collected from artificial substrates among various literature values and the present study. Values calculated from authors' data for varied exposure periods throughout the summer (May to September)

Reference	Locality	Average Percentage Organic Matter
Nielson, 1953	Cloverleaf Lake, Calif.	70
	Edith Lake, Calif.	65
	Genevieve Lake, Calif.	59
Newcombe, 1950	Sodon Lake, Mich.	47
Castenholz, 1961	Pacific Ocean, Oregon coast	42
Newcombe, 1950	Walnut Lake, Mich.	41
Cushing, 1967	Columbia River, Wash.	36
Castenholz, 1960	Alkali Lake, Wash.	34
	Falls Lake, Wash.	33
Present study	Pine River, Mich.	32
King and Ball, 1966	Red Cedar River, Mich.	26
Nelson et al., 1969	White Oak Creek, Tenn.	19

production values (Table 8) to percentage organic matter (Table 10) for the same ecosystems shows that as production rate increases organic matter decreases.

The considerable variation in percentage organic matter (Table 10) is indicative of the variation in ecosystems and methods of measuring organic weight. Obviously considerable error will be caused by measuring dry weight and then estimating organic matter from percentages in the literature.

Macrophytes

Qualitative

Three species of Potamogeton (pondweeds) were the most abundant aquatic vascular plants in the Pine River study area (Table 11). Numerous beds of Nasturtium officinale with occasional small beds of Veronica catenata occurred along margins of the stream, especially around station 1. Other sparsely distributed submerged macrophytes growing in small numbers were: Sagittaria latifolia, Sparganium sp., Ludwigia palustris, Potamogeton interruptus, and P. natans. A complete list of aquatic vascular plants and common stream-bank terrestrial plants is in Appendix B.

Beds of pondweeds up to 100 m long were noted at stations 2 and 5. In the larger beds, plants covered the bottom completely across the stream except for 1 or 2 m next to the banks where shrubs and trees shade the stream.

Largest weed beds were found where stream bottom was gravel, water depth 0.3 to 0.7 m, and stream-bank trees and shrubs lacking. Areas with large weed beds were especially prevalent adjacent to bridge crossings and in farmed areas where trees and shrubs had been removed for roads and farming.

The weed bed sampled at station 1 consisted exclusively of Potamogeton alpinus (Table 11). This pondweed, a broad-leaved form with little branching and short stems, rarely grew above 10 cm from the stream bottom and was found throughout the study area. At station 2 a large bed of P. pectinatus and P. foliosus was sampled. These narrow-leaved forms grew to lengths of about one meter in gravel areas where water depths ranged from 0.3 to 1.0 m. The plant bed sampled at station 4 consisted of P. pectinatus, P. alpinus, and P. foliosus, while at station 5 a plant bed of P. pectinatus and P. alpinus was sampled. In the sampled weed beds density of plants was uniform; whereas, near the fringes of beds distribution was patchy. There appeared to be no zonation of species in plant beds.

From visual observations in 1969 of weed beds that were a mixture of broad and narrow-leaved forms in 1968; it appeared that narrow-leaved forms were more extensive at the expense of broad-leaved forms. Sculthorpe (1967) mentions that linear, ribbon-type leaves of aquatic plants

Table 11. Percentage species composition of submerged aquatic plants in the Pine River study area during summer 1968

Station	Species								
	Potamogeton alpinus	*Potamogeton pectinatus*	*Potamogeton foliosus*	*Potamogeton interruptus*	*Nasturtium officinale*	*Veronica catenata*	*Sagittaria latifolia*	*Sparganium* sp.	*Fissidens* sp.
	Percentage composition of species in the entire stretch of river, up and downstream 1 km from each station								
1	50	-	-	-	45	2	Tr.[a]	Tr.	2
2	10	75	10	Tr.	5	Tr.	Tr.	Tr.	-
4	15	75	5	-	5	Tr.	Tr.	Tr.	-
5	15	80	-	-	5	Tr.	Tr.	Tr.	-
	Percentage composition of species in each sampled weed bed								
1	100	-	-	-	-	-	-	-	-
2	-	70	30	-	-	-	-	-	-
4	20	70	10	-	-	-	-	-	-
5	40	60	-	-	-	-	-	-	-

[a]Tr. = trace (less than 1%).

probably evade tearing more effectively than broad membranous leaves. He also states that because of light extinction in plant beds narrow-leaved species have a competitive advantage. Thus narrow-leaved forms in the Pine River undoubtedly have a competitive advantage over broad-leaved forms because they can withstand stronger currents and more efficiently utilize available light. Narrow-leaved forms probably crowd out P. alpinus in weed beds because of the light extinction factor. Since narrow-leaved forms grow to lengths of one meter they effectively shade out P. alpinus.

All species of Potamogeton found in the Pine River have been previously recorded in Michigan by Oosting (1931). Potamogeton alpinus and P. interruptus were not reported in Montcalm or Isabella Counties (counties in which the study area was located). Potamogeton alpinus has been reported in other counties of the lower peninsula and appears to be distributed throughout the state. Potamogeton interruptus, an introduced species, was reported only from the northern part of the lower peninsula (Oosting, 1931). The occurrence of P. interruptus in the Pine River indicates the distribution of this species has increased in the past 40 years in Michigan.

Quantitative

Most literature on aquatic macrophytes can be separated into: (1) descriptive studies of such factors as

distribution, chemical composition, and general abundance of species; and (2) quantitative studies of standing crop biomass and rates of production. Some investigations have been combinations of the two categories often correlating distribution and standing crop with such environmental factors as light, chemical composition of the water, substrate composition and texture, and other variables (Wetzel, 1964a). Use of aquatic vascular plants as waterfowl and animal food has also been studied (Martin et al., 1951). Besides direct investigations on aquatic macrophytes other studies have dealt with plants indirectly concentrating on energy flow thru the total ecosystem (e.g., Odum, 1957). Although aquatic plants as a group have been studied less than terrestrial plants, more investigations on hydrophytes are appearing in the literature because of the importance of macrophytes in aquatic ecosystems. Undoubtedly as more aquatic plants become nuisances in lakes and streams as a result of man's activities in fertilizing waterways, qualitative and quantitative studies of hydrophytes will increase.

Historical review.--After the turn of this century naturalists and curators of botanical gardens made descriptive studies on aquatic plants then considered exotic species. Because of the adventive spread of introduced species, e.g., Eichhornia crassepies, Elodea canadensis,

and Salvinia auriculata, descriptive studies were and continue to be made on these species.

Although descriptive studies on aquatic vascular plants are numerous (for a review of the literature see Sculthorpe, 1967), quantitative studies of hydrophyte standing crop and rate of production have been exiguous. As Wilson (1939) and later Penfound (1956) observed, the number of published studies on weight of total crop of rooted hydrophytes are very few. Standing crop measurements have been made since the 1920's, but estimates of plant production rates have only appeared in the literature during the past 15 years.

To measure standing crop biomass of aquatic plants, biologists have used gravimetric analysis of plant samples harvested from known sample areas. For estimates of the rate of macrophyte production, three general methods have been commonly used: (1) gravimetric analysis of croppings at different time periods during the growing season, (2) measurement of oxygen production by plants in closed vessels, and (3) measurement of ^{14}C uptake by plants in closed vessels. Wetzel (1964a, b, 1965, 1969a) presents literature reviews, evaluations and criticisms of the oxygen and ^{14}C methods. Gravimetric analysis of cropped plants at different time periods is the oldest method and was used in this study. For reviews and evaluation of the gravimetric method see Wetzel (1964a), Westlake (1965),

and Boyd (1967). Following is a review of the literature on standing crop biomass and primary production rate measurements by the gravimetric method. To date the majority of the literature has been on lakes.

Wetzel (1964a) reported that Petersen (1912) was one of the first workers to measure standing crop of aquatic plants gravimetrically by placing a square frame randomly over the bottom and removing the enclosed vegetation. One of the first published, extensive quantitative studies on vascular hydrophytes was performed by Rickett (1921) on Lake Mendota, Wisconsin. By hand cropping plants in 0.25 m^2 areas from different lake depths and areas, Rickett was able to estimate summer standing crop of hydrophyte species for the whole lake. With techniques developed while working on Lake Mendota, Rickett (1924) also estimated the total standing crop of plants in Green Lake, Wisconsin. Rickett's work was part of a general investigation of biological production on Green Lake and a summary of the investigations was made by Juday (1924).

Most early quantitative investigations on vascular aquatic plants were performed on Wisconsin lakes because of the pioneering work and direction of C. Juday. Wilson (1935) determined standing crops of plants from dredge samples in a medium-hard lake of northern Wisconsin. In Sweeney Lake, Wisconsin, Wilson (1937) also used dredge

samples to determine total standing crop and types of plants present. Wilson (1941) studied plant succession and made measurements of standing crop of 38 species of aquatic plants in Trout Lake, Wisconsin. A comparison of summer crops of plants and animals among four Wisconsin lakes, two hard water and two soft water, showed that standing crops were two to three times higher in hard water lakes (Juday, 1942). In Weber Lake, Wisconsin, Potzger and Van Engel (1942) compared differences in morphology and standing crops of rooted aquatic plants between two years in which a change in water level occurred. Recently, the diversity and quantity of hydrophytes in Lake Mendota were investigated by Lind and Cottam (1969). They found that total macrophyte biomass was predominantly one species, whereas Rickett (1921) found the contribution to total biomass was distributed over many species. Other qualitative studies on hydrophytes in Wisconsin lakes have been made by Schuette and Hoffman (1921), Denniston (1922), Schuette and Alder (1927, 1929a, b), Fassett (1930), Juday (1934), Manning et al. (1938), and Swindale and Curtis (1957).

Low and Bellrose (1944), in 19 Illinois lakes, collected plants from 0.5 m^2 areas to measure standing crops of seed and vegetation of 28 species of aquatic plants. They also compared plant standing crops among lakes with stabilized, semi-stabilized, and fluctuating

water levels. Nygaard (1958) measured standing crop of aquatic plants by diving and sampling 0.05 m^2 areas of lake bottom. He found maximum standing crop in dry weight at 1 and 2 m and a secondary maximum at 10 m in Lake Grane Langsø, Denmark. Standing crops at different depths were measured to show quantitative changes in submerged hydrophytes in a Utah marsh (Robel, 1962). Fish (1963) measured standing crops of Lagarosiphon before and after treatment with an arsenic herbicide in two lakes in New Zealand. Using garden shears to cut hydrophytes from 1 m^2 areas, Straškraba (1963) measured standing crops in two fishponds in southern Czechoslovakia. Assuming maximum standing crop to be annual production, Straškraba determined the contribution of hydrophytes to total production of the two ponds. Bernatowicz and Pieczyńska (1965) used the same assumption as Straškraba to estimate yearly production of emergent and submergent macrophytes in Lake Tałtowisko, Poland. Standing crop of macrophytes was measured by cropping at time of blooming in Mikołajskie Lake, Poland; and the biomass was assumed to be equal to yearly production (Kowalczewski and Wasilewski, 1966). Errors and assumptions using maximum standing crop of macrophytes to estimate yearly production are discussed by Westlake (1965, 1969a, b).

Pieczyńska and Szczepańska (1966) used cropping methods to estimate standing crop of hydrophytes in four

Polish lakes. Standing crops of hydrophytes were measured before and after herbicide treatments in Michigan ponds to determine effects of the herbicides (Sohacki, 1965). In Smyslov Pond, Czechoslovakia, Kořínková (1967) measured standing crops of littoral hydrophytes in enclosed and unprotected plant beds to determine predation pressure of carp on the plants. The following have recently published studies on hydrophyte biomass estimated by cropping plants: Bernatowicz et al. (1968), Goulder (1969), and Boyd and Hess (1970).

The preceding studies on measurement of standing crops of hydrophytes have added significant knowledge to the limnology of lakes. Sculthorpe (1967) compared standing crops of different lakes from published values and commented on the differences between types of lakes and plant depth distributions. He indicated that as a result of seasonal and annual variations, standing crops provide only limited information on growth of communities. Although estimates of standing crops add to the limnology of lakes, greater and more meaningful information is gained from measurements of the rate of production of aquatic vascular plants. As with biomass measurements, lakes have received the most attention in measurements of the rates of production of aquatic vascular plants by cropping.

Penfound (1956) was one of the first investigators to estimate rate of primary production from croppings of aquatic macrophytes at different time periods during the growing season. Comparing production rates from different communities of terrestrial and aquatic vascular plants, he found rates to vary greatly with amount of light, water, and available nutrients. He also stressed that caution should be exercised when comparing primary production rates from cropping methods because the magnitude of values depends upon time of harvest.

In Lake Ösbysjön, Sweden, production rates of submerged hydrophytes were highest in spring, lower in summer, and negative in the fall (Forsberg, 1959). Forsberg (1960) was first to express production rates of hydrophytes in grams ash-free dry weight (organic weight) per square meter. Knight et al. (1962) used croppings of aquatic macrophytes (harvest method) to compare rate of production of macrophytes with rates of phytoplankton and periphyton production in Michigan ponds. They found production rates of macrophytes in the shallow ponds were high compared with phytoplankton production rates. The ^{14}C and harvest methods were used to measure production rates of Ruppia maritima in Borax Lake, California (Wetzel, 1964a). Wetzel's comparison of the two methods indicated that Ruppia was near its maximal rate of growth earlier in the growth season than when highest standing crop was found.

In an irrigation ditch in Japan, Ikusima (1966) measured standing crop and production rate of Vallisneria by the harvest method. Westlake (1966) used the harvest method to estimate the production of Glyceria maxima. Maximum standing crop was in September and 40% of the plant's biomass was roots. Using dredge samples to collect macrophytes, Gehring (1969) compared rate of macrophyte production to rates of phytoplankton and periphyton production in two Michigan ponds. Boyd (1969) used the harvest method to measure production rates of two species of emergent vascular hydrophytes in lakes and rivers of Alabama. In another production study using the harvest method for emergent macrophytes, Boyd (1970) found the most rapid uptake of several nutrients occurred earlier than maximum growth rates. Davies (1970) compared production rates measured by the ^{14}C method and the harvest method in Marion Lake, British Columbia, and found the harvest method yielded lower rates.

Clearly the above studies on lakes indicate that quantitative estimates of hydrophyte production rates can be made by the harvest method. As Wetzel (1969a) and Davies (1970) stated the harvest method does yield rates lower than the ^{14}C method which is assumed to measure net production. Although the ^{14}C method may be more accurate in measuring instantaneous rates of macrophyte production in lentic ecosystems, the ^{14}C and oxygen

enclosure methods cannot be used accurately in flowing waters. Westlake (1967) has demonstrated that current greatly affects metabolism of aquatic vascular plants. Therefore, any method that restricts current from lotic macrophytes will yield questionable results. Obviously until a better method is developed, the harvest method will be used to estimate production rates of hydrophytes in lotic waters. The following is a literature review of standing crop and production rate measurements by the harvest method in lotic ecosystems.

Edwards and Owens (1960) were among the first to measure production rate of aquatic macrophytes by the harvest method in a river. They cropped plants across the river width in 1.8 m strips during June and September in the River Ivel, England. Production rate was determined by dividing the increase in standing crop weight by the time between the two sampling periods. Another English biologist, Westlake (1961) measured standing crop of hydrophytes by the harvest method in a polluted stream, River Colne, England. In another investigation of the River Ivel, Owens and Edwards (1961) compared hydrophyte production rates for different areas of the river. They concluded that enrichment by sewage effluent had no obvious effect on growth of macrophytes in the river. They also concluded that growth of macrophytes was primarily determined by amount of available solar radiation. With methods

developed in River Ivel investigations, Owens and Edwards (1962) determined summer production rates of macrophytes in four English rivers.

The harvest method was used by Vannote (1963) in a community production study of the Red Cedar River, Michigan. Vannote calculated a percentage stocking density of macrophytes in the river so that the estimate of production rate was for the entire river and not just the plant bed. In another ecological study of the Red Cedar, King and Ball (1967) used methods similar to those of Vannote to estimate macrophyte production rates. Their estimates of macrophyte production rates were for the entire river length while Vannote's were for one 3.5 km section. Linton (1967) measured standing crops of macrophytes in five zones of the Red Cedar. He used amount of macrophytes as a parameter in describing dynamics of rock bass populations in the five river zones. Investigations on macrophyte production rates in the Red Cedar have been summarized by Ball et al. (1969).

Macrophyte standing crop was measured by the harvest method as part of a study to determine the effects of macrophytes on nitrogen and phosphorus concentrations in a small stream in Sweden (Stake, 1967, 1968). As part of an investigation of factors affecting growth of rooted aquatic plants, Peltier and Welch (1968) used the harvest method to estimate rate of macrophyte production in the

Holston River, Tennessee. Distribution and intensity of plant growth were closely related to available light reaching stream bottom. Hannan and Dorris (1970) used the harvest method to measure standing crops of macrophytes as part of a study on macrophyte succession after dredging in the San Marcos River, Texas.

Evidently from the above works on rivers, the harvest method has yielded worthwhile estimates of hydrophyte standing crop and rates of production. As stated previously the ^{14}C and oxygen enclosure methods can give estimates of macrophyte production rates in lentic waters. However, the two methods as they have been developed cannot be used successfully in lotic waters because they negate the effects of current. Until a more accurate method is found the harvest method will be used in lotic environments to estimate biomass and production rates. From previous investigations in the literature and the Pine River study, several errors associated with the harvest method have been found and will be discussed in the next section.

Evaluation of the harvest method.--Some errors and criticisms of the harvest method are presented and discussed by Westlake (1965, 1969a) and Wetzel (1965). The following discussion is on major errors and assumptions of the harvest method as used in the Pine River to estimate net production rates of aquatic vascular plants.

1. Mechanical losses: Evidently, losses due to mechanical action of current on vascular aquatic plants are slight. Hydrophytes in lotic waters have adapted to water current forces and tearing or breakage of plant parts is slight in rivers under normal flow conditions. But at times of flooding when currents are relatively high, losses of plant biomass may occur. From observations in the Pine, no plants or plant parts floated downstream except in late August, September, and October when plants began breaking loose from the bottom. High discharge occurred during May in the Pine, but current did not appear to be strong enough to tear the small growths of plants from the substrate.

2. Grazing losses: Because aquatic macrophytes are utilized as food by waterfowl, mammals, reptiles, and fish, there will be losses of plant material by grazing. Mammals and reptiles which might feed on aquatic plants were very rarely observed in the study area. Twice during the summer three or four ducks were observed in the study area, but the extent that ducks and fish fed on the sampled plant beds was undetermined. Because no signs of grazing on plants in the sampled beds were observed, grazing losses were assumed to be very slight in the Pine. Westlake (1965, 1969b) discusses the consequences and corrections needed if grazing of plants is obvious.

3. Sampling losses: If plants are not carefully removed from the substrate, losses of plant material can

result. Losses of material may be high if sampling is performed by dredge or diving in deep areas. All sampled plant beds in the Pine were in water depths less than one meter and plants were removed while wading in the stream. Extreme care was taken in removing macrophytes by hand. Plants were removed in small handfulls by gently pulling from the substrate. At the time of maximum standing crop in July and August, 30 to 45 minutes were required to carefully remove all plants from a one meter square area. No pieces of plants were noticed floating downstream during or after sampling. As an added precaution a net can be set behind the sampling area to collect lost plant pieces.

4. Death losses: Losses of plants due to death during the growing season may be considerable in some situations (Westlake, 1965). In many tropical and subtropical communities there is no pronounced seasonal periodicity of biomass; death losses equal growth increments. Therefore, production rates from biomass changes in tropical communities can only be made if the rate of turnover can be determined. Temperate submerged macrophytes usually have seasonal periodicity and standing crop changes lead to estimates near net production rates unless death losses cannot be determined. In healthy communities, losses during the growing season are usually only 2-15% before the maximum biomass is sampled (Westlake, 1969b).

From observations on the Pine, losses due to death were estimated to be less than 5% before maximum standing crop occurred. Before maximum standing crop was reached no dead plants were observed. When linear-leaved species were 1 m long in July and August, a few dead leaves near plant bases were found. The amount of lower dead leaves did not appear to be greater than 1% of an individual plant biomass.

Losses due to death of plants should be estimated in order to make accurate estimates of production rates by the harvest method. Death losses will be a major source of error in the harvest method, unless these losses can be quantified.

5. Underground organs: Many submerged and emergent macrophytes have a large portion of their biomass buried (Westlake, 1965, 1966; Sculthorpe, 1967; Szczepański, 1969). Harvesting of these species without sampling roots and underground organs would underestimate standing crop. Harvested samples in the Pine included roots. Most roots were collected when plants were pulled from the substrate. But to insure complete collection of roots, the substrate was dug up by hand to a depth of 10 cm to remove all roots and underground organs. Removal of roots appeared to be complete. Observations during the year after sampling revealed no growths in sampled areas except on the fringes, where new growth was occurring from vegetative propagation.

Potamogeton sampled in the Pine are perennials and have storage organs which remain in the substrate from year to year. Therefore, estimates of standing crop and production rates are higher than the actual year's growth because previous year's storage organs were harvested. Sifting weed bed substrates by hand in March revealed very few storage organs. Although a quantitative measure of previous year's storage organs was not determined, it is assumed that less than 5% of the standing crop was previous year's storage organs.

6. Weight variations: Because of differences in techniques and procedures, fresh weight values of hydrophytes can be quite variable. This variability makes comparisons of biomass measurements by the harvest method difficult. More useful comparisons can be made if plant material is oven dried and ashed to determine ash-free dry weight (organic weight). Temperatures for these measurements have generally been set at 105 C and 550 C (Westlake, 1965, 1969a; Wetzel, 1965).

Some error may have been introduced by ashing at 550 C because macrophytes in the Pine had carbonate encrustation. Magnesium carbonate decomposes at temperatures above 350 C (Westlake, 1965). Amounts of magnesium carbonate were not determined, but it is assumed that the amount was small in the total carbonate deposits and error was slight. Wetzel (1965) has stated that

errors resulting from loss of magnesium carbonate by ashing at 550 C are probably small among calcareous plants. Although the proportion of magnesium carbonate in marl deposits is variable, usually amounts are less than 3% (Blatchley and Ashley, 1900, as cited in Wetzel, 1965). Calcium carbonate starts decomposing at temperatures above 550 C (Westlake, 1965) and it was assumed that no losses occurred during ashing.

7. Distribution variation: Variable spatial distribution of plants in weed beds can cause errors in estimating biomass per area. Because of variable physical characteristics within a section of stream (i.e., substrate size, current velocity, available light, and water depth) spatial distribution can vary considerably. Some of this error can be reduced by increasing the number of samples and harvesting a large area at a sampling site. Although advantageous to harvest large and numerous samples, it is often difficult or impossible because stream submerged weed beds are often small in size and processing of large and numerous samples is tedious.

Individual sample area size in this study was 1 m^2 and three replicates were harvested at each sampling period. I believe sample size was large enough, but not the number of replicates. As will be discussed later under (Standing crop and rate of production), variation about mean biomass at some sampling dates was high. More

replicates (five to ten) would have decreased variations about the mean and trends in summer production rates would have been more clearly delineated. Also, time of maximum standing crop would have been more clearly defined.

While death and grazing losses and spatial distribution can cause errors in estimating production rates by the harvest method, I believe the method yields reliable estimates of net primary production. In this study, although quantitative measures of biomass losses were not made, it is assumed that less than 5% of total biomass was lost before maximum standing crop was measured. Because losses were offset to some extent by perennial underground organs, no correction factor was used in estimating standing crop and production rates. Biomass differences over a short period are a valid measure of net production rates (Westlake, 1965).

Standing crop and rate of production.--Growth curves of macrophytes at four stations in the Pine are sigmoid to time of maximum standing crop in August (Figure 8). After maximum standing crop was reached biomass declined until all plants detached from the substrate in October. Growth curves of macrophytes in the Pine are similar to the hypothetical growth curve of Westlake (1965).

Figure 8. Standing crop biomass (g organic matter m^{-2}) of submerged macrophytes at four stations in the Pine River, summer 1968. Vertical lines represent one standard error on each side of the mean. Curved lines fitted by inspection.

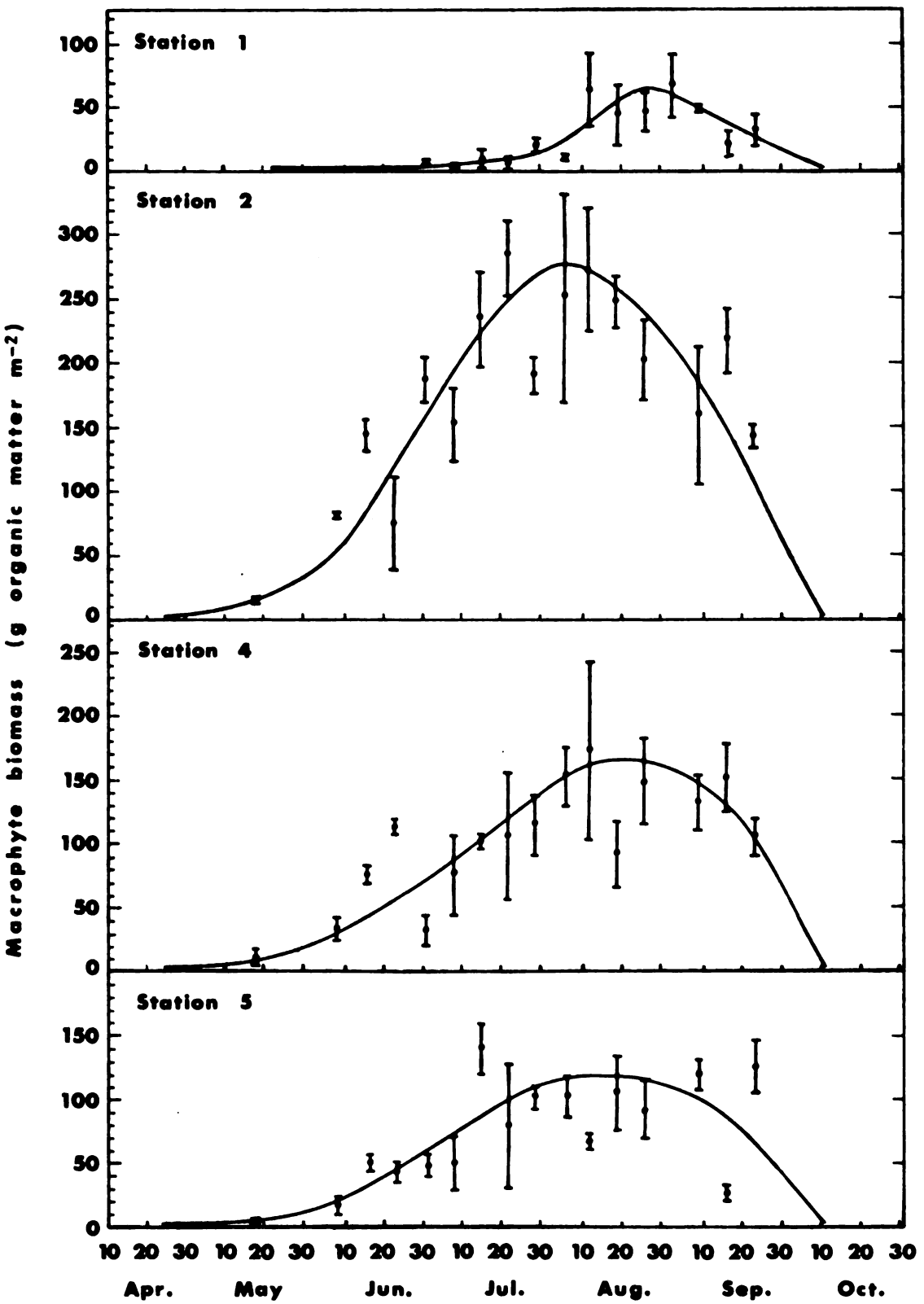
Station 1
Station 2
Station 4
Station 5
Macrophyte biomass (g organic matter m-2)
0
50
100
150
200
250
300
10 20 30 10 20 30 10 20 30 10 20 30 10 20 30 10 20 30 10 20 30
Apr.
May
Jun.
Jul.
Aug.
Sep.
Oct.

Figure 8

Maximum standing crop at station 2 occurred sooner and with higher biomass than any other station. Evidently better conditions for growth existed at station 2 compared with the other stations. Reasons why maximum biomass was reached sooner in the growing season (about 10 days) at station 2 compared with the other stations are unknown. Differences in plant species at the stations does not appear to be the answer. Macrophytes at station 2 were predominantly Potamogeton pectinatus (see Table 11), but this was also the predominant species at station 4 and 5.

Undoubtedly higher maximum biomass at station 2 was partly due to species composition at the four stations. Both species at station 2 were narrow-leaved forms. Plants at station 1 were broad-leaved while those at 4 and 5 were a mixture of broad and narrow-leaved species. While the broad-leaved species only grows to about 10 cm from the substrate, narrow-leaved forms grow to 1 m lengths from the substrate. Obviously narrow-leaved forms more efficiently utilize the area above the substrate for growth. Because standing crop biomass was measured on a substrate area basis, the contribution of biomass per area is greater for narrow-leaved forms. This may explain why station 2 with only narrow-leaved species had higher standing crop per area than the other stations.

Why plants appeared at station 1 four weeks later than at the other stations (Figure 8) is not known. At stations 4 and 5 the same species present at station 1 appeared earlier in the spring. Lower water temperature or less available light may be the factors causing later germination and a shorter growing season.

Variation about mean biomass for some sampling periods was high (see standard errors in Figure 8). At other sampling dates variation was low. Evidently the randomly high and low variations were due to variable spatial distribution of plants in macrophyte beds. As mentioned previously under Evaluation of the harvest method, I believe more replicate samples at each sampling date would have decreased high variation. Part of the reason for spatial variation of plants was the variable physical conditions of substrate size, current, water depth, and available light. With random sampling of only three one-meter square areas, it was not uncommon for one of the selected areas to contain a large rock. Also some sampled areas were near the edge of weed beds where distribution was patchy. These sampled areas that were partly bare of plants caused low estimates of standing crop. Since they comprised one third of the replicates on some dates, variation was large. Ideally ten replicates would probably have given a better estimate of standing crop for each sampling date.

Net production rates of macrophytes (Figure 9) were greatest before maximum standing crop was reached in August at stations 2, 4, and 5. Wetzel (1964a) and Davies (1970) also found production rates greatest before maximum standing crop was reached. This is as expected since production rates are highest during the exponential phase of growth.

Macrophyte growth at station 1 was atypical because production rates were highest at the time of maximum standing crop in August. At stations 2, 4, and 5 production rates were low during May, but during June and July production rates were high. Evidently conditions during June and July were optimal for growth at the downstream stations, but not optimal until August at station 1.

Because of a lack of variance homogeneity a non-parametric, Kruskal-Wallis ranking test (Bradley, 1968) was used to compare the median macrophyte production rates (g organic matter m^{-2} day^{-1}) at the four stations. The analysis showed that production rates between stations were significantly different ($P(x^2) = 39.3$) at the 0.1% level (df=3). Difference in production rates between stations 1 and 2 is probably significantly different. Probably there is no significant difference between production rates at stations 4 and 5.

Some difference in production rates was due to differences in plant species at the four stations.

Figure 9. Net primary production rates of submerged macrophytes at four stations in the Pine River, summer 1968. Values were determined by dividing measured standing crop biomass by the number of days since the start of the growing season (April 24 for stations 2, 4, and 5; May 22 for station 1). Vertical lines represent one standard error on each side of the mean.

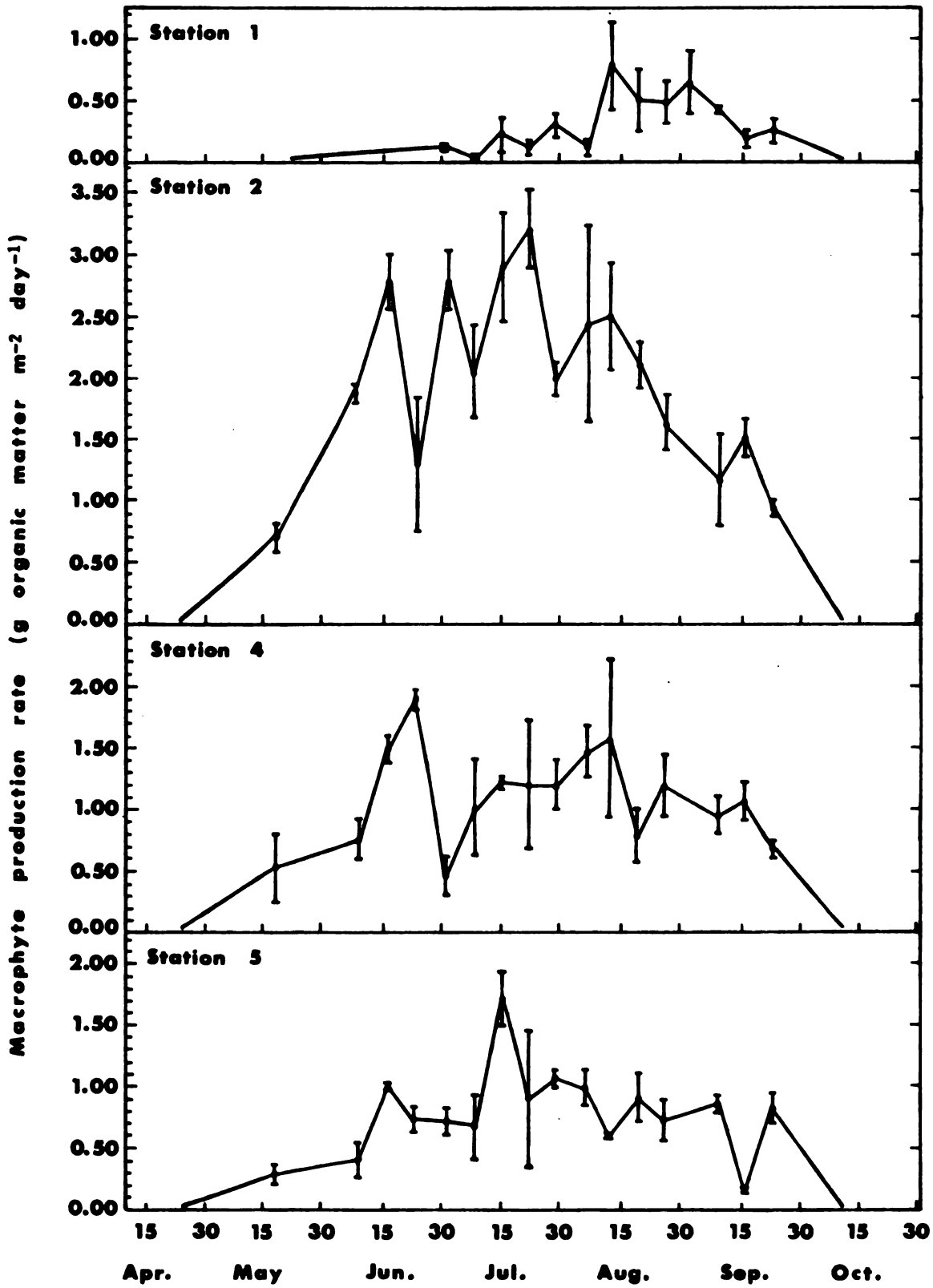
Station 1
Station 2
Station 4
Station 5
Macrophyte production rate (g organic matter m-2 day-1)
1.00
0.50
0.00
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
2.00
1.50
1.00
0.50
0.00
2.00
1.50
1.00
0.50
0.00
15 30 15 30 15 30 15 30 15 30 15 30 15 30
Apr. May Jun. Jul. Aug. Sep. Oct.

Figure 9

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Potamogeton alpinus is probably not as productive on a substrate area basis as the narrow-leaved species. Although some difference in production rates between species exists, it appears that other factors are contributing to macrophyte production rate differences between stations.

Low production rates at station 1 were not correlated with any measured chemical parameters. Nitrate and phosphate concentrations were higher at station 1 than station 2 (see Appendix A). The South Branch enters the Pine below station 1 and may be adding some minor nutrient that is limiting macrophyte growth at station 1. However, this does not appear to be the total answer.

I believe physical characteristics at the four stations were the main factors causing production rate differences. Periphyton production rates were also lower at station 1 compared to station 2 and it was hypothesized that stream cover was limiting growth at station 1. It appears that available light was also limiting macrophyte growth at station 1. The extensive, shade canopy of stream-bank trees and shrubs limits light reaching the stream at station 1 for a great portion of the day. At station 2 the canopy has been partially removed for farming and road building. The wide stream width at station 2 and lack of shading allowed more light to reach the stream and be available for plant growth.

Other investigators have also found that light was the primary factor determining growth of submerged macrophytes. Owens and Edwards (1961) concluded that in the River Ivel, growth of macrophytes was primarily determined by amount of solar radiation. Peltier and Welch (1968) also concluded that distribution and intensity of plant growth were closely related to light actually reaching stream bottom and available for growth.

Although production rates at stations 4 and 5 may not be significantly different from rates at station 2, they were lower at 4 and 5. Lower rates at 4 and 5 may have been caused by: (1) differences in plant species at 4 and 5 compared to station 2; (2) competition for nutrients between macrophytes and periphyton; (3) lack of some nutrient which was being taken up by plants at station 2; and (4) differences in physical characteristics at the stations.

In summary aquatic vascular plant, net production rate and maximum standing crop were highest at station 2. Station 1 had the lowest production rate and standing crop, while stations 4 and 5 were similar in macrophyte production. Evidently high production rates at station 2 compared to station 1 were caused by physical characteristics of the stream causing light to be more available for growth at station 2.

Comparison of standing crops and production rates.--Maximum standing crop of macrophytes in the Pine was similar to that found in most rivers (Table 12). Although somewhat higher than crops in other temperate regions (Red Cedar, English rivers), macrophytes in the Pine were not as dense or luxurious as aquatic plants in more southern latitudes. Evidently the longer growing season in Florida and Texas results in larger standing crops of submerged macrophytes.

The maximum standing crop from the Pine in Table 12 was from station 2 and consisted of mostly Potamogeton pectinatus. Maximum standing crop in the Holston River, Tennessee was also predominantly P. pectinatus (Peltier and Welch, 1968). The Holston River is an enriched, large river and luxuriant aquatic plants have become a nuisance by clogging steam plant intakes (Peltier and Welch, 1968). While the Pine is a small river, macrophyte standing crops approach the size of crops in the Holston River.

Standing crops of submerged macrophytes in lakes and ponds range in values about the same as found for rivers in Table 12 (for comparisons of standing crops in different habitats see Westlake, 1963; Sculthorpe, 1967). Emergent macrophyte standing crops in some environments are two to four times greater in biomass than crops of submerged macrophytes (see Penfound, 1956;

Table 12. Maximum standing crops of submerged macrophytes in rivers (measured by the harvest method)

Reference	River	Dry weight ($g\ m^{-2}$)
Westlake, 1961	River Colne, England	123
Ikusima, 1966	Koaidame (irrigation ditch), Japan	280
Vannote, 1963	Red Cedar River, Michigan	326
Owens and Edwards, 1962	River Ivel, England	320
	Chess	322
	Yare	381
	Test	385
Natelson, 1955 (as cited in Penfound, 1956)	Three Florida spring-river systems	411 423 525
Present study	Pine River, Michigan	444
Peltier and Welch, 1968	Holston River, Tennessee	457
Edwards and Owens, 1960	River Ivel, England	519
Odum, 1957	Silver Springs, Florida	621
Hannan and Dorris, 1970	San Marcos River, Texas	638

Bernatowicz and Pieczyńska, 1965; Sculthorpe, 1967; Boyd 1967, 1969, 1970, for crops of emergent macrophytes). Emergent macrophytes can reach high standing crops because they have the best of both environments, in the sense of more or less unrestricted supplies of gaseous carbon dioxide and light, and of water and dissolved nutrients (Sculthorpe, 1967).

Submerged macrophyte production rates in the Pine were low to medium when compared with other habitats (Table 13). Caution must be used in comparing rates in the literature because of differences in methods used by investigators. Although the majority of investigators listed in Table 13 harvested numerous samples at each sampling date, they only sampled two to six times during the growing season. This type of sampling, in my estimation, yields high estimates of macrophyte production rates. If sampling is carried throughout the entirety of the growing season production values are lower because of slow growth very early in the season and after maximum standing crop is reached. If plants had been sampled at the Pine stations on only four or five dates (two early in the season and two or three at the time of maximum standing crop) production rates would have been higher. Rate values are also higher if calculated by dividing weight increment by the time period between

Table 13. Comparison of net production rates of submerged macrophyte beds as measured by the harvest method for one growing season (values in grams oven dry matter per meter square of macrophyte bed per day)

Reference	Locality	Mean production rate ($g\ m^{-2}\ day^{-1}$)
Gehring, 1969	Pond, Michigan	0.67
Wetzel, 1964a	Borax Lake, California	1.1[a]
Ikusima, 1965	Irrigation ditch, Japan	1.2[a]
Present study	Pine River, Michigan	
	Average	1.58
	Station 1	0.65
	2	2.83
	4	1.57
	5	1.28
Owens and Edwards, 1961	River Ivel, England	
	Reach A	1.12[b]
	B	1.60
	C	2.88
	X	3.99
Hannan and Dorris, 1970	San Marcos River, Texas	2.00[a]
Forsberg, 1959	Lake Ösbysjön, Sweden	2.1[a]
Knight et al., 1962	Ponds, Michigan	
	Average of four ponds	3.39
Peltier and Welch, 1968	Holston River, Tennessee	
	Average of two stations	4.16[b]
Forsberg, 1960	Lake Ösbysjön, Sweden	4.7[b]
Odum, 1956	Silver Springs, Florida	
	Average for three years	5.51
Owens and Edwards, 1962	River Test, England	5.91[b]
	River Yare, England	8.86

[a]Rate calculated from author's data by dividing standing crop by number of days from start of the growing season.

[b]Rate calculated from author's data by dividing increment of standing crop by the time period between samples.

samples. This calculation method had to be used for four of the references because total time of the growing season was not given.

With these considerations in mind, it appears that average macrophyte production rate for the whole study area was moderate compared to rates in other aquatic habitats. Also, the production rate at station 2 was high compared to rates in other rivers and lakes. Evidently, production rates of submerged macrophytes are somewhat higher in rivers than in lakes and ponds, but ranges of net production rates for lentic and lotic habitats are generally the same.

A comparison of submerged macrophyte production rates for the entire, river-bottom area revealed the Pine to be greater in production than the Red Cedar River (Table 14). While 20% of the bottom area in the Pine study area was stocked with aquatic plants, production rate was greater than in the Red Cedar where 44% of the river bottom was stocked with plants. Although the whole Pine study area had a higher macrophyte production rate than the rate in the whole Red Cedar, sections of the Red Cedar were as productive as the Pine. The production rate found by Vannote (1963) for one section of the Red Cedar was about the same as the production rate at station 2 in the Pine.

Table 14. Comparison of net production rates of submerged macrophytes for the entire area of the river bottom. Values from the Red Cedar determined by a random sampling procedure, those from the Pine by visual estimation of percentage plant cover

Reference	Locality	Percentage bottom area covered by plants	Growing season net production rate (g dry matter m^{-2} day^{-1})
King, 1964	Red Cedar River, Michigan (Whole river)	44[a]	0.146
Present study	Pine River, Michigan		
	Average of four stations	20	0.38
	Station 1	5	0.03
	2	34	0.96
	4	24	0.37
	5	23	0.30
Vannote, 1963	Red Cedar River, Michigan (3.5 km section)	50	1.37

[a]Value from Linton (1967).

Production rates for the Pine in Tables 13 and 14 are for the predominant macrophytes--Potamogeton. Although Potamogeton were the major macrophyte producers in summer, some macrophyte production by other species contributed to total yearly primary production in the river. Nasturtium officinale and Veronica catenata were found throughout the study area, and were especially prevalent at station 1. These two perennial species grew throughout the year and did not detach from the substrate in the fall. Yearly production of organic matter by these species was not determined. Obviously, an estimate of total yearly organic matter production by macrophytes from production rates in Table 13 or 14 would underestimate the actual amount produced in the study area.

Percentage organic matter.--Percentage organic matter at all stations decreased slightly from May to September (Figure 10). Carbonate encrustation was especially noticable on plants in August and September. Apparently the increase in carbonate deposits caused the decrease in percentage organic matter as summer progressed.

Average summer percentage organic matter for plants at the four stations were: station 1, 57%; stations 2 and 4, 71%; and station 5, 63%. The cause for differences in percentages between stations may be

Figure 10. Percentage organic matter (ash-free dry weight divided by dry weight) of submerged macrophytes at four stations in the Pine River during summer, 1968.

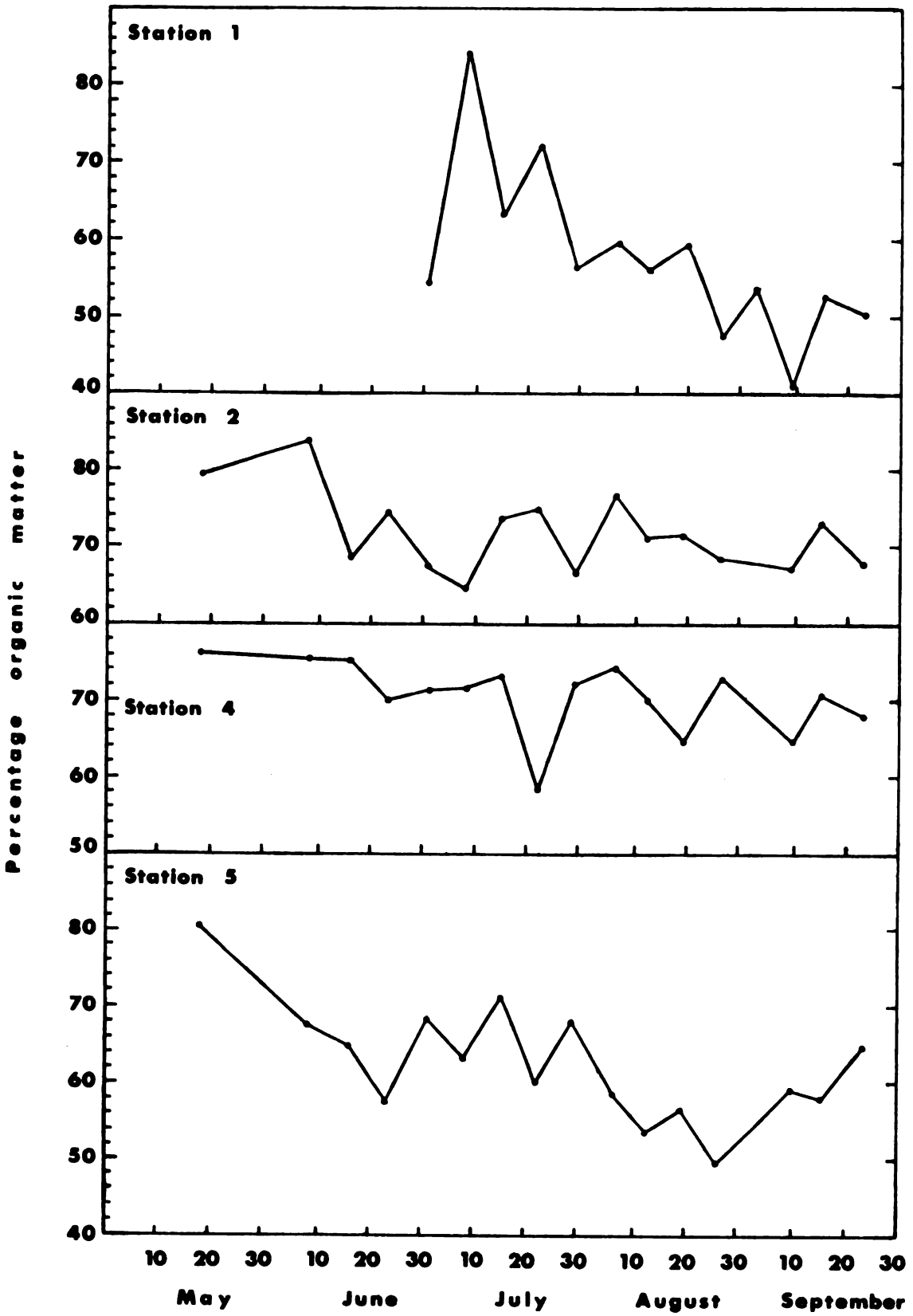
Station 1
Station 2
Station 4
Station 5
Percentage organic matter
80
70
60
50
40
10 20 30 10 20 30 10 20 30 10 20 30 10 20 30
May
June
July
August
September

Figure 10

due to differences in species composition at the four stations. Plants sampled at station 1 were all Potamogeton alpinus. Apparently this species has a lower percentage organic matter than the narrow-leaved species at station 2. Sampled plants at station 5 were 40% P. alpinus (see Table 11) and average percentage organic matter at this station was lower than at station 2. Although plants sampled at station 4 were 20% P. alpinus the average percentage organic matter was similar to that at station 2.

Percentage organic matter for Potamogeton in the Pine was somewhat lower than percentages found by other investigators. Bernatowicz and Pieczyńska (1965) found two species of Potamogeton to have 68 and 80% organic matter in Lake Tałtowisko, Poland. Peltier and Welch (1968) found hydrophytes, (majority was P. pectinatus) in the Holston River, Tennessee, to average 71% organic matter. Three species of Potamogeton in the San Marcos River, Texas, averaged 81, 84, and 85% organic matter (Hannan and Dorris, 1970). Sculthorpe (1967) lists six species of Potamogeton which ranged from 62 to 87% organic matter. Carbonate deposits undoubtedly caused lower percentages in the Pine. Percentage organic matter may be lower than 65% of the dry weight in plants growing in calcareous waters where heavy encrustations of marl may be deposited on foliage (Sculthorpe, 1967).

Total Net Primary Production

Primary producers in the Pine River study area were periphyton and aquatic vascular plants. During summer (May to September) of 1968, net rate of periphyton production was 0.28 g organic matter m^{-2} day^{-1}, while macrophyte production rate was 0.29 g organic matter m^{-2} day^{-1}. Summer, net primary production rate at each station was: (1) 0.23, (2) 0.95, (4) 0.53, and (5) 0.56 g organic matter m^{-2} day^{-1}.

To determine the annual net primary production rate a correction factor was needed because rate of periphyton production in the winter months will be lower. Grzenda (1960) found the rate of periphyton production in the Red Cedar River to be 0.56 g organic matter m^{-2} day^{-1} annually and 0.78 g m^{-2} day^{-1} during summer. Assuming the same summer to annual rate ratio, annual rate of periphyton production in the Pine would be 0.20 g m^{-2} day^{-1}. On an annual basis macrophyte production rate was 0.13 g m^{-2} day^{-1}.

The total area of river bottom in the study area (20 river km between stations 1 and 5) was calculated from surface measurements to be approximately 3.0×10^5 m^2. Annual amount of organic matter produced in the study area was estimated to be 22 metric tons (0.20 g m^{-2} day^{-1} x 365 days x 3.0×10^5 m^2) by periphyton and 14 metric tons (0.13 g m^2 day^{-1} x 365 days x 3.0×10^5 m^2) by

aquatic vascular plants. Because of the irregular topography of stream bottom and additional area of macrophyte surfaces, area colonized by periphyton was obviously greater than surface measurements indicated. Nelson et al. (1969) found the total bottom area of a stream estimated by ^{32}P uptake to be four times greater than the bottom area calculated from surface measurements. They concluded that the value obtained by uptake data was a better estimation of total bottom area than surface measurements of length and width. Multiplying annual production of periphyton by four gives 88 metric tons of periphyton organic matter.

Measured periphyton and macrophyte production rates in the Pine indicated that rates of summer production were similar for the two primary producers. On an annual basis, rate of periphyton production was one and a half times as great as the macrophyte rate. Amount of organic matter produced annually by periphyton was evidently seven times greater than annual macrophyte production.

The annual net primary production rate for the Pine during 1968 in dry weight was 0.74 g dry matter m^{-2} day^{-1}, with the periphyton rate calculated as 0.57 g m^{-2} day^{-1}. The macrophyte rate was 0.17 g m^{-2} day^{-1}. Using Odum's method of adding 30% for converting net production rates to gross production rates (Odum, 1959),

the annual gross rate of primary production would be 0.96 g dry weight m^{-2} day^{-1}. This value ranks the Pine River study area in Odum's second magnitude of production rates with shallow lakes and ponds, ocean coasts, average forests, moist grasslands, and ordinary agriculture. The value for the Pine is on the low end of Odum's range of values and indicates that the Pine is moderately low in gross rate of primary production compared to major environments of the world.

SUMMARY

Periphyton

1. Periphyton biomass and production rate were determined gravimetrically after accrual from 2 to 14 weeks on Plexiglas substrates.

2. During summer (May to September) diatoms were the dominant algae in the periphyton. Cladophora glomerata was collected abundantly on substrates during August and September. Cocconeis was a pioneer genus on artificial substrates, while Navicula was a dominant genus on substrates with a pioneer growth.

3. Turnover times at the four stations were calculated at station 1, 28; 2, 30; 4, 25; and 5, 14 days.

4. Growth curves from May to July were sigmoid with a carrying capacity of 5 to 8 (station 1) and 10 to 20 (station 2, 4, and 5) g organic matter m^{-2}, which was reached after 6 to 7 weeks of exposure. Carrying capacity biomass was highest at station 5.

5. Production rates were lowest during May and highest at all stations, except station 1, in June and July. Highest rate at station 1 occurred in August. Highest production rate at any station was 0.864 g organic matter m^{-2} day^{-1} at station 5 during June.

6. Rainfall caused low production rates by scouring of the stream bed and decreasing available light from overcast skies and high water. Scouring was very appreciable when rainfall was over 2 cm in a 24 hour period.

7. Average summer production rates were: station 1, 0.208; 2, 0.268; 4, 0.272; and 5, 0.374 g organic matter m^{-2} day^{-1}. The rate at station 1 was significantly different from the rate at station 5.

8. Stream cover appeared to be the major parameter limiting periphyton production at station 1 compared to the downstream stations.

9. Substrates in riffles usually showed highest production rates compared to rates in pools and shaded areas. Lowest rates were found in shaded areas.

10. Production rates in the Pine were moderate to high compared with periphyton production rates measured by other investigators in lakes and streams.

11. Percentage organic matter was low when production rates were high. Compared to values from other investigations on lakes and streams percentage organic matter was low in the Pine.

Macrophytes

1. Macrophyte biomass and production rate were gravimetrically determined after harvesting plants from weed beds.

2. Three species of Potamogeton were the dominant aquatic vascular plants.

3. Sigmoid growth curves of submerged macrophytes were typical of perennial plants.

4. Maximum standing crop was greatest at station 2 and occurred sooner in summer (August) than at the other stations. Plants at station 1 germinated later and reached maximum standing crop later in the season than at the downstream stations.

5. Average summer production rates in plant beds were: station 1, 0.65; 2, 2.83; 4, 1.57; and 5, 1.28 g organic matter m^{-2} day^{-1}. Production rates were greatest before maximum standing crop occurred, except at station 1 where highest production rate occurred at time of maximum standing crop.

6. Stream cover limiting available light was evidently the major parameter causing low macrophyte production at station 1 compared to the downstream stations.

7. Maximum standing crop in the Pine was similar to crops found in other rivers, although lower than emergent plant standing crops.

8. Production rates in the Pine were average compared to rates in other rivers and lakes.

9. Percentage organic matter decreased from May to September, apparently due to increased carbonate

encrustation later in summer. Values for Potamogeton in the Pine were low compared to percentages of Potamogeton in other streams and lakes.

Total Net Primary Production

1. Summer net primary production rates at each station were 1, 0.23; 2, 0.95; 4, 0.53; and 5, 0.56 g organic matter m^{-2} of stream bottom day^{-1}.

2. Average annual rate of net primary production was estimated at 0.33 g organic matter m^{-2} day^{-1}.

3. Annually the amount of organic matter produced in the study area was estimated at 88 metric tons by periphyton and 14 metric tons by macrophytes.

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APPENDICES

APPENDIX A

CHEMICAL DATA OF THE PINE RIVER

Appendix A. Chemical data of the Pine River (all concentrations in ppm, methods listed on last page)

Station[a]	Time	Temp. C		D.O.	pH	Alkalinity		Hard.	Cl-	Carbon		Phosphate		Nitrate
		Air	HOH			phth	M.O.			Total	Org.	Total	Ortho	NO_3-N
12/15/1967														
(1)	1000	-5.5	0.5	12.8	7.5	---	---	---	---	----	----	.100	----	----
(2)	1130	-3.0	0.5	14.2	7.3	---	---	189	---	----	----	.064	----	----
(3)	1330	-1.0	1.0	14.0	7.2	---	---	---	---	----	----	.058	----	.716
(4)	1400	-1.5	1.0	15.4	7.4	---	---	---	7.9	----	----	.053	----	----
(5)	1530	---	---	15.1	7.6	---	---	---	---	----	----	.040	----	.577
4/6/1968														
(1)	1030	7.0	3.9	12.2	7.6	---	144	179	7.2	37.0	0.9	.158	----	.145
(2)	1330	8.0	6.0	12.8	7.7	---	142	191	7.3	43.5	8.9	.064	----	.069
(3)	1405	11.0	8.2	12.6	7.9	---	161	195	7.2	33.5	----	.072	----	.055
(4)	1500	11.0	8.1	13.3	7.9	---	162	196	6.9	59.5	20.0	.021	----	.200
(5)	1630	11.2	8.3	13.5	7.8	---	169	211	9.8	63.0	21.8	.086	----	.092
4/24/1968														
(1)	1030	16.0	10.5	11.4	7.7	---	207	214	7.3	63.0	12.5	.286	----	.147
(2)	1230	18.0	12.0	10.2	7.5	---	222	219	7.4	21.0	----	.116	----	.178
(3)	1330	18.0	12.5	10.5	7.8	---	218	223	7.0	62.0	8.8	.140	----	.094
(4)	1500	18.0	14.0	10.8	7.7	---	223	224	6.8	67.0	12.6	.077	----	.170
(5)	1600	19.0	15.0	11.0	7.8	---	226	224	9.0	67.0	26.5	.064	----	.276
5/4/1968														
(1)	1030	6.0	9.5	10.5	---	---	194	231	6.5	62.0	14.7	.227	----	.225
(2)	1230	9.0	9.5	8.8	---	---	190	227	7.4	60.5	14.1	.089	----	.072
(3)	1330	10.0	9.5	11.0	---	---	206	232	6.5	62.0	11.7	.072	----	.193

Appendix A.--(continued)

Station[a]	Time	Temp. C		D.O.	pH	Alkalinity		Hard.	Cl-	Carbon		Phosphate		Nitrate
		Air	HOH			phth	M.O.			Total	Org.	Total	Ortho	NO_3-N
5/4/1968														
(4)	1530	10.5	9.6	11.8	---	---	209	229	6.6	60.5	9.5	.044	----	.206
(5)	1630	9.0	9.7	12.1	---	---	213	233	10.4	62.0	10.0	.059	----	.189
5/18/1968														
(1)	1945	15.6	15.0	8.3	7.5	---	197	208	6.2	64.0	15.9	.146	----	.155
(2)	1745	17.0	16.0	10.3	7.7	---	183	218	7.0	63.0	18.4	.077	----	.157
(3)	1700	21.0	15.0	10.4	7.8	---	201	224	7.2	63.0	14.0	.094	----	.160
(4)	1400	17.0	14.6	11.6	7.6	---	198	222	7.0	62.0	13.7	.012	----	.214
(5)	1000	18.0	11.0	9.6	7.6	---	200	227	9.5	60.5	11.7	.072	----	.255
6/1/1968														
(1)	0945	15.0	14.4	6.3	7.2	---	142	180	7.5	59.0	24.4	.202	----	.125
(2)	1100	14.0	15.0	6.9	7.2	---	145	184	7.5	59.0	23.6	.082	----	.128
(3)	1245	14.4	14.4	7.4	---	---	161	191	7.5	62.0	22.7	.090	----	.078
(4)	1300	15.0	15.0	7.7	7.4	---	156	191	7.0	60.5	22.4	.077	----	.050
(5)	1500	15.0	15.0	7.8	7.4	---	168	198	9.0	62.0	20.8	.092	----	.258
6/8/1968														
(1)	1030	24.5	19.5	6.8	---	---	172	202	5.5	64.0	22.0	.400	----	.165
(2)	1300	31.0	22.0	9.4	7.6	---	178	214	6.0	63.0	19.6	.188	----	.164
(3)	1400	30.5	21.0	7.1	7.4	---	186	220	6.5	63.0	17.6	.062	----	.235
(4)	1600	30.0	23.0	9.4	---	---	178	229	7.5	62.0	18.6	----	----	.081
(5)	1800	30.0	24.5	9.6	8.0	---	187	223	11.0	63.0	17.4	.069	----	.260

Appendix A.--(continued)

Station[a]	Time	Temp. C		D.O.	pH	Alkalinity		Hard.	Cl-	Carbon		Phosphate		Nitrate
		Air	HOH			phth	M.O.			Total	Org.	Total	Ortho	NO_3-N
6/16/1968														
(1)	1000	15.0	15.0	8.3	7.4	---	183	208	6.0	56.0	11.4	.096	----	.142
(2)	1100	14.5	16.0	9.1	7.6	---	189	222	7.0	50.5	4.4	.194	----	.335
(3)	1230	16.0	16.5	9.2	7.3	---	187	229	7.0	54.0	8.4	.051	----	.160
(4)	1430	21.0	17.0	10.8	7.5	---	188	227	5.5	52.0	13.4	.144	----	.242
(5)	1800	21.0	19.0	11.0	8.1	---	192	230	9.5	52.0	5.2	.060	----	.075
6/23/1968														
(1)	0930	18.5	15.5	9.7	7.3	---	185	226	5.0	48.0	2.9	.147	----	.186
(2)	1015	22.0	17.0	9.6	7.4	---	188	228	7.0	48.0	2.4	.134	----	.123
(3)	1200	23.0	17.0	11.4	7.6	---	193	231	7.0	10.0	---	.086	----	.370
(4)	1300	25.5	19.0	9.1	7.8	---	185	230	6.5	50.0	4.9	.090	----	.387
(5)	1345	28.0	20.0	10.9	8.0	10.7	196	232	9.5	50.0	2.2	----	----	.049
7/1/1968														
(1)	1010	21.0	20.0	6.9	7.2	---	173	210	9.5	56.0	13.8	.333	----	.474
(2)	1045	21.0	20.5	7.2	7.3	---	180	224	8.5	56.0	12.1	.252	----	.383
(3)	1110	21.5	20.5	7.1	7.4	---	185	228	7.5	60.0	14.9	.134	----	.394
(4)	1130	22.0	20.5	8.4	7.5	---	186	226	8.0	60.0	14.6	.144	----	.381
(5)	1200	21.5	20.5	8.0	7.6	---	190	234	8.5	64.0	12.6	.149	----	.505
7/9/1968														
(1)	1000	24.5	19.0	7.0	7.9	---	195	228	6.0	26.0	----	.292	----	.574
(2)	1030	24.5	20.5	8.0	8.0	4.0	215	240	7.4	26.0	----	.200	----	.545
(3)	1130	25.0	20.5	7.6	8.1	5.0	215	238	7.0	26.0	----	.152	----	.461
(4)	1300	26.5	20.5	7.8	8.4	9.0	225	234	7.4	16.0	----	.116	----	.280
(5)	1400	26.5	21.0	10.0	8.4	9.0	237	237	10.8	20.0	----	.116	----	.559

Appendix A.--(continued)

Station[a]	Time	Temp. C		D.O.	pH	Alkalinity		Hard.	Cl-	Carbon		Phosphate		Nitrate
		Air	HOH			phth	M.O.			Total	Org.	Total	Ortho	NO_3-N
7/15/1968														
(1)	1030	29.5	22.0	7.0	7.4	---	183	219	5.0	56.0	11.4	.152	----	.520
(2)	1145	30.5	24.5	9.1	---	---	179	221	6.5	54.0	10.3	.158	----	.430
(3)	1345	39.0	23.5	9.6	---	---	184	228	6.4	56.0	11.1	.128	----	.405
(4)	1400	32.0	25.5	10.1	---	5.5	179	231	6.2	54.0	8.9	.122	----	.447
(5)	1630	33.0	27.0	11.2	---	9.5	180	228	9.4	56.0	9.6	.096	----	.371
7/24/1968														
(1)	1045	28.0	17.8	7.9	8.8	---	177	226	4.6	49.0	5.8	.203	----	.241
(1a)[b]	1115	29.0	21.3	5.4	8.2	---	183	226	10.0	24.0	----	.104	----	.299
(2)	1145	30.0	20.1	10.0	8.5	1.1	179	228	6.7	46.0	2.1	.106	----	.523
(3)	1230	33.8	19.1	8.6	8.5	---	191	236	6.2	48.0	1.4	.106	----	.530
(4)	1400	----	----	10.8	9.1	5.0	184	235	6.0	47.0	0.9	----	----	.585
(5)	1330	----	----	11.4	8.8	5.0	172	233	7.3	47.0	3.8	.104	----	.635
7/29/1968														
(1)	1030	18.5	16.0	8.1	8.3	---	182	224	4.2	56.0	11.6	.152	----	.496
(1a)	----	24.0	18.0	5.8	8.1	---	182	220	9.4	45.0	----	.076	----	.278
(2)	----	29.0	18.0	8.2	8.4	---	178	247	6.2	54.0	10.6	.129	----	.345
(3)	1240	26.4	17.8	8.8	8.8	---	186	234	6.2	64.0	18.6	.070	----	.443
(4)	----	23.0	18.0	12.4	---	---	189	233	5.8	56.0	9.9	.084	----	.437
(5)	----	22.0	21.0	11.4	8.9	6.5	176	252	8.2	46.0	1.8	.084	----	.464
8/6/1968														
(1)	1015	25.8	18.9	6.8	8.1	---	187	231	4.5	53.0	7.4	.113	.117	.620
(2)	----	26.8	18.5	7.4	8.2	---	182	211	6.0	52.0	7.6	----	.081	.499

Appendix A.--(continued)

Station[a]	Time	Temp. C		D.O.	pH	Alkalinity		Hard.	Cl-	Carbon		Phosphate		Nitrate
		Air	HOH			phth	M.O.			Total	Org.	Total	Ortho	NO_3-N
8/6/1968														
(3)	----	27.2	19.6	7.4	8.0	---	188	229	6.0	56.0	10.1	.145	.078	.473
(4)	1225	28.9	20.8	9.4	8.4	---	185	228	6.0	46.0	----	----	.066	.536
(5)	----	30.0	22.5	10.8	8.4	5.5	180	191	12.8	52.0	8.1	----	.060	.535
8/12/1968														
(1)	1030	20.0	14.5	8.3	8.0	---	189	228	4.5	55.0	8.9	.184	.129	.668
(1a)	1000	20.0	16.5	5.9	8.1	---	192	234	9.2	56.0	9.2	----	.030	.406
(2)	1130	22.2	16.1	9.8	8.2	---	190	231	7.0	52.0	5.6	----	.069	.586
(3)	1330	22.9	16.1	9.8	8.2	---	198	241	6.5	----	----	.096	.051	.528
(4)	1530	21.5	18.9	11.0	8.5	---	189	245	6.5	53.0	6.9	.096	.057	.608
(5)	1630	23.0	19.4	12.5	8.7	---	186	235	9.8	53.0	7.6	----	.042	.593
8/19/1968														
(1)	1030	26.0	18.5	7.3	7.8	---	191	222	4.2	58.0	11.4	.151	.121	.498
(2)	1130	28.5	20.7	8.7	8.5	---	192	221	6.2	57.0	10.2	.119	.085	.408
(3)	1300	28.5	20.0	7.2	8.2	---	193	234	6.2	63.0	15.9	----	.064	.451
(4)	1400	29.0	22.2	10.5	8.2	---	194	233	6.0	63.0	15.7	.172	.058	.516
(5)	1800	29.5	24.0	9.9	8.4	6.0	193	231	9.0	60.5	11.9	----	.058	.470
8/26/1968														
(1)	1630	15.0	16.9	10.6	8.0	---	196	228	4.7	51.0	3.2	.180	.110	.656
(2)	1400	15.7	16.9	11.0	8.1	---	196	223	6.2	50.0	2.2	.114	.106	.514
(3)	1300	14.9	15.8	8.9	8.1	---	208	236	6.5	51.0	0.2	.091	.080	.446
(4)	1130	14.9	16.0	9.4	8.1	---	207	234	6.5	51.0	0.5	.069	.070	.510
(5)	0940	13.4	15.8	8.8	8.0	---	202	233	10.8	53.0	3.7	.067	.072	.572

Appendix A.--(continued)

Station[a]	Time	Temp. C		D.O.	pH	Alkalinity		Hard.	Cl-	Carbon		Phosphate		Nitrate
		Air	HOH			phth	M.O.			Total	Org.	Total	Ortho	NO_3-N
9/4/1968														
(1)	1100	25.0	10.0	8.8	7.8	---	228	224	7.0	51.0	----	.092	----	.705
(1a)	----	23.0	14.0	6.8	7.8	---	235	230	13.0	57.0	----	.053	.019	.367
(2)	----	25.5	14.0	7.8	7.9	---	227	220	9.0	50.0	----	.096	.042	.533
(3)	----	26.5	13.0	7.6	7.8	---	238	234	10.0	55.0	----	.062	----	.436
(4)	----	28.0	15.0	10.6	8.2	---	244	232	9.5	54.0	----	.067	.026	.605
(5)	1500	28.0	15.5	12.0	8.4	6.0	247	230	13.8	56.0	----	.042	.012	.517
9/9/1968														
(1)	1000	16.2	15.0	7.8	7.8	---	178	222	4.8	54.0	10.6	.090	----	.592
(2)	1200	16.2	15.9	7.8	7.8	---	178	225	6.8	54.0	10.6	.102	----	.496
(3)	1240	16.3	15.2	7.5	8.0	---	185	233	9.5	55.0	9.9	.053	----	.340
(4)	1400	19.0	16.0	9.9	7.8	---	179	230	6.5	51.0	7.3	.048	----	.444
(5)	1515	19.0	17.0	10.2	8.2	---	181	226	9.2	50.0	5.8	.044	----	.548
9/17/1968														
(1)	1100	19.0	10.5	7.4	7.8	---	200	198	7.5	63.0	14.2	.095	.094	.388
(1a)	----	23.0	14.5	9.8	7.8	---	200	218	11.0	63.0	14.2	.037	.017	.300
(2)	----	25.5	14.5	12.2	8.0	---	201	216	9.0	57.0	8.0	.082	.048	.458
(3)	----	21.0	13.5	10.8	8.1	---	204	208	9.0	63.0	13.2	.060	.033	.414
(4)	----	21.0	14.0	11.0	8.3	---	205	206	8.8	57.0	7.0	.057	.025	.488
(5)	1530	21.0	15.5	12.7	8.6	8.0	215	188	13.5	58.5	6.0	.044	.031	.445
9/22/1968														
(1)	1600	20.8	17.2	8.9	7.9	---	190	220	5.5	60.5	14.1	.142	----	.578
(2)	1530	23.4	18.3	11.9	8.3	---	187	240	7.5	63.0	17.4	----	----	.403

Appendix A.--(continued)

Station[a]	Time	Temp. C		D.O.	pH	Alkalinity		Hard.	Cl-	Carbon		Phosphate		Nitrate
		Air	HOH			phth	M.O.			Total	Org.	Total	Ortho	NO_3-N
9/22/1968														
(3)	1330	24.0	17.4	9.0	8.1	---	194	255	7.8	63.0	13.4	----	----	.417
(4)	1300	20.7	17.3	10.1	8.3	---	194	242	8.0	60.5	11.9	----	----	.482
(5)	1000	20.0	16.2	8.3	8.3	---	194	246	11.8	64.0	15.4	----	----	.505
9/28/1968														
(1)	1122	----	10.3	---	---	---	---	245	3.6	----	----	.152	.140	.647
(1b)[c]	1120	----	10.5	---	---	---	---	205	2.3	----	----	.038	.050	.653
10/1/1968														
(1)	1330	20.5	12.0	10.2	8.0	---	---	234	5.0	59.5	----	----	.150	.610
(2)	----	20.0	11.5	14.4	8.4	---	---	242	5.0	58.5	----	.070	.060	.460
(3)	----	24.0	10.5	10.4	8.0	---	---	250	6.5	66.0	----	.055	.034	.496
(4)	----	20.0	11.0	11.4	8.0	---	---	244	5.5	61.0	----	.055	.040	.584
(4b)[c]	----	18.0	13.5	9.6	7.8	---	---	214	17.0	68.0	----	.032	.034	.372
(5)	1530	21.0	12.0	12.0	8.2	---	---	246	7.3	63.0	----	.037	.032	.536
10/6/1968														
(1)	1430	8.9	8.5	10.5	7.6	---	191	236	6.0	59.5	12.9	.050	.112	.686
(2)	1400	8.3	8.4	10.3	7.5	---	188	242	8.0	61.0	15.1	.038	.044	.535
(3)	1300	7.8	8.3	10.8	8.1	---	194	250	8.0	64.0	16.7	.047	.038	.488
(4)	1045	7.8	8.3	11.0	8.0	---	186	248	7.3	63.0	17.6	.088	.038	.554
(5)	1000	8.2	8.3	10.8	7.9	---	196	250	13.0	64.0	16.2	.041	.015	.535

Appendix A.--(continued)

Station[a]	Time	Temp. C		D.O.	pH	Alkalinity		Hard.	Cl-	Carbon		Phosphate		Nitrate
		Air	HOH			phth	M.O.			Total	Org.	Total	Ortho	NO_3-N
10/24/1968														
(1)	1530	6.1	7.8	10.5	---	---	180	232	7.4	55.0	11.1	.175	.103	.437
(2)	1600	6.1	7.8	11.1	---	---	192	272	13.5	58.0	11.2	.070	.073	.386
(3)	1700	6.2	7.8	10.8	---	---	193	248	7.9	60.0	12.9	.044	.050	.350
(4)	1730	6.2	7.7	11.3	---	---	195	246	7.6	72.0	24.4	.044	.044	.439
(5)	1800	7.0	7.7	10.7	---	---	197	258	12.5	62.0	13.9	.038	----	.446
11/15/1968														
(1)	1100	-2.0	-0.5	11.0	7.7	---	---	206	4.0	54.5	----	.109	.072	.401
(2)	----	-2.0	-0.5	12.0	7.8	---	---	230	6.5	56.0	----	.058	.053	.554
(3)	----	-1.5	0.0	12.0	7.8	---	---	230	7.5	56.0	----	.079	.013	.598
(4)	----	0.0	0.0	12.8	8.0	---	---	236	8.0	56.0	----	.069	.009	.538
(4b)	----	1.5	0.0	10.4	7.9	---	---	253	18.5	63.0	----	.065	.032	.450
(5)	1635	2.0	0.5	12.2	7.8	---	---	244	11.0	59.0	----	.052	.018	.581
11/29/1968														
(1)	1330	0.6	2.3	11.8	8.4	---	170	219	8.8	52.0	10.5	.081	.128	.558
(1a)	1310	0.7	1.5	10.5	8.1	---	186	229	11.0	51.0	5.6	.037	.018	.485
(2)	1245	0.7	2.0	11.7	8.5	---	175	223	8.3	54.5	11.8	.021	.054	.531
(3)	1200	0.2	2.3	12.6	8.4	---	183	230	7.5	47.0	2.3	.015	.037	.591
(4)	1030	0.5	2.3	12.8	8.7	---	180	229	6.5	56.0	12.1	.042	.037	.652
(5)	1000	2.0	2.3	12.8	8.6	---	172	230	10.8	60.0	18.0	.042	.047	.573
12/17/1968														
(1)	1115	---	---	12.4	---	---	198	253	6.0	70.0	21.7	.052	.046	.750
(2)	1100	---	---	12.9	---	---	208	261	6.5	70.0	19.2	.125	.109	.762

Appendix A.--(continued)

Station[a]	Time	Temp. C		D.O.	pH	Alkalinity		Hard.	Cl-	Carbon		Phosphate		Nitrate
		Air	HOH			phth	M.O.			Total	Org.	Total	Ortho	NO_3-N
12/17/1968														
(3)	1045	---	---	13.3	---	---	211	269	7.5	70.0	18.5	.031	.011	.742
(4)	1015	---	---	13.6	---	---	205	275	6.5	71.0	21.0	.017	.009	.814
(4b)	1030	---	---	13.6	---	---	211	275	21.0	70.0	18.5	.068	.061	.700
(5)	1000	---	---	13.7	---	---	225	277	8.5	71.0	16.1	.088	.008	.824
1/25/1969														
(1)	1130	-12.0	0.0	----	7.5	---	167	220	8.2	68.0	27.3	.033	----	.710
(1a)	1215	-14.5	-0.5	----	8.4	---	166	220	9.9	60.0	19.5	.040	----	.495
(2)	1230	-14.0	-0.5	----	8.1	---	175	221	8.3	64.0	21.3	.107	.061	.733
(3)	1300	-14.0	0.0	----	8.1	---	179	246	8.4	67.0	23.3	.048	----	.835
(4)	1330	-13.0	0.0	----	7.6	---	180	234	8.8	65.0	21.1	.019	----	.858
(5)	1400	-13.0	0.0	----	8.1	---	168	243	12.2	68.0	27.0	.067	.036	.878
2/27/1969														
(1)	1100	0.0	1.5	14.1	8.6	---	194	253	7.3	67.0	19.7	.145	----	.663
(1a)	----	1.5	1.0	9.6	8.0	---	203	255	7.5	67.0	17.5	----	.019	.558
(2)	----	1.5	1.0	12.5	8.4	---	195	250	6.3	66.0	18.4	.036	.044	.645
(3)	----	0.5	0.5	13.1	8.8	---	208	255	6.5	68.0	17.2	.016	.098	.625
(4)	----	2.0	1.0	14.5	8.7	---	205	248	6.0	67.0	17.0	.010	.098	.743
(5)	1240	6.5	1.0	13.8	8.6	---	204	253	9.0	68.0	18.2	.023	.145	.755
3/15/1969														
(1)	1130	0.2	1.8	13.2	8.7	---	182	235	8.3	60.5	16.1	.118	----	.655
(1a)	1205	0.6	0.6	11.6	8.7	---	201	256	9.5	63.5	14.5	.036	.052	.608
(2)	1230	0.9	2.2	14.1	8.2	---	179	249	9.3	55.5	11.8	.041	.132	.660

Appendix A.--(continued)

Station[a]	Time	Temp. C		D.O.	pH	Alkalinity		Hard.	Cl-	Carbon		Phosphate		Nitrate
		Air	HOH			phth	M.O.			Total	Org.	Total	Ortho	NO_3-N
(3)	1250	2.2	1.7	15.4	8.3	---	183	249	8.5	56.5	11.8	.036	.100	.668
(4)	1330	1.3	3.3	16.6	8.5	---	190	247	8.5	64.5	17.1	.008	.079	.701
(5)	1630	1.7	4.4	15.8	8.5	9.8	191	247	12.8	63.5	16.9	.046	----	.685

[a](1) Blanchard Road crossing; (2) Fremont Road crossing; (3) Schmeid Road crossing; (4) Tamarak Road crossing; (5) Crystal Road crossing (see Figure 2 for locations).

[b](1a) South Branch at Brinton Road.

[c](1b) Pony Creek at confluence with Pine River (4b) Wolf Creek at confluence with Pine River.

Methods:

Temperature--pocket thermometer.
pH--Sargent portable pH meter (12/15/1967 to 7/1/1968), Beckman pH meter Model N (7/9/1968 to 3/15/1969).
Dissolved oxygen--Winkler (Azide modification). APHA, AWWA, and WPCA. 1965. Standard methods for the examination of water and wastewater. 12th edit. Amer. Pub. Health Ass., Inc. New York. 769 p.
Alkalinity--APHA (1965).
Hardness--EDTA titrimetric. APHA (1965).
Chloride--Mercuric nitrate. APHA (1965).
Carbon--Beckman Carbonaceous Analyzer.
Phosphate--Stannous chloride. APHA (1965).
Nitrate--modified brucine. Jenkins, D. and L. L. Medsker. 1964. Brucine method for determination of nitrate in ocean, estuarine, and fresh waters. Anal. Chem. 36:610-612.

APPENDIX B

AQUATIC PLANTS AND ALGAE IN THE PINE RIVER STUDY AREA, PLUS THE MORE COMMON TERRESTRIAL PLANTS BORDERING THE STREAM

Appendix B. Aquatic plants and algae in the Pine River study area, plus the more common terrestrial plants bordering the stream

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Algae

- Chlorophyta (green algae)
  - Cladophoraceae
    - Cladophora glomerata (L.) Kuetzing. Found throughout the study area, predominantly around station 1 and upstream. Very luxuriant growths appeared at the end of August, 1968, at station 1. Thinned-out at the beginning of October.
  - Zygnemataceae
    - Spirogyra sp. Few small masses appeared in late September upstream from station 2 to the South Branch confluence.
- Chrysophyta
  - (Diatoms)
    - Dominant genera in the periphyton during the summer months.
      Navicula spp. Cocconeis spp. Diatoma sp.
      Melosira sp. Gomphonema spp. Rhoicosphenia spp.
    - Genera of rare occurrence.
      Amphora spp. Achnanthes sp. Nitzschia spp.
      Synedra sp. Stephanodiscus sp. Cymbella sp.

Higher plants

- Bryophyta (mosses)
  - Fissidentaceae
    - Fissidens sp. (flat-fork moss) One large bed above station 1 in a shaded area of the stream.
- Pteridophyta (ferns)
  - Equisetaceae
    - Equisetum fluviatile L. (swamp horsetail) Along banks at station 4.
  - Polypodiaceae
    - Adiantum pedatum L. (maidenhair fern) In swampy woods
    - Onoclea sensibilis L. (sensitive fern) Along wooded banks.
- Spermatophyta (seed-bearing plants)
  - Pinaceae
    - Picea spp. (spruce) In forested areas.
    - Tsuga canadensis (L.) Carr. (hemlock) In forested areas.

Appendix B.--(continued)

Pinus spp. (pine) In forested areas.
Cupressaceae
Thuja occidentalis L. (arbor vitae) In forested areas.
(Angiosperms, stream-bank forms)
Gramineae (grasses) Many species.
Cyperaceae (sedges) Few species.
Araceae
Symplocarpus foetidus (L.) Nutt. (skunk cabbage) Wet areas.
Salicaceae
Populus spp. (aspens and populars) Sparse stream cover.
Salix spp. (willows) Stream cover, from station 3 upstream.
Betulaceae
Betula spp. (birches) In forested areas.
Alnus spp. (alders) Predominant stream cover, whole area.
Fagaceae
Quercus spp. (oaks) In forested areas.
Ulmaceae
Ulmus spp. (elms) In forested areas.
Ranunculaceae
Caltha palustris L. var. palustris (marsh marigold) Wet areas around station 1.
Anacardiaceae
Rhus spp. (sumacs) Margins of wooded areas.
Aceraceae
Acer spp. (maples) In forested areas.
Cornaceae
Cornus Amomum Mill. (silky dogwood) Stream cover, station 3 and upstream.
C. stolonifera Michx. (red osier) Stream cover, but sparse.
Ericaceae
Vaccinium spp. (blueberry) In wet areas.
(Aquatic forms, emergent)
Typhaceae
Typha latifolia L. (common cat-tail) Common in wet areas, but few plants growing in the stream.
T. angustifolia L. (narrow-leaved cat-tail) Roadside ditches, but sparse.
Alismataceae
Sagittaria latifolia Willd. (arrow-head) Sparse.

Appendix B.--(continued)

Cyperaceae

Scirpus sp. (bulrush) Sparse.

S. acutus Muhl. (hardstem bulrush) Common near gently sloping stream-banks.

(Submergent)

Sparganiaceae

Sparganium sp. (bur-reed) Submersed, ribbon-leaf form common, but sparse.

Najadaceae

Potamogeton natans L. (floating brown-leaf) Few beds in still water above station 2.

P. alpinus Balbis. (red pondweed) May be a hybrid of P. alpinus and P. gramineus. Common throughout the study area. As abundant as P. pectinatus. Appears to be crowded-out in some areas by the narrow-leaved pondweeds.

P. foliosus Raf. (leafy pondweed) Bright-green plant with short leaves; emerges after and flowers later than P. pectinatus. Third most abundant pondweed; found in beds with P. pectinatus.

P. pectinatus L. (sago pondweed) Predominantly from station 2 downstream. First of the narrow-leaved pondweeds to emerge in the spring. Very thick growths where the stream was wide and the substrate gravel.

P. interruptus Kit. ? May be a variety of P. pectinatus. A European species, previously reported only from northern Michigan. Longer and wider stems and leaves than P. pectinatus. Found in beds of P. pectinatus at station 2.

Alismataceae

Sagittaria latifolia Willd. (arrow-head) Submersed narrow-leaved form common, but sparse.

Cruciferae

Nasturtium officinale R. Br. (water-cress) Very common throughout the area.

Onagraceae

Ludwigia palustris (L.) Ell. var. americana (DC.) Fern. and Griscom. (false loose-strife) Few plants above station 2.

Appendix B.--(continued)

Scrophulariaceae

Veronica catenata Pennell. (water speedwell) Sterile light-green patches throughout the area. It and *Nasturtium officinale* are the only abundant angiosperms present in the water during winter months.

(Floating)

Lemnaceae

Spirodela polyrhiza (L.) Schleiden (big duckweed) Few plants found at station 2.

Lemna minor L. (lessor duckweed) Very thick in the South Branch.

Keys used in identification:

Fassett, N. C. 1966. A manual of aquatic plants. Univ. Wis. Press. Madison, Wis. 405 p.

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Smith, G. M. 1950. The fresh-water algae of the United States. 2nd edit. McGraw-Hill Book Co., Inc. New York. 719 p.