DEPRESSION OF PRIMARY PRODUCTIVITY BY SUSPENDED SEDIMENT AND DISSOLVED HUMIC MATERIAL IN LIMNOCORRAL EXPERIMENTS AT SOUTHERN INDIAN LAKE, NORTHERN MANITOBA

by

Stephanie Jane Guildford

Submitted to the faculty of the Graduate School in partial fulfillment
of the requirements for the degree of Master of Science
in the Department of Botany, University of Manitoba.

December 1984

DEPRESSION OF PRIMARY PRODUCTIVITY BY SUSPENDED SEDIMENT AND DISSOLVED HUMIC MATERIAL IN LIMNOCORRAL EXPERIMENTS AT SOUTHERN INDIAN LAKE, NORTHERN MANITOBA

BY

STEPHANIE JANE GUILDFORD

A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

ABSTRACT

Large *in situ* enclosures (10 m diameter, nominal volume 2.3×10^5 L) were used in controlled experiments to test hypotheses concerning the responses to impoundment of a large reservoir (Southern Indian Lake) in northern Manitoba. The hypotheses investigated in this thesis involve the influence of the two types of flooded shoreline material, inorganic glacio-lacustrine clay sediment and organic moss-peat material from the boreal forest floor, on phytoplankton primary production, biomass, and nutrient status.

The fine-grained inorganic sediments were not a significant source of P to algae as indicated by the physiological indicators of nutrient status: alkaline phosphatase activity, P debt, and N/P and, P/C composition ratios. The major effects of these sediments were reduced light penetration, primary production and zooplankton standing crops.

Moss-peat material was a significant source of dissolved humic material, phosphorus and nitrogen. Increased concentrations of dissolved N and P were observed after the moss-peat addition and physiological indicators of algal nutrient status showed no N or P deficiency. After an initial increase, primary production and algal biomass declined relative to the controls. Enrichment experiments supported the hypothesis that a micronutrient, possibly Fe, was chelated by dissolved humic material and was limiting algal growth. After one year of inundation the inhibitory influence of the moss-peat material was no longer observed.

The results of the limnocorral experiments showed that flooding of glacio-lacustrine clay and moss-peat material could explain many of the primary productivity and nutrient status responses observed after the flooding of Southern Indian Lake. In the lake, primary productivity and phytoplankton biomass, on average, were approximately unchanged by impoundment, presumably due to the combined effects of decreased light by suspended sediments (and increased water column depth) and increased P loading from flooded moss-peat material.

ACKNOWLEDGMENTS

I am deeply grateful to my supervisor Pat Healey. His patience and guidance in all aspects of this project have been invaluable.

Several people working on the Southern Indian Lake limnocorral project allowed me to use portions of their data. In particular I would Like to thank Cory Anema for chemical analyses, Hedy Kling for phytoplankton counts, Greg McCullough for hydrogeological data and Doug Ramsey for zooplankton counts.

Karen Cooper, Sandra-Lee Konrad and Margaret Treble provided expert laboratory and field assistance. Construction, maintenance and sampling of the limnocorrals was an arduous, cooperative task involving most of the above mentioned people as well as the following: Drew Bodaly, Bob Fudge, Donna Rystephanuk, Renee Sauve and Neil Strange.

I would like to acknowledge Togwell Jackson for providing me with key references in the humic literature and Len Hendzel for helpful discussions. Sharon Ryland typed the first draft.

Lastly I would like to thank my husband Bob Hecky for his continuous encouragement and support.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

This thesis examines the separate effects of two different types of flooded material, inorganic clay soil and organic moss-peat soil, on phytoplankton nutrient status and primary productivity using large enclosures as experimental systems in a reservoir in northern Manitoba.

The most commonly reported sequence of events during and after reservoir formation is: flooding of soils, release of nutrients, increases in phytoplankton biomass and primary productivity, increases in secondary production, exhaustion of nutrients and decline of productivity to normal or below normal levels (Ellis 1936, Rodhe 1964, Rzoska 1966, Chamberlain 1972, Campbell et al. 1975, Duthie and Ostrofsky 1975, Baxter and Glaude 1980, Ostrofsky and Duthie 1980). As more studies of a variety of reservoirs are undertaken, a more complex picture is emerging. Kelly et al. (1978) observed increased N and P concentrations in five lakes involved in a hydroelectric development in Nova Scotia together with a decrease in chlorophyll. He suggested algae were light limited due to increased suspended sediments. Jackson and Hecky (1980) cited Fe as the probable limiting nutrient in two northern reservoirs containing relatively high concentrations of humic material and phosphate. They found a good correlation between humus-chelated Fe and low rates of primary productivity. In a series of reservoirs on the Volga River, levels of primary productivity were quite variable from one reservoir to another (Pyrina 1979) and in some of these reservoirs high levels of secondary production were due to bacterial respiration of organic detritus rather than primary productivity (Romanenko 1979).

An intensive, multidisciplinary study of a reservoir before, during and after impoundment was conducted at Southern Indian Lake, Manitoba from 1973 to 1978. A detailed description of the study has been published in the Canadian Journal of Fisheries and Aquatic Sciences volume 41(4), 1984. Since the work discussed in this thesis is a direct result of the Southern Indian Lake (SIL) study, a brief description of the lake and impoundment will be given.

Southern Indian Lake is a large (2,400 km^2 after flooding), shallow lake on the Churchill River in northern Manitoba. The geographic setting of SIL is on the Precambrain Shield over which glacial lacustrine sediments from glacial Lake Agassiz were deposited. The predominant vegetation surrounding the lake is that of the boreal forest. In 1976 the water level of SIL was raised 3 m in order to divert the Churchill River southward to hydroelectric generating stations on the Nelson River (Newbury et al. 1984).

The most important physical change to SIL during and after impoundment was large scale shoreline erosion. Flooding reduced the length of exposed bedrock controlled shoreline from 76 to 14% of the lake's total. In the year of impoundment and the following two years an annual average of 4×10^6 tonnes of mineral sediment was eroded into the lake. This is about 20 times the normal sedimentary input from the Churchill River. The minimum estimate for stabilization of 90% of SIL shorelines is 35 years (Newbury and McCullough 1984). Increased mean depths and increased light scattering caused by higher concentrations of suspended solids from shoreline erosion significantly reduced the mean water column light intensity of the mixed layer (Hecky 1984). The biological responses to impoundment were closely related to the reduction in light penetration (Hecky 1984).

The phytoplankton of SIL changed from being predominantly P limited to light limited. The response was not uniform around the lake. There was significant variation with respect to various chemical and biological parameters before flooding (Hecky and Guildford 1984). In some areas of the lake where reduction in mean water column light was most extreme, primary productivity became light limited and was lowered by impoundment (Hecky and Guildford 1984). In a few protected, shallow bays where erosion of clay shorelines was minimal and the highest proportion of flooded material was organic, the response to flooding was similar to the classic trophic upsurge where chlorophyll and primary productivity increase dramatically. However in much of the lake the explanation for changes in primary productivity and nutrient status was not so obvious.

One of the most disturbing changes in the lake after impoundment was an increase in the level of methyl mercury in the flesh of two economically important species of fish (Bodaly et al. 1984). Levels of Hg became so high that the local community on SIL was advised not to eat these species. To investigate this serious problem, experiments using large enclosures were conducted at SIL. Enclosures were chosen because they permitted the isolation of specific aspects of flooding in situ. Different types of shoreline material were added separately to enclosures along with radioactive Hg. Intensive study of water chemistry and all levels of the food chain followed in order to determine where and how Hg entered the food chain.

The purpose of this thesis is to study the separate effects of the two main types of flooded terrestrial material at SIL on the nutrient status and primary productivity of the phytoplankton community at SIL by using the large enclosure experiments. Specifically the questions asked are these:

1) Are SIL inorganic shoreline sediments a significant source of available P and if so did this contribute to the overall decrease in P deficiency observed in the lake after impoundment or did P deficiency decrease because light limitation due to increased suspended sediments replaced P deficiency?

2) Would moss-peat material added separately to an enclosure stimulate primary and secondary production as suggested by the classic trophic upsurge reservoir response or would the material depress primary productivity as observed by Jackson and Hecky (1980)?

Laboratory studies have shown that anywhere from 0 to 50% of total phosphorus associated with sediments can be used by algae (Helfrick and Kevern 1973, Smith et al. 1978, Dorrich et al. 1980, Williams et al. 1980, Grobbelaar 1983). Light limited primary productivity due to high concentrations of suspended sediments has been reported by Marzolf and Osborne (1972), Kelly (1978, in Baxter and Glaude 1980) and Hecky and Guildford (1984).

The organic moss-peat layer of soil is a source of humic matter as well as nutrients. Humic substances are amorphous, heterogeneous complexes of refractory organic matter ranging in molecular weight from hundreds to tens of thousands (Schnitzer and Khan 1972). Probably the most important feature of humic matter is the metal chelating ability which arises predominantly from two functional groups, -COOH and phenolic -OH. In natural waters, humic matter has been reported as both beneficial to algae (Prakash and Rashid 1968, Giesy 1976, Toledo et al. 1980, DeHaan et al. 1982) and deleterious (Sakamoto 1971, Jackson and Hecky 1980, Francko and Heath 1983, Devol et al. 1984).

This thesis contains two major sections: 1) sediment-algal interactions which are the results and discussion of the sediment enclosure experiments and 2) moss-peat algal interactions which are the results and discussion of the moss-peat enclosure experiments. There are two smaller sections: 1) a presentation of three enrichment experiments conducted using water from the moss-peat limnocorrals and 2) a comparison of the limnocorral experiments with the observations made in the lake after impoundment.

Experimental Design

Study area

Figure 1 gives the location of SIL. Figure 2 is a more detailed map of the lake showing the seven regions defined by the Freshwater Institute study (Newbury et al 1984). Figure 3 indicates the area in Wupaw Bay where the enclosures were situated.

Sediment enclosures

SIL shoreline sediment was added to three limnocorrals throughout two summer seasons. Sufficient sediment was added weekly or biweekly to maintain a Secchi disc value comparable to some moderately and extremely turbid areas in the lake. A fourth limnocorral had no sediment added

FIGURE 1. The geographical setting of Southern Indian Lake and the Churchill River Diversion (from Newbury et al 1984).

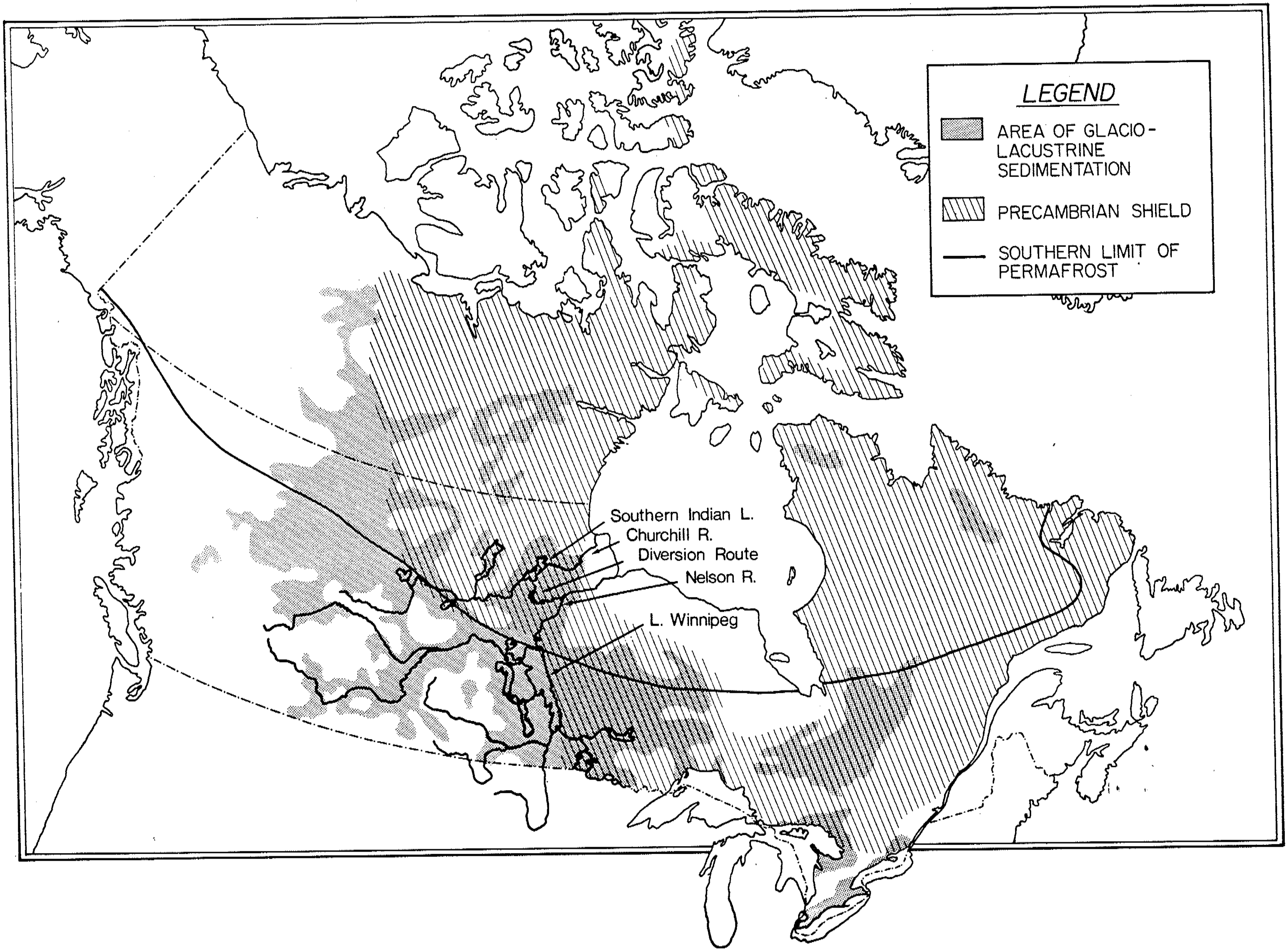
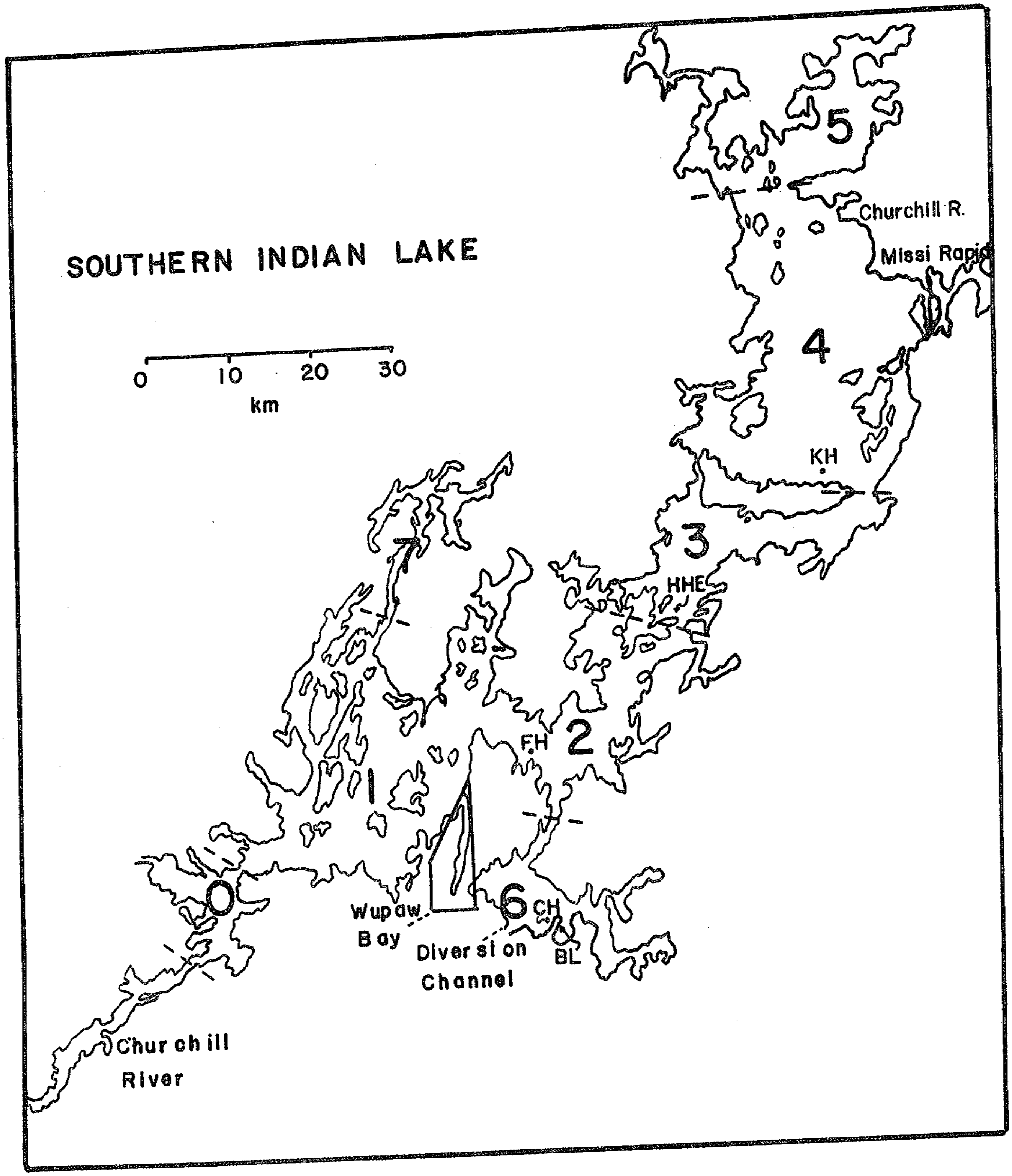
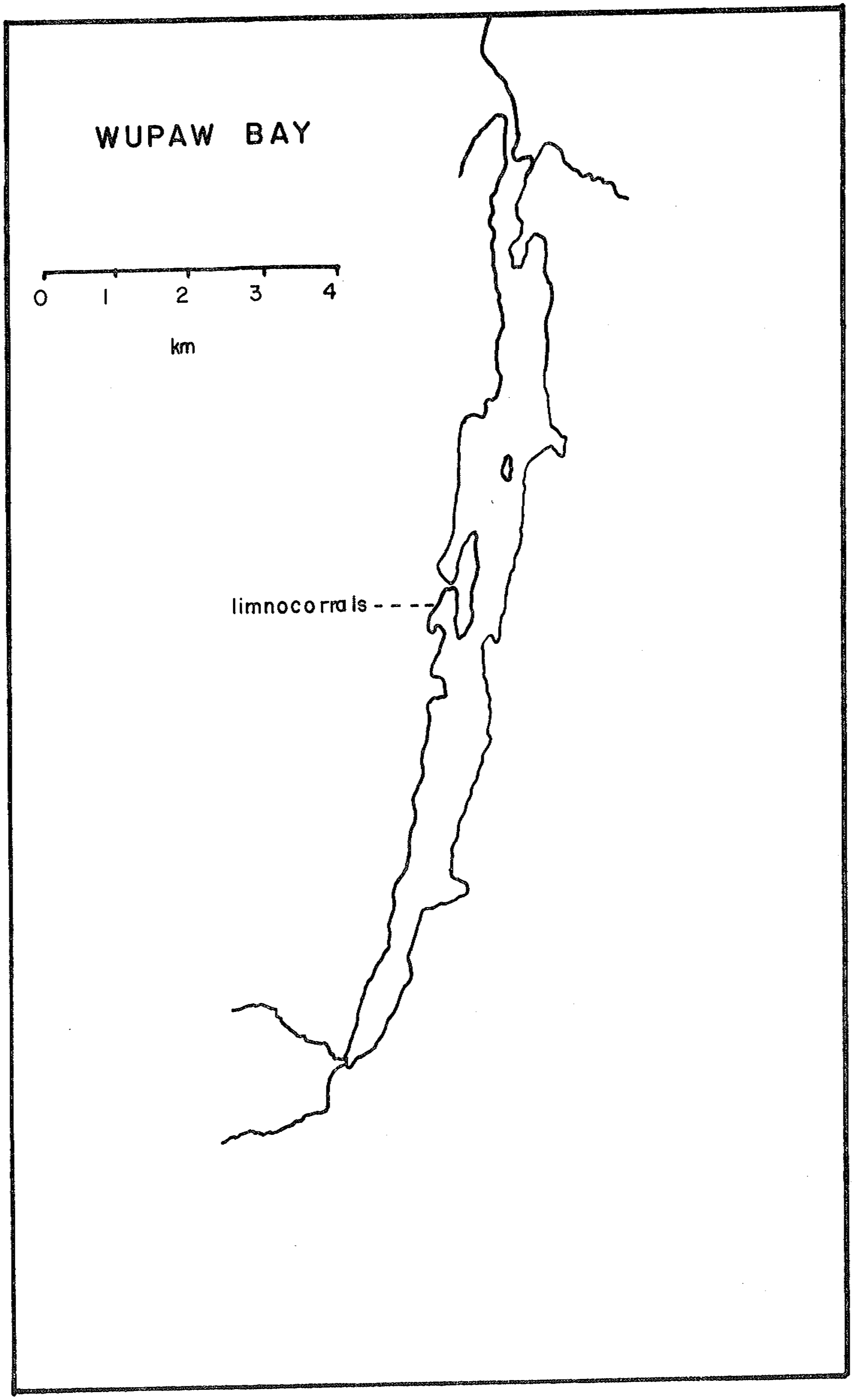

LEGEND
AREA OF GLACIO-LACUSTRINE SEDIMENTATION
PRECAMBRIAN SHIELD
SOUTHERN LIMIT OF PERMAFROST
Southern Indian L.
Churchill R.
Diversion Route
Nelson R.
L. Winnipeg

FIGURE 2. Map of Southern Indian Lake. Numbers denote regions defined by Newbury et al (1984). Letters denote shoreline sediment sampling sites.



SOUTHERN INDIAN LAKE
0
10
20
30
km
5
Churchill R.
Missi Rapid
4
KH
3
HHE
7
2
FH
1
0
6
CH
Wupaw Bay
Diversion Channel
BL
Churchill River

FIGURE 3. Map of Wupaw Bay showing the location of the limnocorrals.


WUPAW BAY
0 1 2 3 4
km
limnocorrals

but was covered with a screen to reduce light penetration to the same degree as the sediment. This was done to observe the effect of reduced light alone without the influence of the sediments. One limnocorral was artificially enriched with nitrogen and phosphorus over one summer to observe the effect of increased nutrients without the influence of sediment or reduced light.

<u>Moss-peat enclosures</u>

Moss and peat material taken from a SIL shoreline was added to three limnocorrals. The vegetation was added all at one time to simulate flooding. Two other limnocorrals were designed to observe the effect of moss-peat vegetation that had been flooded for some time. One limnocorral was installed over a mossy area that was flooded during the 1976 impoundment. The effect of moss-peat after one year under water was observed by monitoring a moss-peat limnocorral two years in row. At the beginning of the second summer the sides of the limnocorral were lowered for a few days to allow circulation of lake water.

Four untreated limnocorrals were studied as controls. One of these was studied two years in succession. Each year samples from the lake just outside the limnocorrals were studied as well.

The response of the algae to the various treatments was monitored by measuring primary productivity, algal biomass and nutrient status indicators on a regular basis each summer. Since the limnocorrals were part of a larger study involving several people other than myself I was able to obtain water chemistry and zooplankton data to help interpret the algal response.

In addition to the routine measurements on the moss-peat limnocorrals three enrichment experiments (two in the lab and one *in situ*) were conducted using water from one of the moss-peat limnocorrals.

METHODS

Description of the limnocorrals

The limnocorrals were made of fibre-reinforced translucent polyethylene supplied and sewn into cylinders 10 m in diameter and 4 m deep by Curry Industries (601-3 Bowman Ave. Winnipeg, Manitoba, R2K 1F7). Five of the limnocorrals had plastic floors sewn in while the remaining eleven were open to the sediment. The limnocorrals were supported by styrofoam and wood collars and secured with sandbags and anchors (Fig. 4). The treatments, type of bottom, depth and volume of each limnocorral are given in Table 1. The volume of each limnocorral was calculated by mixing tritium (^3H) into the limnocorrals and immediately measuring the ^3H concentration. Dilution of the tritium concentration over time gave an estimate of leakage. The limnocorrals are identified by letters to indicate the treatment and numbers to indicate the year and limnocorral number (Table 1). For example control limnocorral number one used in 1981 is C81-1.

Moss-peat Addition

The material added to the moss-peat limnocorrals was mainly sphagnum and feather moss and underlying peat from a nearshore area in Wupaw Bay. The material was collected by hand down to the permafrost (about 50 cm). In 1981 the moss-peat material was added over a period of 2 days by emptying uniform tub-fulls into the limnocorrals.

FIGURE 4. A cross-sectional view of a limnocorral to show the basic structure and the method used to suspend large containers *in situ* for the enrichment experiment.

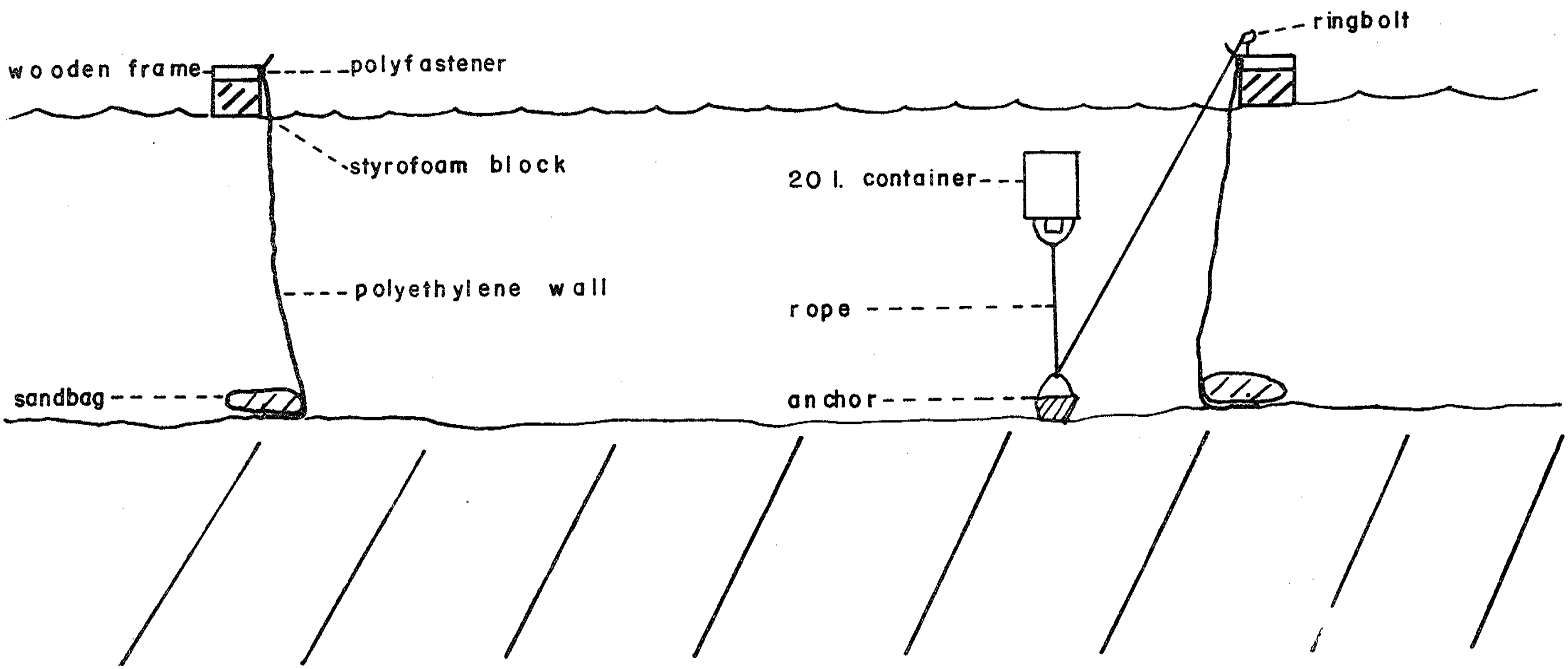

wooden frame
polyfastener
styrofoam block
polyethylene wall
sandbag
ringbolt
20 l. container
rope
anchor

TABLE 1. Limnocorral code names, treatments, bottom type, volume, and depth.

Name	Treatment	Bottom Type	Volume (m^3)	Depth (m)
C81-1	Control	natural	221	2.81
LM81-2	Low moss; 63 Kg moss-peat added June 21,1981 (day 173).	natural	275	3.50
PN81-3	Phosphorus and nitrogen added bi-weekly.	plastic	241	3.07
LS81-4	Low sediment; sediment added bi-weekly to maintain Secchi depth of 0.50 m.	plastic	316	4.02
C81-5	Control	plastic	273	3.48
HS81-6	High sediment; sediment added bi-weekly to maintain Secchi depth of 0.30 m.	plastic	318	4.01
C81-7	Control	plastic	273	3.48
L81-8	Lake			
FM82-1	Flooded moss; limnocorral installed over moss-peat vegetation flooded in 1976.	natural	161	2.05
SC82-2	Screen; surface completely covered with one thickness of black fibreglass screen.	natural	215	2.70
LM82-3	Low moss; 52 Kg moss-peat added June 28,1982 (day 180).	natural	279	3.60
HM82-4	High moss; 104 Kg moss-peat added June 28,1982.	natural	211	2.70
OC82-5	Control; used for 2 years (previously LC81-1)	natural	261	3.30
C82-6	Control	natural	231	2.90
HS82-7	High sediment; sediment added weekly to Secchi depth of 0.35 m.	natural	225	2.90
OM82-8	Old moss; moss-peat limnocorral studied for 2 years (previously LM81-2).	natural	254	3.20
L82-9	Lake			

Occasionally tubs were weighed to estimate the amount of material added, and sampled for chemical analysis. During the addition the water in the limnocorral was mixed using a small battery-operated outboard trolling motor mounted inside the limnocorral. The moss and peat floated at the surface for about a week before becoming water-logged and sinking. In 1982 the hand picked moss and peat material was formed into uniform bales using chicken wire and submerged in the limnocorral overnight. This was done to saturate the material more quickly so it would sink to the bottom when the chicken wire was removed from the limnocorral the following day and thus more closely simulate flooding of attached moss. After the moss and peat addition and initial mixing with the outboard motor, the moss-peat limnocorrals remained untreated throughout the summer.

Sediment Addition

Sediment was collected from SIL shoreline site FH (Fig. 2) in large plastic barrels. The weight of sediment in each barrel was measured and sub-samples were taken for dry weight, grain size and total carbon, nitrogen and phosphorus (C,N,P) analyses. Sediment additions were made by pumping water from the limnocorral into the sediment barrel which was stirred to create a suspension. The submersible pump was then placed inside the sediment barrel and the sediment-water mixture pumped into the limnocorral. The trolling motor was operated to mix the suspended sediment into the limnocorral. The pumping was repeated until the desired amount of sediment was added. Sufficient sediment was added to reduce the Secchi disk readings to values similar to those found in parts of the lake after flooding. In 1981 Secchi depths of 0.3 m in the high sediment limnocorral (HS81-6) and 0.5 m in the low sediment limnocorral (LS81-4) were maintained. In 1982 a Secchi depth of 0.35 m was maintained in HS82-7. Since the larger sediment particles did not remain in suspension it was necessary to add sediment every two weeks to maintain the desired Secchi readings. In 1982 sediment was added weekly to reduce fluctuations in light due to sedimentation between treatments.

Phosphorus and Nitrogen Enrichment

Limnocorral PN81-3 was artificially enriched with phosphorus and nitrogen. Nitrogen was added as $NaNO_3$ on two occasions only (25 g on June 21 and 20 g on July 15). Nitrogen additions were stopped to see if N deficiency could be induced when it became clear that P was the limiting nutrient under the initial treatment regime. Phosphorus in the form of $NaH_2PO_4 \cdot 2H_2O$ was added at approximately 2 week intervals from June 21 to August 21, 4 g each time. The nutrients were dissolved in 400 ml double distilled water and then mixed into the limnocorral with the trolling motor.

Screen Covered Limnocorral

Limnocorral SC82-2 was covered with a screen to reduce light penetration to the same degree that light was reduced by the sediment in HS82-7. The screen was made by sewing 1.5 m wide strips of black fibreglass window screen into a circle 10 m in diameter which was stapled onto the wooden collar supporting the limnocorral. Ten square blocks (20 cm on a side) of styrofoam floating on the water surface inside the limnocorral supported the screen.

Sample Collection

Samples were collected in 2 L dark brown Nalgene bottles using an integrating sampler similar to that described by Fee (1976). The sampler was operated by lowering the weighted bottle fitted with a small diameter inlet and outlet port up and down through the euphotic zone. The depth of 1% light penetration in the limnocorrals was usually 2.5 m or more. Since the depth of the limnocorrals was approximately 3.0 m the sampler was lowered no deeper than 2.5 m to avoid stirring up the bottom. In 1981 net samples were collected by dragging a 10 uM mesh plankton net through the water. All water samples were stored in light tight insulated coolers. Most of the analyses were begun within 8 hours of sampling.

Water samples were collected bi-weekly from June 20 to August 24, 1981 and weekly from June 30 to August 23, 1982. Samples were routinely taken from the PN81-3 and sediment limnocorrals on days that were about halfway between the nutrient and sediment additions to avoid any pulse response to the treatment.

Field Measurements

Temperature profiles were measured each time a water sample was collected. Readings were taken at 0.5 m intervals using either a Whitney-Montedoro model CTU-3A or a Yellow Springs Instruments temperature/ conductivity meter. Temperature calibrations were made against a thermometer and were accurate to 0.1^{o}C.

Secchi disc measurements were made using a 25cm disc with alternating black and white quadrants. Measurements were made in the shade. The values reported are the averages of the depth of disappearance and reappearance of the disc. Readings made by four observers at the same station differed by 15% at a mean depth of 1.8 m.

Irradiance was measured from 0 to 2.5 m at 0.5 m intervals using a Li-Cor (Li-Cor Ltd., Box 4425, 4421 Superior St., Lincoln, Nebraska 68504) quantum sensor and meter. This instrument measures the total quanta of photosynthetically active radiation. These data were used to calculate the vertical light extinction coefficient (k) (Hutchinson 1957) and the mean water column light intensity over 24 hours, I_{24} (Fee, 1979, Ramberg 1979, and Hecky and Guildford 1984).

The vertical extinction coefficient, k, is the slope of the line derived by linear regression of the natural logarithm of the irradiance measurements versus depth. The light extinction coefficient was partitioned using the method of Hutchinson (1957) to determine the per cent extinction due to upward scattering by suspended particles (P_s), absorption by chlorophyll (P_{chl}), and absorption by other material (P_a). The light extinction due to upward scattering was found by:

$$P_s = 100 \left(\frac{S_s}{z + \frac{S_s}{2} - 0.03} \right) \quad (1)$$

where $S_s = (5.9)(z)(R_p)$ (2)

and where z is the light extinction coefficient corrected for the assumption that all light is coming from the zenith position (at the latitude of SIL the correction factor is 1.2, Hecky et al. 1979), R_p is the ratio of upwelling light measured just below the water surface to incoming light at the surface, and 0.03 is the extinction coefficient of pure water. The light extinction attributable to chlorophyll is calculated as

$$P_{chl} = \frac{100\,(0.016)\,A}{z} \qquad (3)$$

where A is the concentration of chlorophyll a, 0.016 is the extinction coefficient for chlorophyll suggested by Bannister (1974) in units of m^2 mg^{-1} chl. The light extinction attributable to absorption by dissolved material is

$$P_a = 100 - (P_s + P_{chl}) \qquad (4)$$

The quantity I_{24} is found by the following integral formula:

$$I_{24} = \frac{1}{z}\int_0^{z_m} I_o e^{-kz}\,dz \qquad (5)$$

where I_{24} = mean light intensity of the mixed layer over 24 hours, z = mean depth of the mixed layer, z_m = maximum depth, k = extinction coefficient, I_o = daily integral surface irradiance. I_{24} was calculated using equation (6) which is the solution for the integral in equation

(5):

$$I_{24} = I_o\left(\frac{1 - \frac{1}{e^{kz}}}{kz}\right) \tag{6}$$

Laboratory measurements

Water samples were analyzed for chlorophyll a, particulate carbon, nitrogen and phosphorus (CNP), dissolved inorganic carbon (DIC), total dissolved nitrogen (TDN), total dissolved phosphorus (TDP), soluble reactive phosphate (SRP), pH, humic color, primary productivity, adenosine tri-phosphate (ATP), alkaline phosphatase activity, and phosphorus and nitrogen debt. The methods for chlorophyll a, CNP, DIC, TDN, TDP, and SRP are those of Stainton et al. (1977).

Humic color

The absorbance at 455 nanometers (A_{455}) of filtered and centrifuged water samples was read routinely as a relative estimate of humic content of the water. Various wavelengths in the vicinity of 455 nm have been used as indicators of humic content (Schnitzer and Khan 1972 (465 nm) , Gjessing 1976 (430 nm), Jackson and Hecky 1980 (465 nm)).

Primary Production

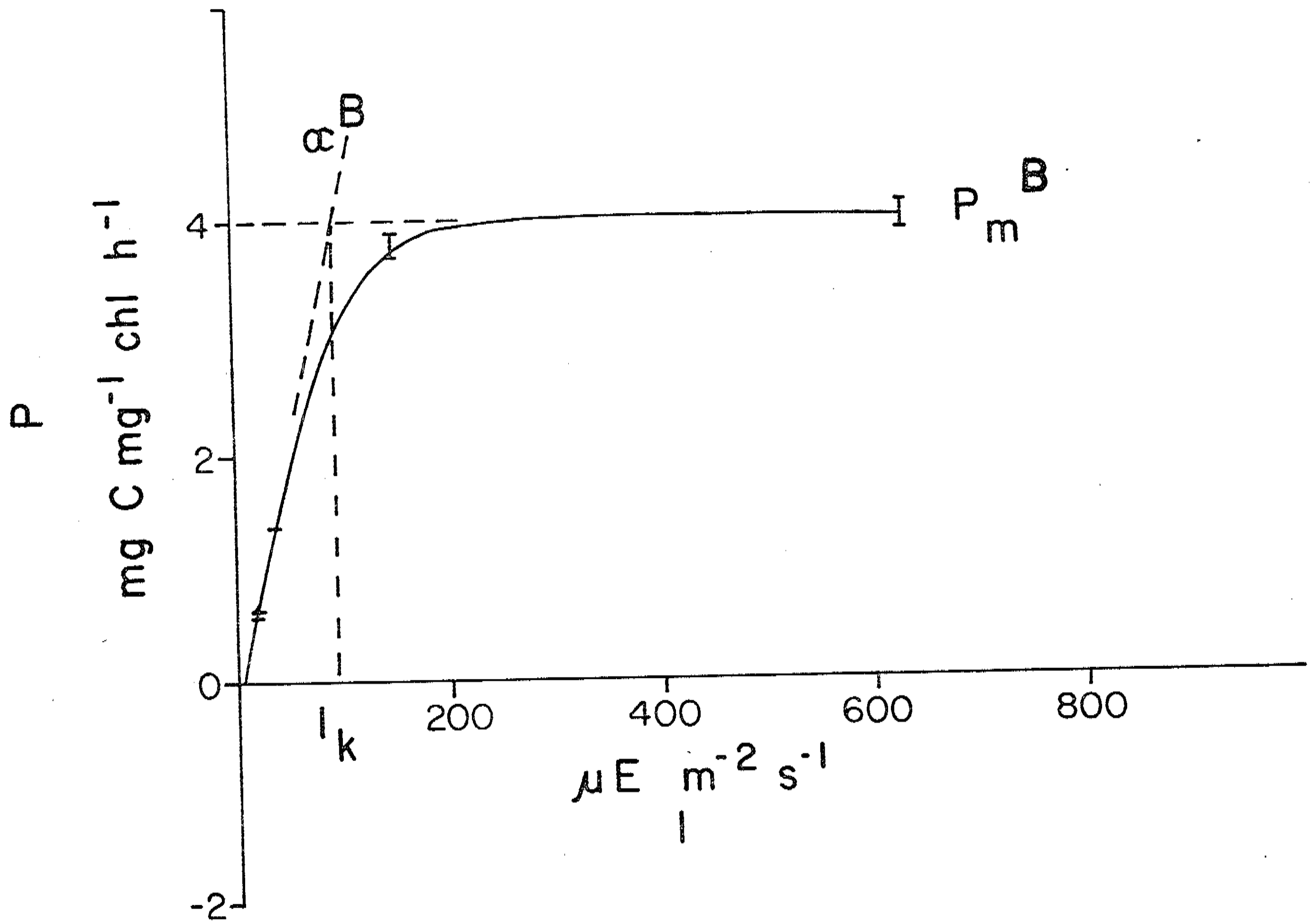
Rates of primary production were measured using a ^{14}C incubator technique similar to that described by Shearer and Fee (1974). The plan for the incubator used is given by Shearer (1976). Samples were subsampled for DIC, then inoculated with ^{14}C as sodium bicarbonate to a concentration of approximately 0.15 uCi/ml. Subsamples were immediately taken for standardization and counted in a Packard liquid scintillation counter containing an automatic external standard. The remainder of the labelled water sample was siphoned into ten 60 ml bottles. Two bottles were incubated in the dark and the remainder at four different light intensities for 3 hours. At the end of the incubation the samples were acidified and bubbled with air to remove any label that had not been converted to the organic form. Subsamples were counted on a Packard liquid scintillation counter.

The rate of ^{14}C uptake at each light intensity was calculated using the following equation:

$$C_o = \frac{(DIC)(^{14}C_a)\left(\frac{V_b}{V_a}\right)(f)}{(t)(^{14}C_b)} \qquad (7)$$

where C_o is photosynthesis (mg C L^{-1} h^{-1}), DIC is in mg L^{-1}, $^{14}C_a$ is activity of ^{14}C in the aliquot counted (dpm), $^{14}C_b$ is the activity of ^{14}C added to the incubation bottle (dpm), v_b is the volume of the incubation bottle (ml), v_a is the volume of the aliquot counted (ml), t is the incubation time (hours) and f is an isotopic correction to account for the preferential uptake of ^{12}C (Lind 1979). A typical light response curve is given in Fig. 5 where carbon uptake values have been normalized to chlorophyll and dark uptake values have been subtracted from the light values. The uptake curve has three parameters which are discussed in the results: P_m^B, I_k, and alpha^B. P_m^B is the maximum rate

FIGURE 5. Parameterization of the incubator-determined curve of photosynthesis per unit chlorophyll (P) against irradiance (I). P_m^B is the maximum rate of carbon fixation, α^B is the initial slope of the function considered linear through the lowest two irradiances in the incubator, and I_k is the interception of α^B with P_m^B. I_k is taken to be the nominal irradiance at the onset of light saturation. The solid curved line is the function $P = P_m^B \tanh(\alpha^B I/P_m^B)$ of Platt and Jassby (1976), which fits most of the data well. Vertical bars indicate the range of replicates (from Hecky and Guildford 1984).



α^B
P_m^B
P
mg C mg^{-1} chl h^{-1}
4
2
0
-2
I_k
200
400
600
800
μE m^{-2} s^{-1}
I

of primary productivity measured in the incubator. $Alpha^B$ is the slope of the line connecting the two lowest carbon uptake values. I_k is the intersection of $P_m{}^B$ and $alpha^B$, and it is the irradiance at which photosynthesis begins to be saturated. The coefficient of variation for $P_m{}^B$ was 5% at 13.4 mg C m^{-3} h^{-1}.

Daily integral primary productivity was calculated using the computer program designed by Fee (1973). The program combines the light response of the algae from the incubator with the light penetration measurements made at the time of sampling to give an estimate of primary productivity per square meter of lake surface. Then using actual or simulated (cloudless) solar irradiance (Fee 1977), daily integral production is calculated. At Southern Indian Lake solar irradiance was monitored using an Eppley pyranometer located on a high point of land, the South Indian Lake airport. To make comparisons between primary productivity on different days the cloudless irradiance data was used.

ATP

ATP was extracted from water samples and measured using the method described by Rudd and Hamilton (1973). The water sample was filtered onto a 0.22 uM nominal pore size membrane filter which was immediately extracted in a boiling solution of 0.5 M Tris buffer. The ATP in the extract was measured photometrically using the firefly lantern extracts, luciferin and luciferase. The coefficient of variation for a Wupaw Bay water sample containing 1.0 ug l^{-1} ATP was 16% (n = 18). Normally three replicates were done for each sample.

Water samples from the sediment limnocorrals contained high concentrations of suspended sediments. To test whether the sediments might interfere with the ATP extraction or photometric analysis, three sets of extractions were done using increasing amounts of sediment. These experiments are described in Appendix 1. All the data indicate that sediment interferes with ATP measurement; however, it was not possible to quantify the problem accurately. The experiments showed that ATP may be underestimated by 20 to 90% at high sediment concentrations. For this reason ATP measurements from the sediment limnocorrals were not used.

Alkaline phosphatase activity

Alkaline phosphatase activity was used as an indicator of phosphorus deficiency. The method is described in Healey and Hendzel (1979). Most phytoplankton produce enzymes capable of breaking down organic phosphorus compounds; usually the enzyme activity increases with phosphorus deficiency. Alkaline phosphatase activity was measured by incubating water samples with O-methyl-fluorescein phosphate and observing the rate of appearance of O-methyl-fluoroscein which becomes fluorescent when the phosphate bond is hydrolyzed. Activity was measured in the whole water sample and in the filtrate of the sample (<0.45 um), the difference being the activity associated with the phytoplankton and other seston. The rate of alkaline phosphatase activity was calculated from the linear portion of the slope of the line of fluorescence versus time. The line was usually linear over a one hour time period with a correlation coefficient of 0.99. The method is very reproducible. Perry (1972) using enriched natural samples found a coefficient of variation of 3% at a level of 1.6 umole P $L^{-1}h^{-1}$. The activities in the limnocorrals ranged from 0 to 2.8 umole P $L^{-1}h^{-1}$. The alkaline phosphatase activity was usually normalized to ATP, although in some instances chlorophyll a (chl) was also used. Levels of 0.02-0.10 umoles P ug ATP^{-1} h^{-1} and 0.003-0.005 umoles P ug chl^{-1} h^{-1} indicate moderate P deficiency. Levels greater than 0.1 umole P ug ATP^{-1} h^{-1} and 0.005 umole P ug chl^{-1} h^{-1} indicate severe deficiency. These values were suggested by Healey and Hendzel (1979) and are based on work using cultures and natural samples including Southern Indian Lake water.

P debt and N debt

P debt was used as another indicator of phosphorus deficiency. Enough P is added to the water sample to saturate P uptake. The total P taken up is an indication of the degree of phosphorus deficiency. The technique is described in Healey (1973). Immediately following the addition of a final concentration of 10 uM KH_2PO_4 to 100 ml water samples, triplicate subsamples were taken and filtered. After 24 hours in the dark at room temperature final triplicate subsamples were taken, filtered and analyzed for SRP. The difference between initial and final is the P debt. The assay for N debt was similar except a final concentration of 10 uM NH_4Cl was added. Levels greater than 0.5 umole P ug ATP^{-1} or 0.075 umole P ug chl^{-1} indicate P deficiency and greater than 1.0 umole N ug ATP^{-1} or 0.15 umole N ug chl^{-1} indicate N deficiency. The correlation coefficients for the standard curves for both N and P analyses were usually 0.99. If one of the 3 triplicate subsamples was quite different it was not used.

Composition Ratios

Five composition ratios, N/C, P/C, N/P, ATP/C and chlorophyll a/C, were examined for indications of nutrient status. Indicator values suggested by Healey and Hendzel (1980) are in Table 2. Composition ratios involving P were not reliable indicators of nutrient status in the sediment limnocorrals. This was due to the large proportion of detrital P associated with the inorganic sediments added to these limnocorrals (see Appendix 2).

Sediment analysis

Subsamples of shoreline sediment added to the sediment limnocorrals were air-dried or oven-dried at $60^{o}C$ then ground and total CNP determined using the same procedures described for seston samples.

Readily available P was estimated by extracting shoreline sediments with distilled water. This analysis was performed on four shoreline sediment samples collected from different areas of SIL (locations in Fig. 2). About 100 mg of dried sediment was combined in a centrifuge tube with 30 ml double distilled water (DDW) and agitated on a shaker overnight. The mixture was then centrifuged for 200 minutes at 13,000 G, 10,000 RPM, the supernatant was collected and analyzed for SRP and TDP. The pellet was re-extracted a second and third time, and the combined supernatants analyzed for SRP and TDP. The pellet was then resuspended in 15 ml DDW and filtered onto a preweighed GF/C filter. The filtrate was analyzed for SRP and TDP, and the filter-retained solids were analyzed for total P.

TABLE 2. Composition ratios that indicate nutrient deficiency. Units are ug mgC^{-1} except for N/P which is ug ug^{-1}.

Ratio	Type of deficiency	Degree of deficiency none	moderate	deficient
N/C	N	>140	80-140	<80
P/C	P	>20	10-20	<10
N/P	P	<10		>10
Chl/C	general	>20	10-20	<10
ATP/C	general	>2.0		<2.0

Enrichment Experiments

Three enrichment experiments were conducted on water from the moss-peat limnocorrals to test the hypothesis that these limnocorrals were iron limited. Two experiments were done in the lab and one *in situ*.

Enrichment Experiment I (August 4-11, 1981)

Four 300 mL aliquots of water from each of the moss-peat limnocorral(LM81-2) and control limnocorral (C81-1) were poured into 500 mL Erlenmeyer flasks which had been acid washed and autoclaved. The two sets of four flasks were given the following treatments: 1) no treatment, 2) trace metal solution (final concentrations are in Table 3), 3) Na_2 EDTA (final concentration 0.874 mg L^{-1}), 4) Na_2EDTA (final concentration 0.874 mg L^{-1}) + $FeCl_3$ $6H_2O$ (final concentration 2.34 uM Fe) and then loosely covered with aluminum foil and incubated at room temperature (26-27^oC). The flasks were lit from below by Vita-Lite fluorescent lamps delivering 54 uE $m^{-2}sec^{-1}$. The flasks were moved daily to compensate for variability in the lights. The flasks were subsampled on August 8 and 11 for primary productivity, DIC, alkaline phosphatase activity, and chlorophyll a. Because of the small volume available in the flasks, primary productivity was measured on one light and one dark bottle only. The light bottle was incubated in the second compartment of the incubator. This light intensity was chosen because during August, primary productivity was saturated in the second compartment. The other analyses were done as described previously.

TABLE 3. Final concentrations of trace elements used in the enrichment experiments. The trace metal solution is a five fold dilution of that used in freshwater medium WC of Guillard and Lorenzen (1972).

Trace metal	Compound ($mg\ L^{-1}$)	Element ($weight\ L^{-1}$)	Element (umole)
Na_2 EDTA	0.874		ca. 2.34 (EDTA)
$FeCl_3 \cdot 6H_2O$	0.630	0.13 mg Fe	ca. 2.34
$CuSO_4 \cdot H_2O$	0.002	0.5 ug Cu	ca. 0.008
$ZnSO_43 \cdot 7H_2O$	0.004	1.0 ug Zn	ca. 0.016
$CoCl_2 \cdot 6H_2O$	0.002	0.5 ug Co	ca. 0.01
$MnCl_2 \cdot 4H_2O$	0.036	0.01 mg Mn	ca. 0.018
$Na_2MoO_4 \cdot 2H_2O$	0.001	0.5 ug Mo	ca. 0.006
H_3BO_3	0.20	0.034 mg B	ca. 3.2

Enrichment Experiment II (August 1-7, 1982)

Water from the moss-peat (LM82-3) and control (C82-6) limnocorrals was collected in 20 L nalgene containers with a 200 um screen placed over the mouth to exclude zooplankton. The containers were covered to keep out sunlight. Three 2400 mL aliquots from each container were siphoned into acid washed sterile Fernbach flasks. The following treatments were given to the two sets of flasks: 1) no treatment, 2) 5.3 g (wet weight) moss-peat dredged from LM82-3, and 3) Na_2EDTA (final concentration 0.874 mg L^{-1}) + $FeCl_3$ $6H_2O$ (final concentration 2.34 uM Fe). The amount of moss-peat material added to flasks was proportional to that added to the moss-peat limnocorral at the beginning of the summer. The flasks were loosely covered with aluminum foil and incubated at room temperature over a bank of Vita-Lite fluorescent lamps delivering 200 uE m^{-2} sec^{-1}. Subsamples (500 ml) were siphoned from each flask on August 2, 4, 5, and 7 and analyzed for ATP, alkaline phosphatase activiy, pH, absorbance at 455 nm, DIC, primary productivity, and chlorophyll a. P debt was measured on August 1 and 7. All analyses were done as described previously.

In situ Enrichment Experiment (August 1 - 10, 1982)

This experiment was similar to Enrichment Experiment II (August 1-7 1982) except that the water was incubated in larger containers *in situ*. The containers were incubated at two depths or covered with screen to test the effect of different light intensities.

Seven 20 L Nalgene containers were filled with water from the moss-peat limnocorral (LM82-3). A 200 um screen was placed over the mouth of each container while filling to exclude zooplankton. Three of the containers received no treatment, two received 50 g wet weight of moss-peat (dredged from LM82-3), and two received Fe and Na_2EDTA solution (final concentrations as in Enrichment Experiment II). One of the control containers was covered with one thickness of black fibreglass screen. One of each set of two containers as well as the screen covered container were positioned in the surface water of LM82-3. The remaining three were anchored at 0.8 m in the limnocorral where they would receive about the same amount of light as the screen-covered container. Fig. 4 illustrates how the containers were suspended in the limnocorral. The containers were subsampled at the beginning of the experiment and on August 3, 6, and 10. Samples were taken by pumping about 1200 mL from each container into brown 2 L nalgene bottles. The containers anchored at 0.8 m were raised to the surface for sampling. Care was taken to avoid exposing these containers to direct sunlight. The samples were analyzed in the same manner as for Enrichment Experiment II.

SEDIMENT LIMNOCORRALS

RESULTS

SIL Shoreline Sediments

The SIL shoreline sediment added to the limnocorrals was primarily inorganic clay. The mean CNP weight ratio was 37:1:1 and about 70% of total carbon was carbonate (based on analyses in Appendix 3). Although rich in total P relative to C and N, only about 2% of total P was extractable into distilled water (Table 4). The total weight of C, N and P added to each sediment-treated limnocorral is given in Table 5.

The sediment was made up of 85% clay and 15% silt sized particles with the majority of particles less than 1.0 um in diameter (G.K. McCullough, unpublished data). The smaller particles remained in suspension scattering and absorbing light. Light extinction (k) increased in sediment-treated limnocorrals in direct proportion to the total suspended solids (TSS, Fig. 6). Mean water column light intensity per day (I_{24}) decreased as TSS and depth increased (Table 6). Partitioning of k into the three components P_s, P_a and P_{chl} showed that in the sediment limnocorrals over 50% of light extinction was due to scattering by suspended particles (Figs. 7 and 8). Seasonal Secchi disk and k values are given in Appendix 4.

Algal biomass indicators

The lower rate of sediment loading in 1981 (LS81-4) increased chlorophyll and suspended C (Table 7, Figs. 9 and 10). In 1982 both the sediment addition (HS82-7) and the screen (S82-2) increased chlorophyll

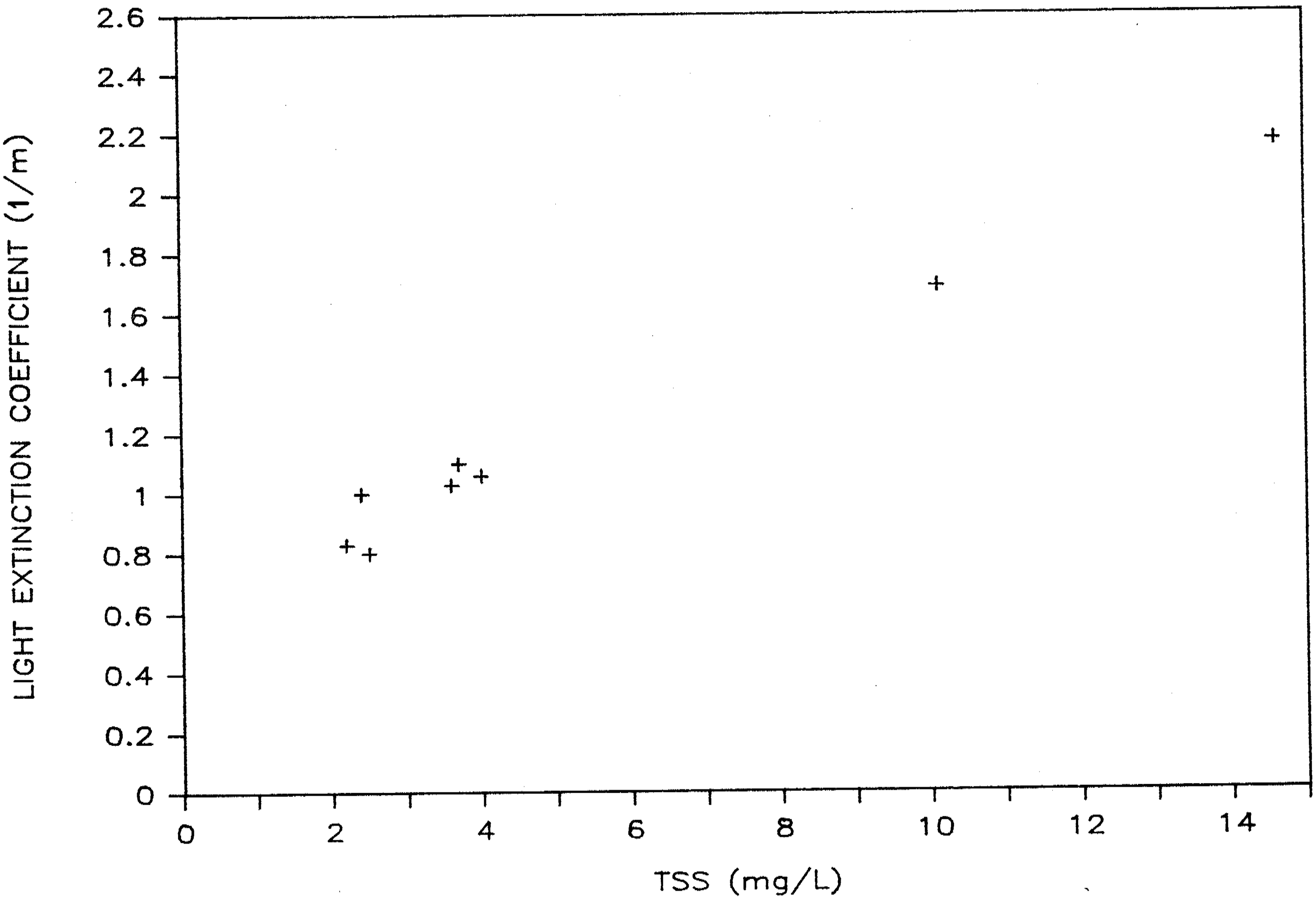
TABLE 4. Total and distilled water extractable P from four Southern Indian Lake shoreline sites in ug mg^{-1} dry weight (Hecky unpublished data). Water extractable TDP is the sum of three distilled water extractions of the sediments. About 90 % of TDP in the extract was SRP. % P is water extractable TDP expressed as a per cent of total P in the sediments. Sample site locations are in figure 2.

Sample	Total P	Water extractable TDP	% P
	(ug mg^{-1})	(ug mg^{-1})	
CH 1	0.55	0.010	1.8
CH 2	0.57	0.009	1.6
BL 1	0.69	0.009	1.3
BL 2	0.68	0.010	1.5
HHE 1	0.69	0.019	2.8
HHE 2	0.67	0.017	2.5
KHE 1	0.57	0.008	1.4
KHE 2	0.59	0.019	3.2

TABLE 5. Total weight of nutrient elements added to each experimental limnocorral with the three different types of treatments.

Limnocorral	Treatment	C (g)	N (g)	P (g)	CO_3-C (g)
LM81-1	moss-peat (63 Kg)	24255	265	25	441
LM82-3	moss-peat (52 Kg)	20020	219	21	364
HM82-4	moss-peat (104 Kg)	40040	437	42	728
LS81-4	sediment (32 Kg)	759	17	19	528
HS81-6	sediment (52 Kg)	1196	26	31	832
HS82-7	sediment (52 Kg)	1196	26	31	832
PN81-3	P&N	none	45	19	none

FIGURE 6. Relationship between k, the light extinction coefficient, and total suspended solids (TSS). The data are from the 1981 limnocorral experiments. TSS was not measured in 1982.



LIGHT EXTINCTION COEFFICIENT (1/m)
2.6
2.4
2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
2
4
6
8
10
12
14
TSS (mg/L)

TABLE 6. Seasonal means of some light related parameters for the sediment, P&N and control limnocorrals. k is the vertical light extinction coefficient, I_{24} is the mean water column light intensity and TSS is total suspended sediments. The season for 1981 was June 20 to August 23(day 171-235). In 1982 the season for the secchi depths was from June 29 to August 30 (day 180-242) and for k July 7 to August 9 (day 188-221).

Limnocorral	Treatment	Depth (m)	Secchi (m)	k (m^{-1})	I_{24} ($E\ m^{-2}\ d^{-1}$)	TSS ($mg\ L^{-1}$)
C81-1	control	2.8	1.84	1.03	20.3	3.6
C81-5	control	3.5	2.43	0.80	20.8	2.5
C81-7	control	3.5	2.44	0.83	20.2	2.2
LS81-4	sediment (33 Kg)	4.0	0.82	1.69	9.2	10.1
HS81-6	sediment (52 Kg)	4.0	0.54	2.17	7.5	14.6
PN81-3	P&N	3.1	1.51	1.10	17.4	3.7
L81-8	lake	3.3	1.47	1.06	17.2	4.0
C82-6	control	2.9	2.09	1.13	18.0	n.d.[1]
HS82-7	sediment (51.5 Kg)	2.9	0.51	2.02	10.6	n.d.
SC82-2	screen	2.7	2.29	1.05	10.6	n.d.
L82-9	lake	3.3	1.30	1.19	15.5	n.d.

1 n.d. = not done

FIGURE 7. Partitioning of the mean light extinction coefficients for the 1981 limnocorrals into the three components; P_s (proportion of light extinction due to scattering by suspended particles), P_{chl} (proportion of light extinction due to absorption by chlorophyll), and P_a (proportion of light extinction due to other absorption processes). L = lake, C = control, PN = phosphorus and nitrogen, LM = low moss, LS = low sediment, and HS = high sediment. All limnocorrals except C81-1 and LM81-2 had plastic bottoms.

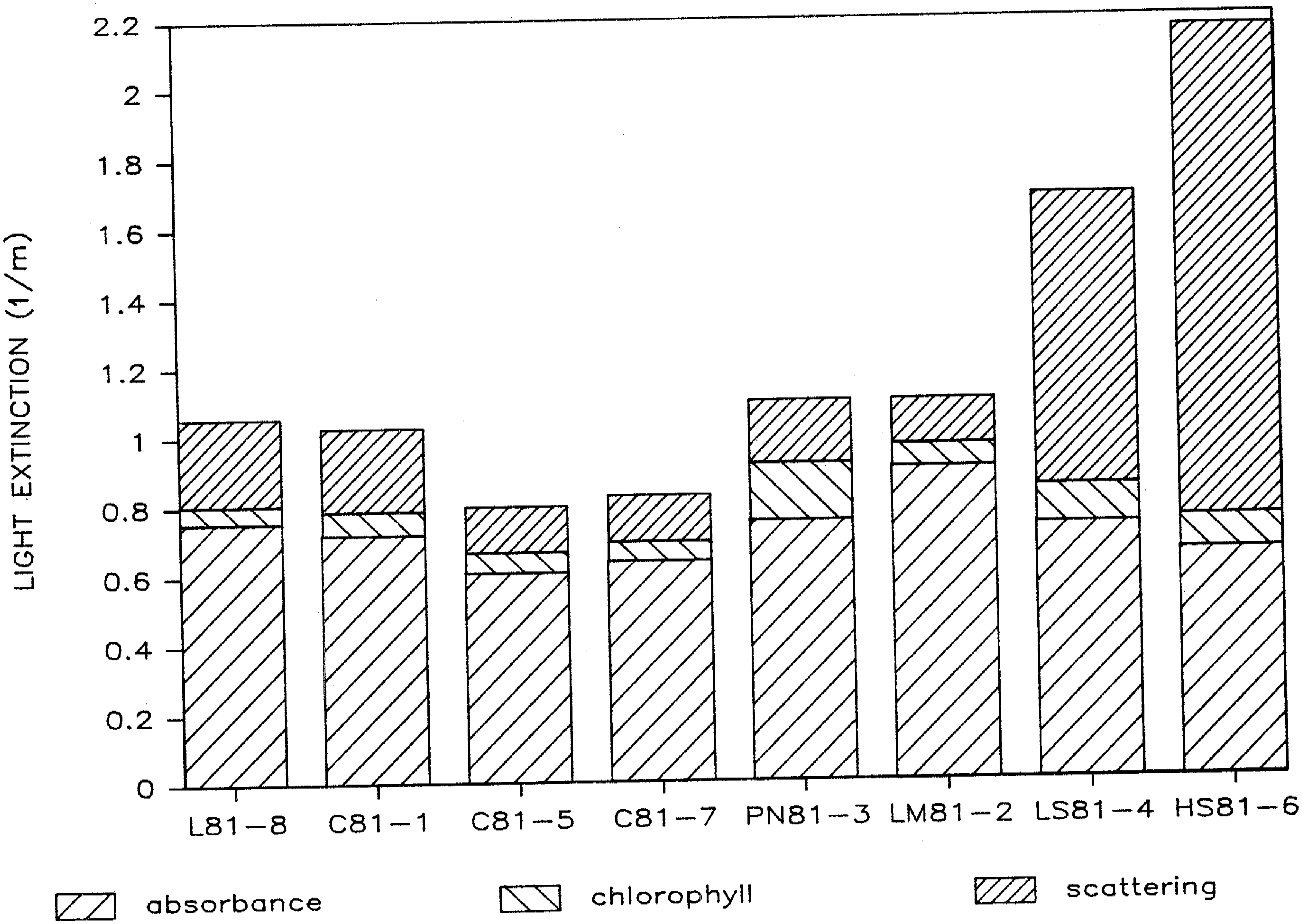

LIGHT EXTINCTION (1/m)
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
L81-8
C81-1
C81-5
C81-7
PN81-3
LM81-2
LS81-4
HS81-6
absorbance
chlorophyll
scattering

FIGURE 8. Partitioning of the mean light extinction coefficients for the 1982 limnocorrals into the three components; P_s (proportion of light extinction due to scattering by suspended particles), P_{chl} (proportion of light extinction due to absorption by chlorophyll), and P_a (proportion of light extinction due to other absorption processes). L = lake, C = control, OC = 1 year old control, OM = 1 year old moss, FM = flooded moss, LM = low moss, HM = high moss, and HS = high sediment. All limnocorrals had natural bottoms.

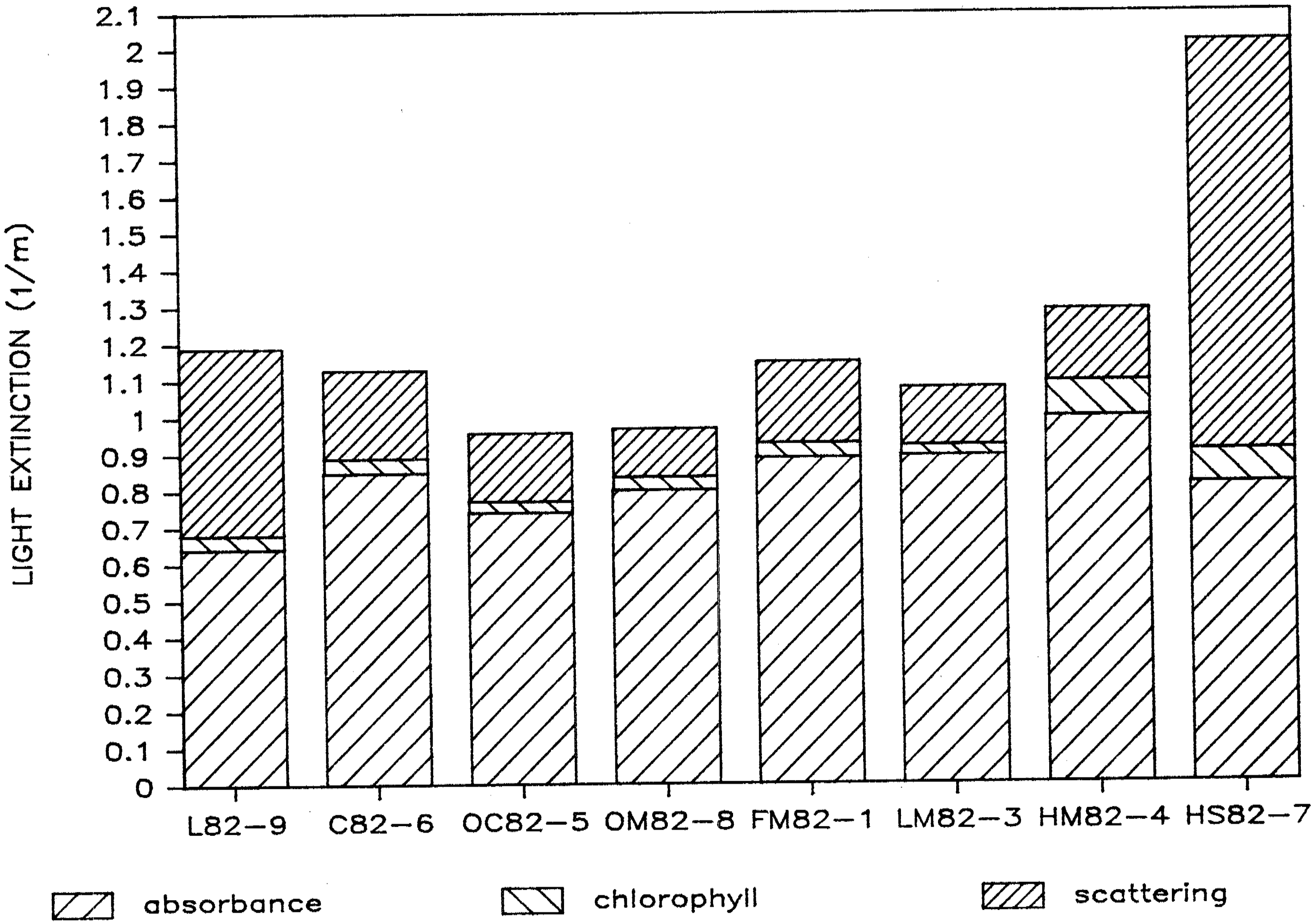

2.1
2
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
LIGHT EXTINCTION (1/m)
L82-9
C82-6
OC82-5
OM82-8
FM82-1
LM82-3
HM82-4
HS82-7
absorbance
chlorophyll
scattering

TABLE 7. Chlorophyll a and suspended carbon data for the sediment and control limnocorrals in 1981 and 1982. The data are time weighted means for July 10 to August 24, 1981 (days 191-236) and July 7 to August 9, 1982 (days 188-221). The experimental limnocorral data are expressed as a percent of the appropriate controls. Individual controls are expressed as a per cent of the mean of the controls for each year in order to show the range of variablity between the controls.

Limnocorral	Treatment	Chlorophyll a		Suspended carbon		Chl/C
		ug L^{-1}	%	ug L^{-1}	%	ug mg^{-1}
C81-8	control	3.9	111	719	98	5.4
C81-5	control	3.6	103	787	107	4.6
C81-7	control	3.0	86	701	95	4.3
LS81-4	sediment (33 Kg)	4.6	131	813	111	5.7
HS81-6	sediment (52 Kg)	2.8	80	474	64	5.9
PN81-3	P&N	11.8	337	1981	269	6.0
L81-8	lake	2.5	71	435	59	5.8
C82-6	control	2.2	100	909	100	2.4
HS82-7	sediment (52 Kg)	3.2	145	1019	112	3.1
SC82-2	screen	2.7	123	909	100	3.0
L82-9	lake	2.1	95	644	71	3.3

FIGURE 9. Chlorophyll a concentrations in the 1981 sediment limnocorral experiments. C = control, LS = low sediment and HS = high sediment. Day 170 is June 19 and day 230 is August 18. All limnocorrals had plastic bottoms.

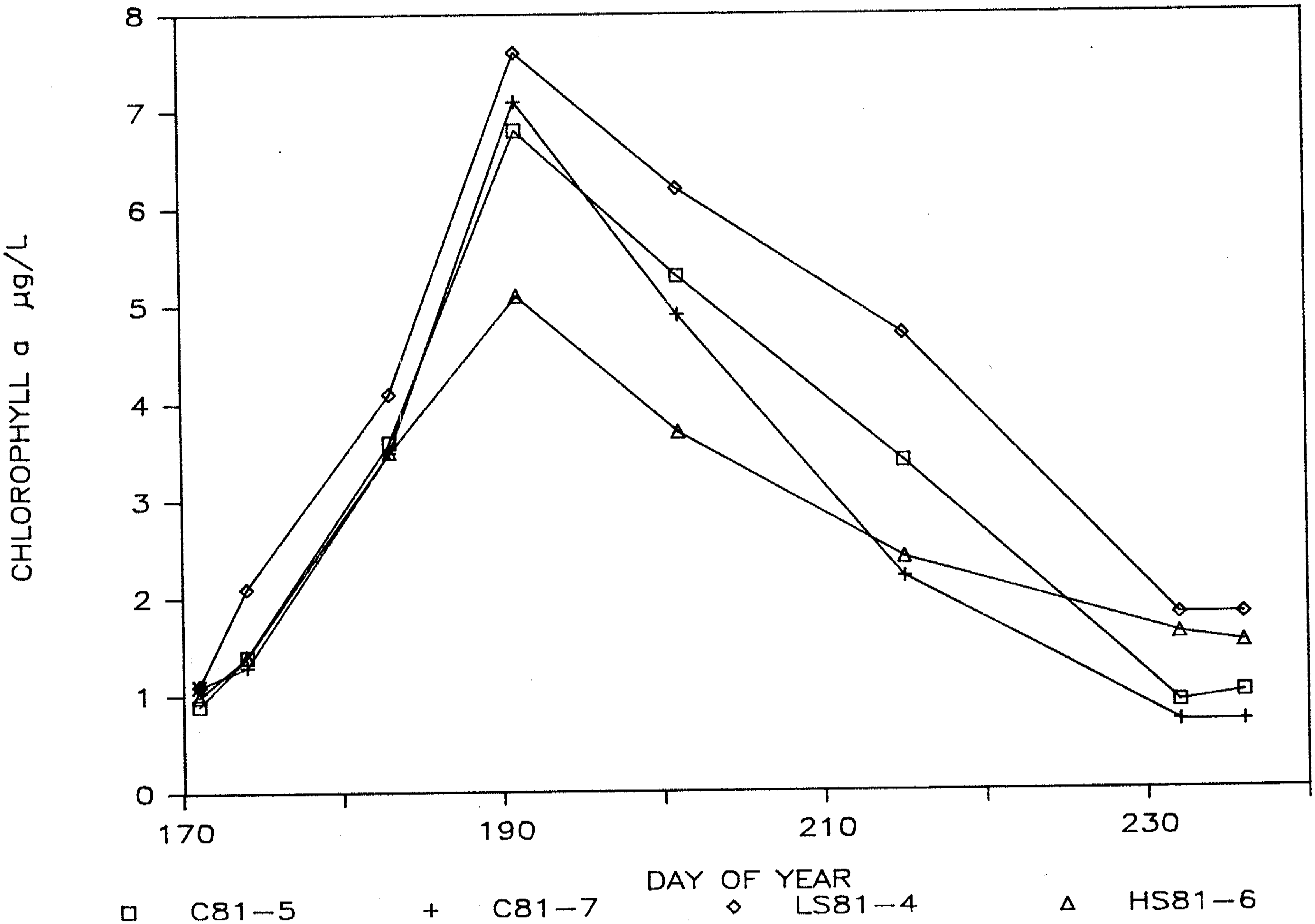
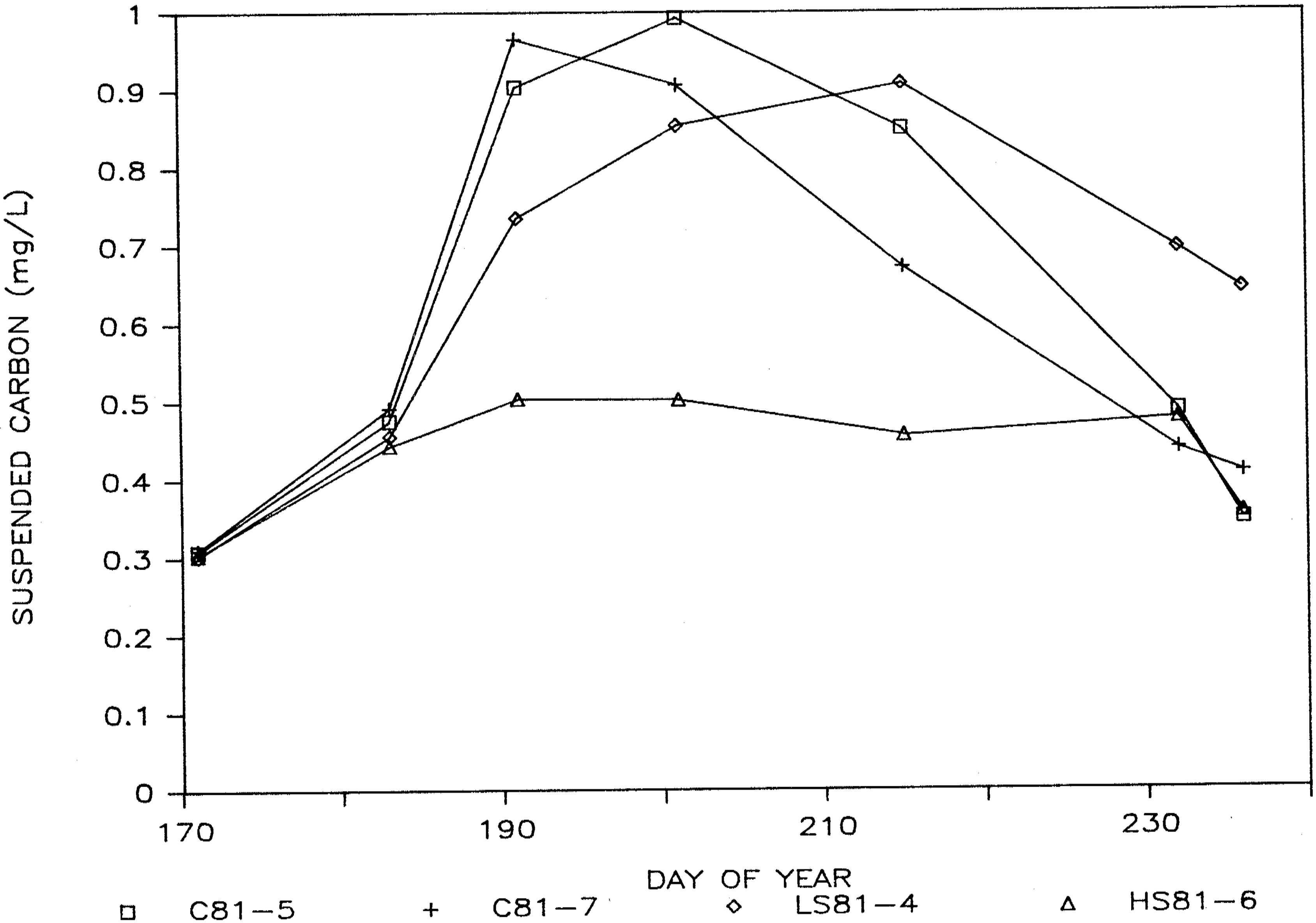

CHLOROPHYLL a µg/L
0
1
2
3
4
5
6
7
8
170
190
210
230
DAY OF YEAR
C81−5
C81−7
LS81−4
HS81−6

FIGURE 10. Suspended carbon concentrations in the 1981 sediment limnocorral experiments. C = control, LS = low sediment and HS = high sediment. Day 170 is June 19 and day 230 is August 18. All limnocorrals had plastic bottoms.


SUSPENDED CARBON (mg/L)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
170
190
210
230
DAY OF YEAR
C81-5
C81-7
LS81-4
HS81-6

but had little or no effect on suspended C (Table 7, Figs. 11 and 12). P and N enrichment tripled chlorophyll and suspended C (Table 7, Figs. 13 and 14). During both years, suspended C and chlorophyll were lower in the lake than in the control limnocorrals (Table 7, Figs. 11 and 14).

Bacteria

Two sets of counts were done on the limnocorrals in 1981. The mean values are given in Table 8. There was little difference in cell numbers between the sediment limnocorrals and controls with plastic floors (C81-5 and C81-7) and the lake. The P+N treatment (PN81-3) had double the bacteria of the controls. The two limnocorrals with sediment bottoms C81-1 and LM81-2 had more bacteria than the plastic bottom limnocorrals.

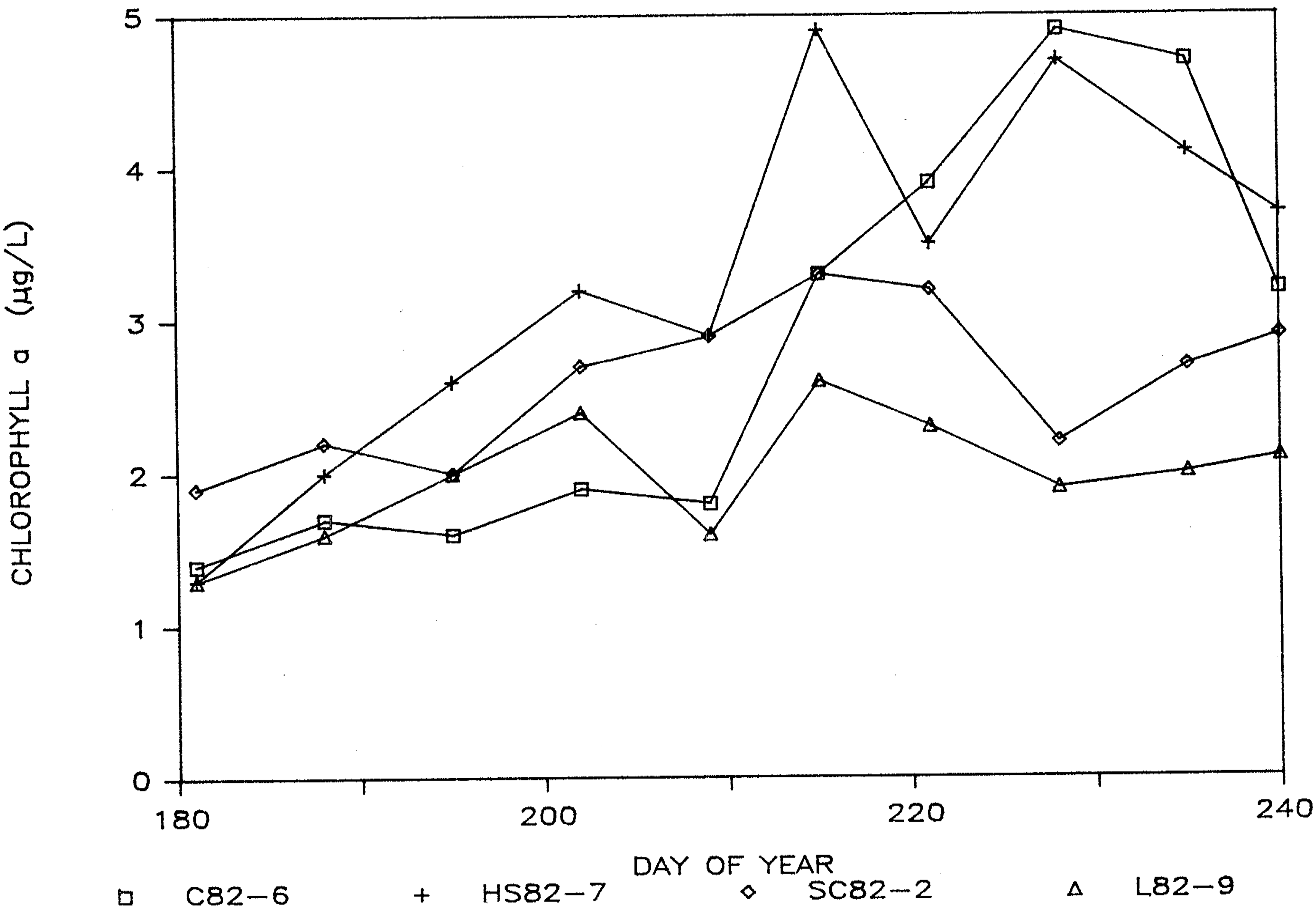
Zooplankton

In both years there were less zooplankton in the sediment limnocorrals than in the comparable controls (Table 9). The type of limnocorral bottom seems to have affected zooplankton numbers. The only control in 1981 which had a natural sediment bottom rather than plastic (C81-1) had the lowest number of zooplankton, but it also had the highest numbers and biomass of fish as well (R.E. Hecky personal communication).

Primary Productivity

Mean integral productivity was 25% to 40% lower in all three sediment limnocorrals and in the screen covered limnocorral than that in the controls (Table 10). Seasonal primary productivity parameters are

FIGURE 11. Chlorophyll a concentrations in the 1982 sediment limnocorral experiments. C = control, HS = high sediment, SC = screen covered, L = lake. Day 180 is June 29 and day 240 is August 28. All limnocorrals had natural bottoms.



CHLOROPHYLL a (µg/L)
0
1
2
3
4
5
180
200
220
240
DAY OF YEAR
□ C82−6
+ HS82−7
◇ SC82−2
△ L82−9

FIGURE 12. Suspened carbon concentrations in the 1982 sediment limnocorral experiments. C = control, HS = high sediment, SC = screen covered, L = lake. Day 180 is June 29 and day 240 is August 28. All limnocorrals had natural bottoms.

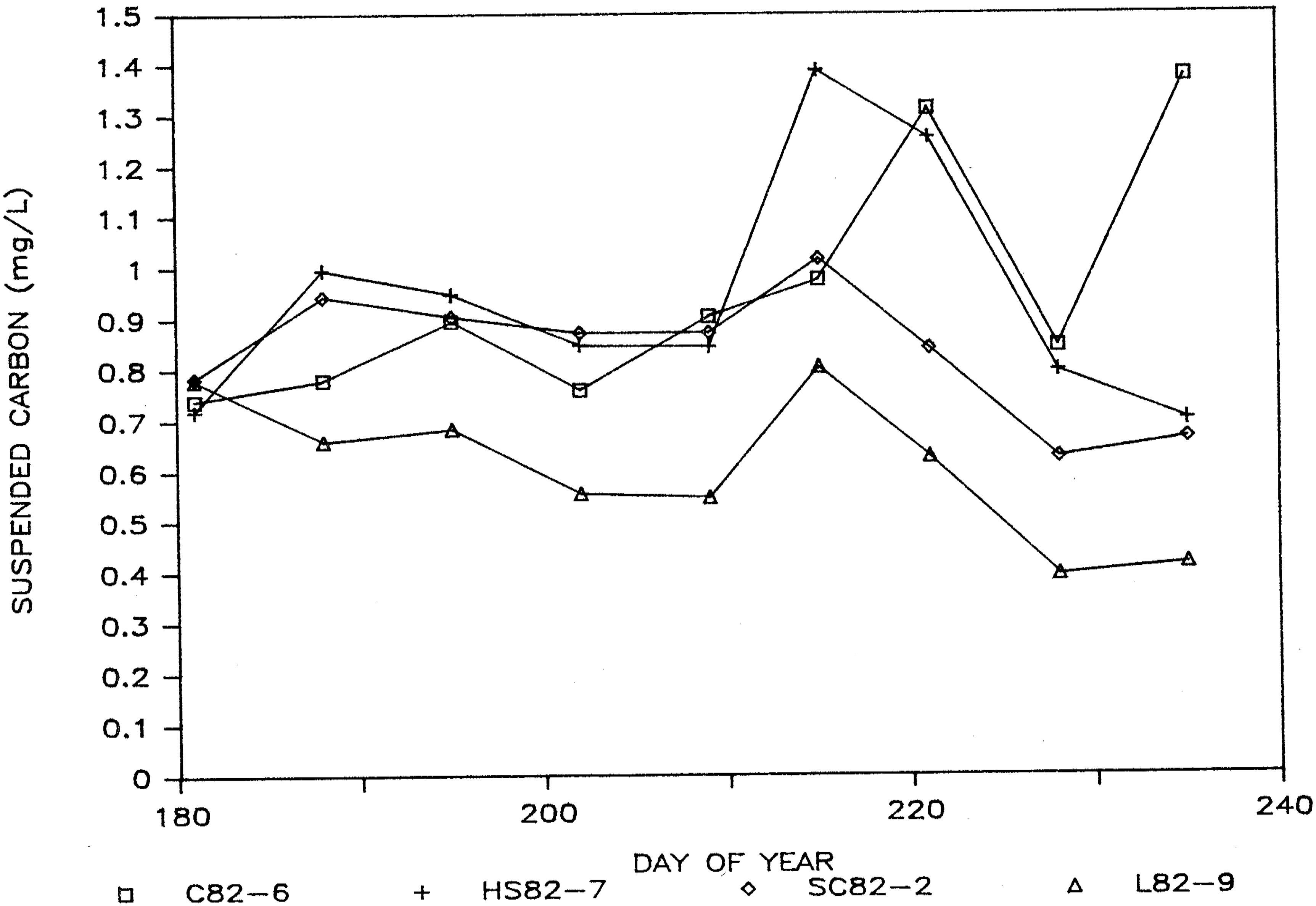

1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
SUSPENDED CARBON (mg/L)
180
200
220
240
DAY OF YEAR
C82-6
HS82-7
SC82-2
L82-9

FIGURE 13. Chlorophyll a concentrations in the 1981 P and N limnocorral, lake and controls. C = control, PN = phosphorus and nitrogen, L = lake. All limnocorrals except C81-1 had plastic bottoms. Day 170 is June 19 and day 230 is August 18.

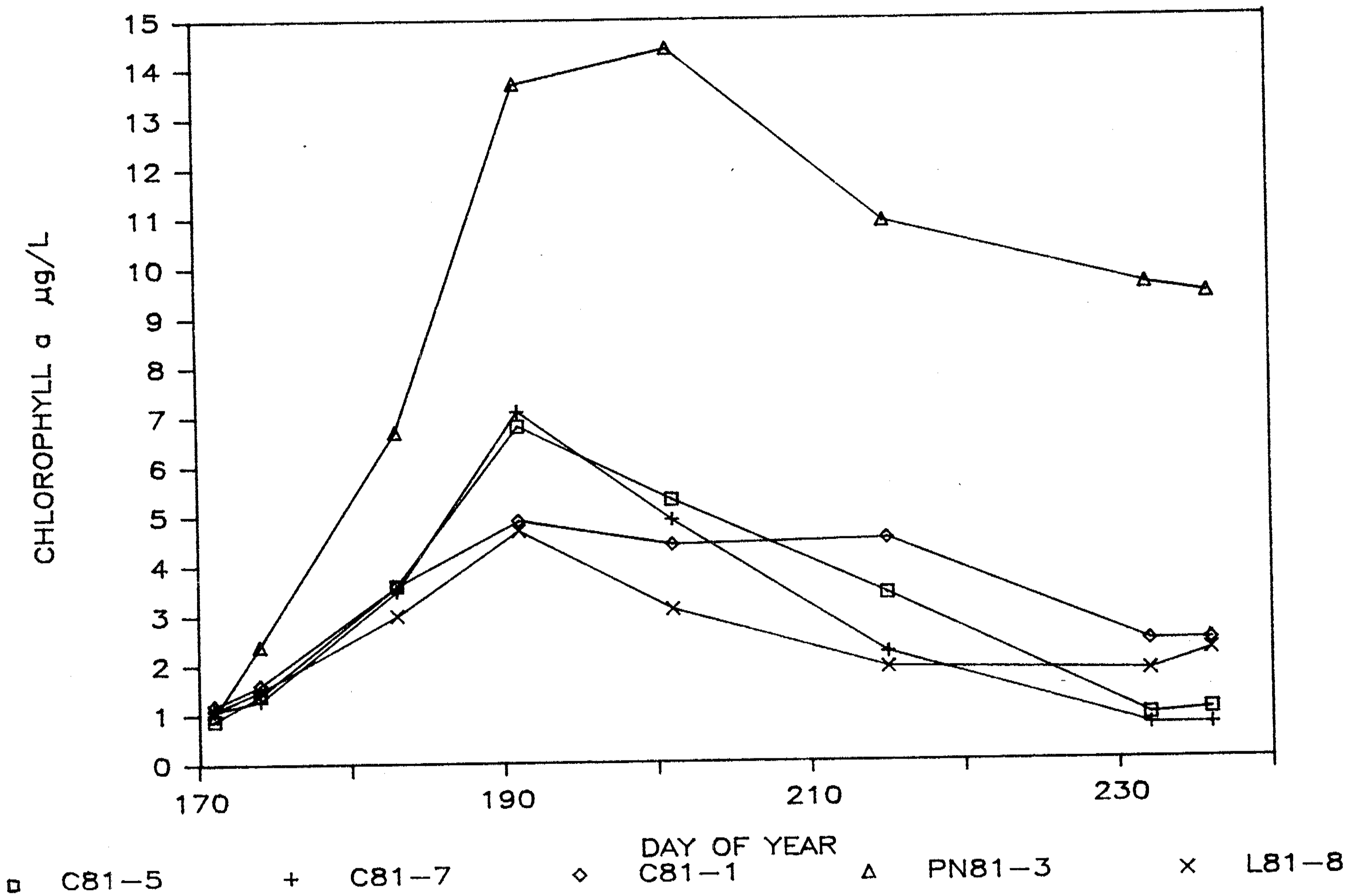

15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
CHLOROPHYLL a µg/L
170
190
210
230
DAY OF YEAR
C81-5
C81-7
C81-1
PN81-3
L81-8

FIGURE 14. Suspended carbon concentrations in the 1981 P and N limnocorral, lake and controls. C = control, PN = phosphorus and nitrogen, L = lake. All limnocorrals except C81-1 had plastic bottoms. Day 170 is June 19 and day 230 is August 18.

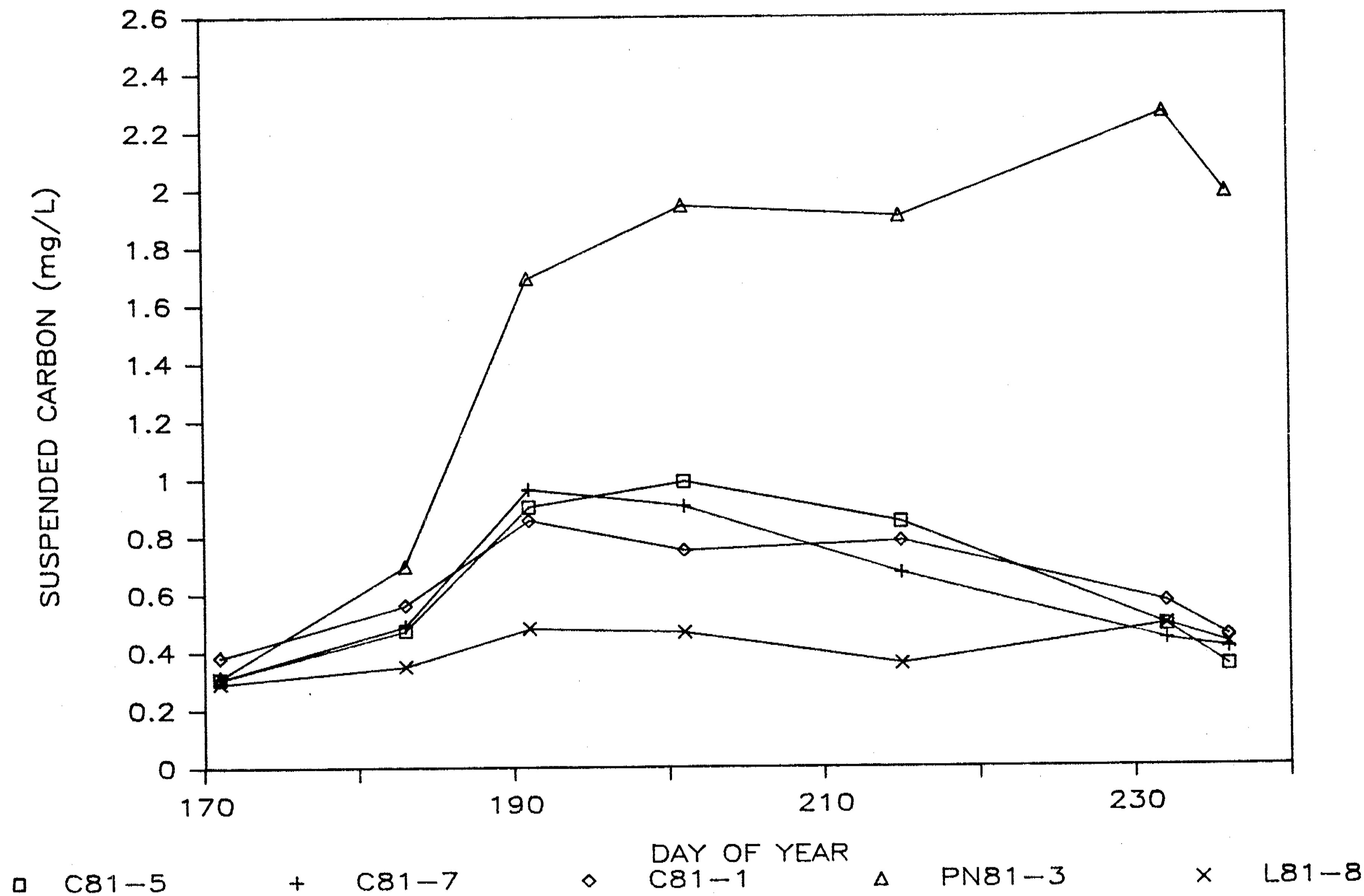

SUSPENDED CARBON (mg/L)
2.6
2.4
2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
170
190
210
230
DAY OF YEAR
C81-5
C81-7
C81-1
PN81-3
L81-8

TABLE 8. Bacteria in the limnocorrals and lake in 1981. Numbers are the average of replicates, one set from July and one from August. H.Kling counted the bacteria using the fluoresence microscopy technique of Hobbie et al (1977).

Limnocorral	Treatment	Bacteria cells ml^{-1}	Bottom type
C81-1	control	2530	natural
LM81-2	moss-peat (63 Kg)	2470	natural
C81-5	control	1750	plastic
C81-7	control	1780	plastic
LS81-4	sediment (33 Kg)	1860	plastic
HS81-6	sediment (52 Kg)	1640	plastic
PN81-3	P&N	3010	plastic
L81-8	lake	1750	

TABLE 9. Mean zooplankton numbers in the sediment and control limnocorrals and the lake in 1981 and 1982. D. Ramsey counted the zooplankton.

Limnocorral	Treatment	Zooplankton animals L^{-1}	Bottom type
C81-1	control	39	natural
C81-5	control	98	plastic
C81-7	control	116	plastic
LS8I-4	sediment (33 Kg)	73	plastic
HS81-6	sediment (53 Kg)	69	plastic
PN81-3	P&N	171	plastic
L81-8	lake	48	
C82-6	control	71	natural
HS82-7	sediment (52 Kg)	27	natural
SC82-2	screen	15	natural
L82-9	lake	42	

TABLE 10. Seasonal means of relevant parameters of primary productivity for the sediment and control limnocorrals in 1981 and 1982. . The data are means for July 10 to August 24, 1981 (days 191-236) and July 7 to August 9, 1982 (days 188-221). The experimental limnocorral data are expressed as a per cent of the appropriate controls. Individual controls are expressed as a per cent of the mean of the controls for each year in order to show the range of variability between the controls. Symbols are explained below.

Limnocorral	Treatment	I.P.	%	I_{24}	%	$Alpha^B$	%	P_m^B	%	I_k	I_{24}/I_k
C81-1	control	500	99	21.1	103	7.07	95	4.80	99	17.1	1.2
C81-5	control	480	95	20.0	98	7.29	98	4.74	98	16.4	1.2
C81-7	control	541	107	20.4	99	8.04	108	5.04	104	17.0	1.2
LS81-4	sediment (33 Kg)	369	73	8.7	43	6.74	90	4.02	83	15.6	0.6
HS81-6	sediment (53 Kg)	239	47	6.7	33	8.42	113	5.22	107	16.0	0.4
PN81-3	P&N	924	182	17.0	83	5.07	68	2.88	59	14.1	1.2
L81-8	lake	449	89	17.4	85	8.74	117	6.30	130	19.3	0.9
C82-6	control	290	100	18.7	100	4.24	100	4.98	100	19.3	1.0
HS82-7	sediment (52 Kg)	208	72	10.6	57	3.40	80	4.50	90	20.6	0.5
SC82-2	screen	181	62	10.2	55	3.08	73	3.48	70	17.3	0.6

I.P. is the daily rate of primary productivity (mg C m^{-2} d^{-1})

I_{24} is the mean water column light intensity during 24 hours (E $m^{-2}d^{-1}$)

$Alpha^B$ is the initial slope of the primary produtivity irradiance curve in the incubator expressed per unit of chlorophyll (mg C E^{-1} m^2 mg Chl a^{-1})

P^B_m is the maximum rate of primary productivity observed in the incubator expressed per unit of chlorophyll (mg C mg Chl a^{-1})

I_k is irradiance at the onset of light saturation (E m^{-2} d^{-1})

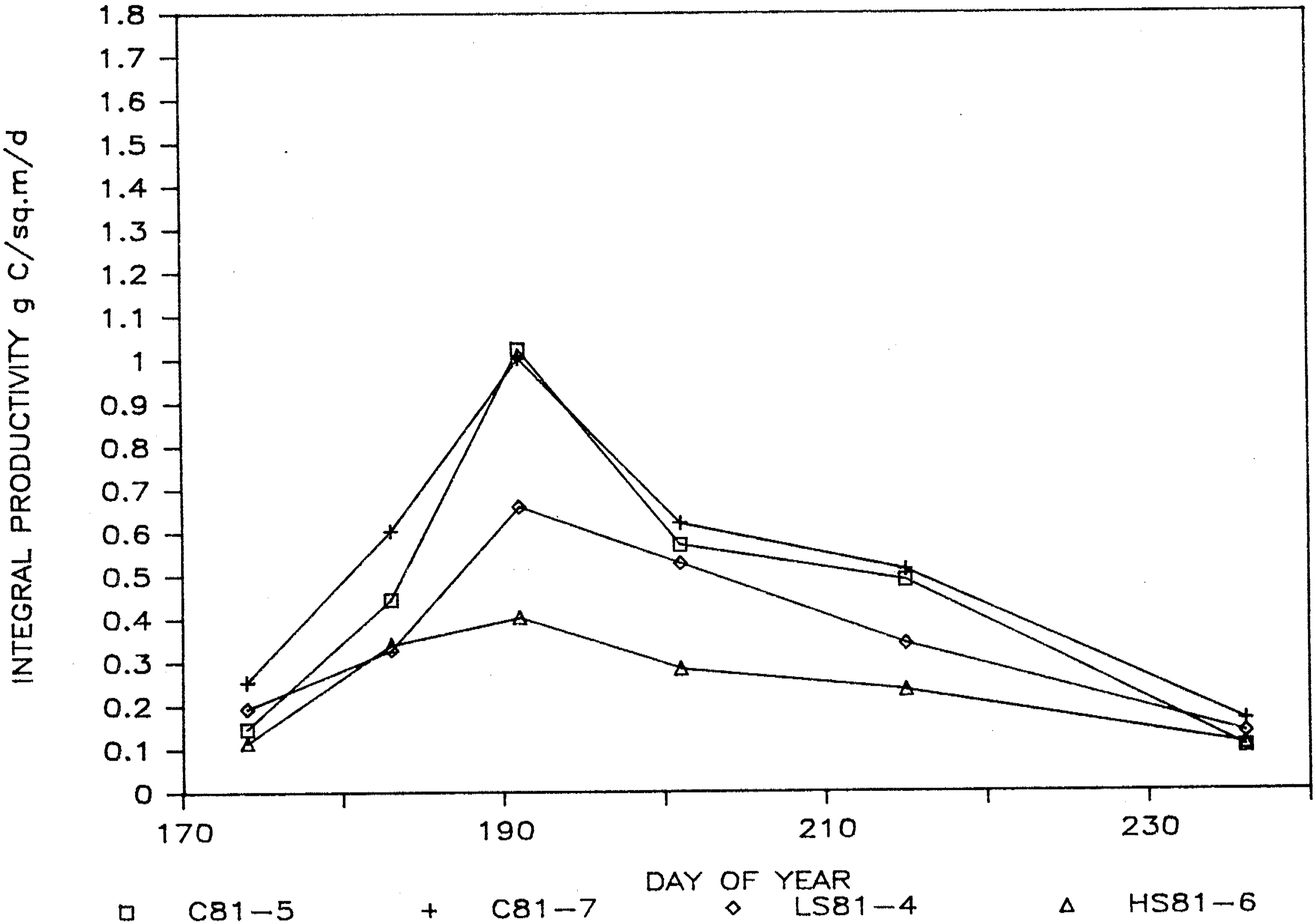
in Appendix 5 and Figs. 15 to 17. In PN81-3 integral productivity was nearly double that in the controls. Integral production was monitored routinely only one year in the bay and it was 10% lower than the controls. Integral production is a function of I_{24} and the light response in the incubator (defined by $alpha^B$ and P_m^B). All treated limnocorrals had lower I_{24} than the controls (Table 10). Low sediment (LS81-4), high sediment (HS82-7), and screened (SC82-2) limnocorrals had lower $alpha^B$ and P_m^B than the controls. The high sediment limnocorral (HS81-6) and the lake (81-8) had higher $alpha^B$ and P_m^B than the controls.

Integral production for all the limnocorrals in 1982 was only one third to one half the levels of 1981. P_m^B values were comparable for both years but $alpha^B$ values in 1982 were about half the values for 1981. I_{24} values were similar for the 2 years but these values have been calculated using cloudless irradiance. Cloudless irradiance was used to facilitate comparisons between primary productivity on different days and in different years. Surface irradiance data for comparable seasons in both years are not available. Water temperatures were lower in 1982 (Fig. 18), and these cooler temperatures may have been caused by lower solar irradiance in 1982.

Indicators of N deficiency

There was essentially no N deficiency in the controls or sediment limnocorrals as indicated by N debt or N/C ratios (Table 11 and Appendix 6). PN81-3 developed N debt large enough to suggest N deficiency on 2 of 3 dates sampled after N additions were stopped and P alone was added (Fig. 19); however, the N/C ratios remained in the no deficiency range

FIGURE 15. Seasonal pattern of daily integral primary productivity in the 1981 sediment limnocorral experiments. C = control, LS = low sediment, and HS = high sediment. Day 170 is June 19 and day 230 is August 18. All limnocorrals except C81-1 had plastic bottoms.



1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
INTEGRAL PRODUCTIVITY g C/sq.m/d
170
190
210
230
DAY OF YEAR
C81−5
C81−7
LS81−4
HS81−6

FIGURE 16. Seasonal pattern of daily integral primary productivity in the 1981 P and N limnocorral, control limnocorrals, and lake. C = control, PN = phosphorus and nitrogen, and L = lske. Day 170 is June 19 and day 230 is August 18. All limnocorrals except C81-1 had plastic bottoms.

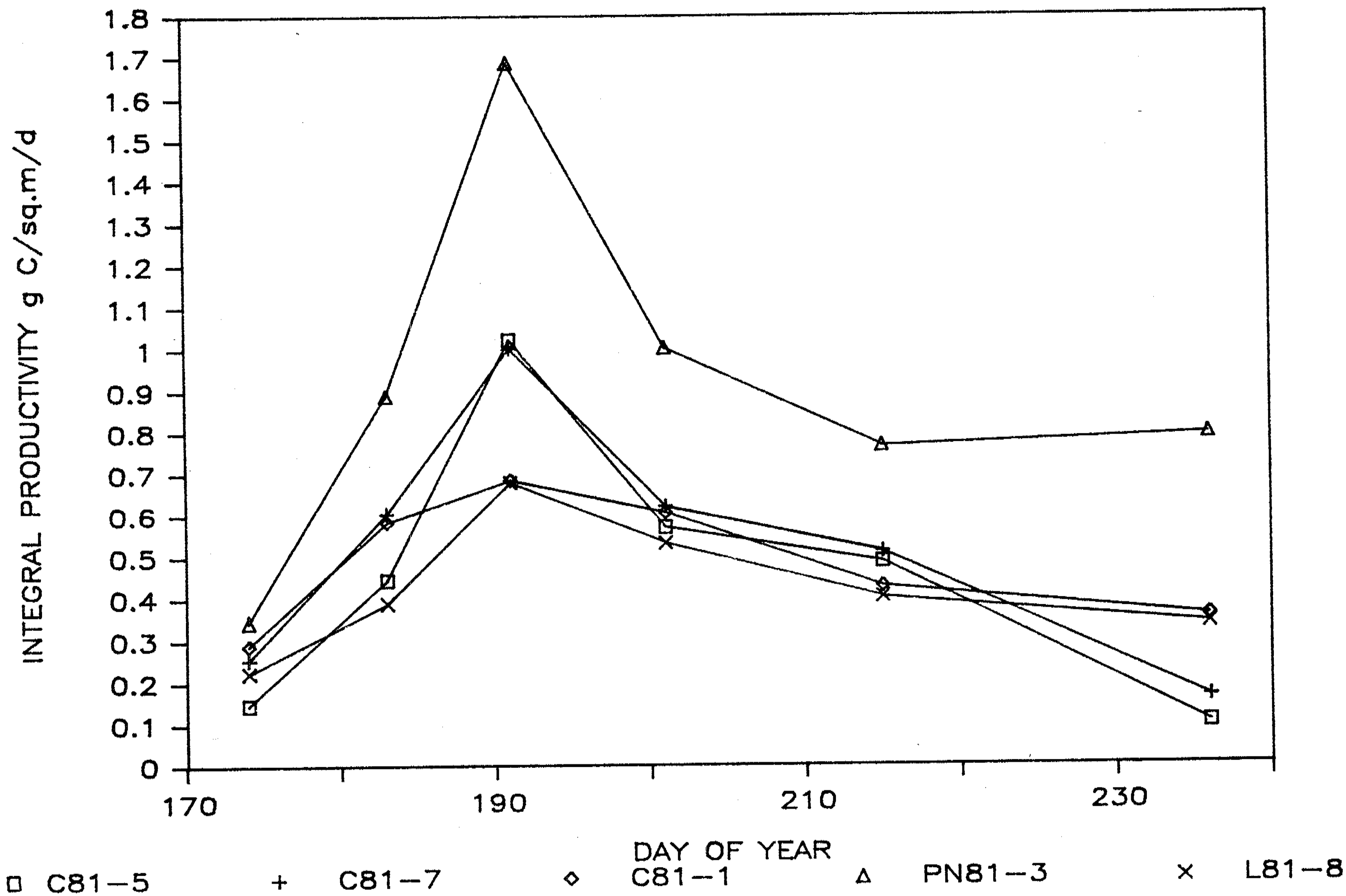
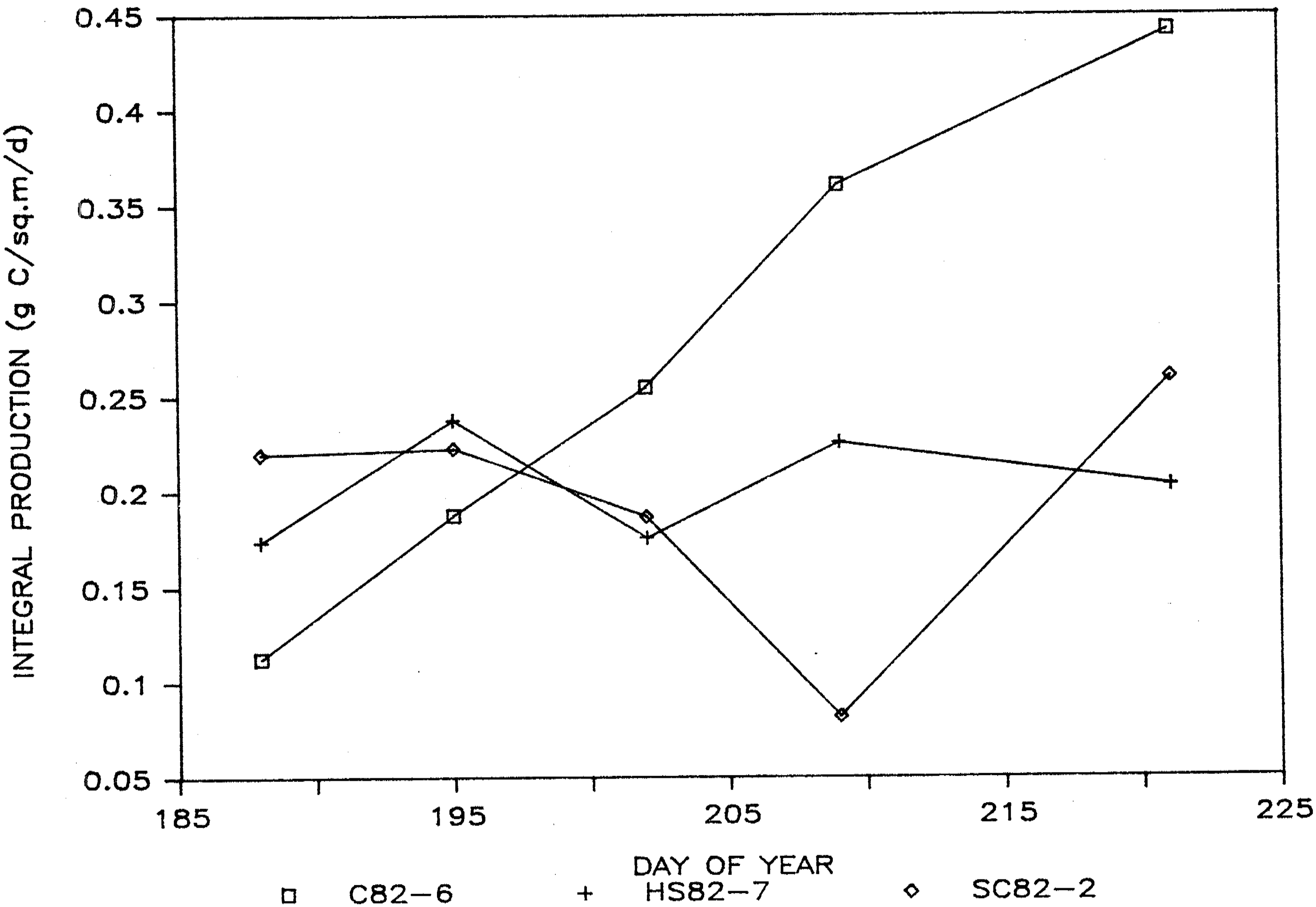

INTEGRAL PRODUCTIVITY g C/sq.m/d
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
170
190
210
230
DAY OF YEAR
C81-5
C81-7
C81-1
PN81-3
L81-8

FIGURE 17. Seasonal pattern of daily integral primary productivity in the 1982 sediment limnocorral experiments. C = control, HS = high sediment, and SC = screen covered. Day 170 is June 19 and day 230 is August 18. All limnocorrals had natural bottoms.



INTEGRAL PRODUCTION (g C/sq.m/d)
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
185
195
205
215
225
DAY OF YEAR
C82−6
HS82−7
SC82−2

FIGURE 18. Seasonal temperatures for Wupaw Bay (3.0 m) during 1981 (+) and 1982 (◇).

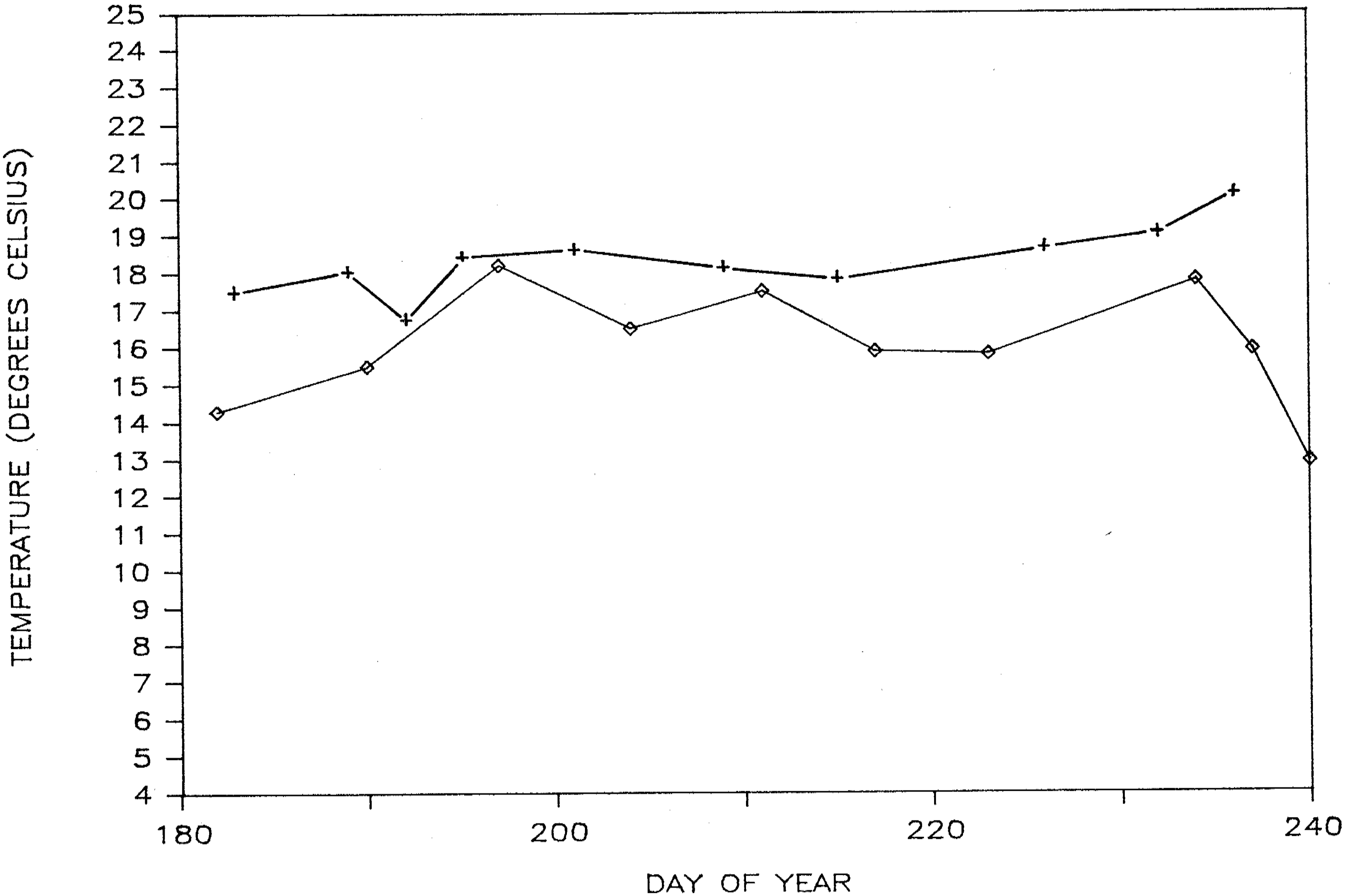
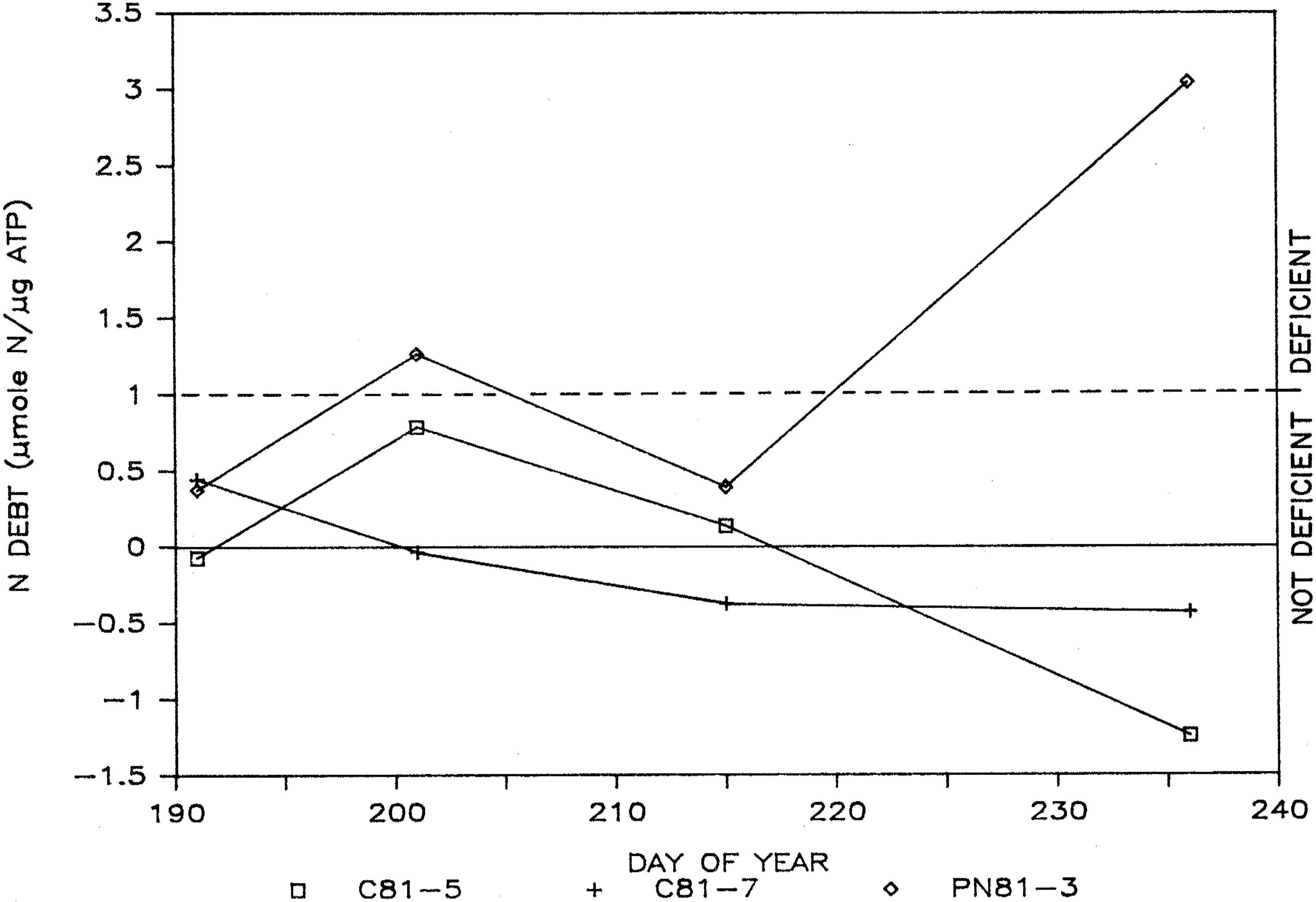

TEMPERATURE (DEGREES CELSIUS)
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
180
200
220
240
DAY OF YEAR

TABLE 11. Mean values for various physiological indicators of N and P deficiency in the sediment and control limnocorrals in 1981 and 1982. P and N headings indicate parameters indicative of P and N deficiency respectively: general indicators cannot on the basis of present evidence be ascribed with any certainty to either N or P deficiency (Healey and Hendzel 1980). Composition ratios are ug particulate P, N, ATP, or chlorophyll a (chl) mg particulate C^{-1}; ug particulate N ug particulate P^{-1}. Nutrient debts are umoles ammonium or phosphate removed in 24 h darkness ug chl^{-1}. Negative debt means net release of nutrient. Alkaline phosphatase activity (Pase) is umole o-methyl fluorescein phosphate hydrolyzed h^{-1} ug chl^{-1}. n.d. = no data.

		N		P				GENERAL	
Limnocorral	Treatment	Ndebt[1]	N/C[2]	Pase[3]	Pdebt[4]	P/C[5]	N/P[6]	Chl/C[7]	ATP/C[8]
C81-1	control	0.101	210	0.146	0.285	14	16	5.5	0.77
C81-5	control	-0.079	190	0.155	0.422	9	21	4.6	0.67
C81-7	control	-0.087	190	0.173	0.476	11	17	4.4	0.80
LS81-4	sediment (33 Kg)	0.060	180	0.124	0.300	16	11	6.2	0.33
HS81-6	sediment (52 Kg)	-0.079	190	0.077	0.192	32	6	6.4	0.42
PN81-3	P&N	0.106	200	0.093	0.383	9	23	6.5	0.45
L81-8	lake	-0.032	160	0.056	0.204	20	9	6.3	1.99
C82-6	control	n.d.	190	0.026	n.d.	11	20	3.0	0.76
HS82-7	sediment (52 Kg)	n.d.	180	0.003	n.d.	21	10	3.5	0.72
SC82-2	screen	n.d.	180	0.019	n.d.	12	17	3.1	1.07
L82-9	lake	n.d.	210	0.008	n.d.	15	15	3.4	1.37

1 >0.15 = N deficiency
2 80-140 = moderate, <80 = severe N deficiency
3 0.003-0.005 = moderate, > 0.005 = severe P deficiency
4 >0.075 = P deficiency
5 10-20 = moderate, <10 = severe P deficiency
6 >10 = P deficiency
7 <10 = deficiency
8 <2.0 = deficiency

FIGURE 19. Seasonal pattern of N debt normalized to ATP in the 1981 P and N limnocorral and controls. The broken horizontal line indicates the occurrence of N deficiency in algae as given by Healey and Hendzel (1980). C = control, PN = phosphorus and nitrogen. Day 190 is July 9 and day 230 is August 18. All limnocorrals had plastic bottoms.


N DEBT (µmole N/µg ATP)
3.5
3
2.5
2
1.5
1
0.5
0
−0.5
−1
−1.5
190
200
210
220
230
240
DAY OF YEAR
DEFICIENT
NOT DEFICIENT
C81−5
C81−7
PN81−3

at all times.

Indicators of P deficiency

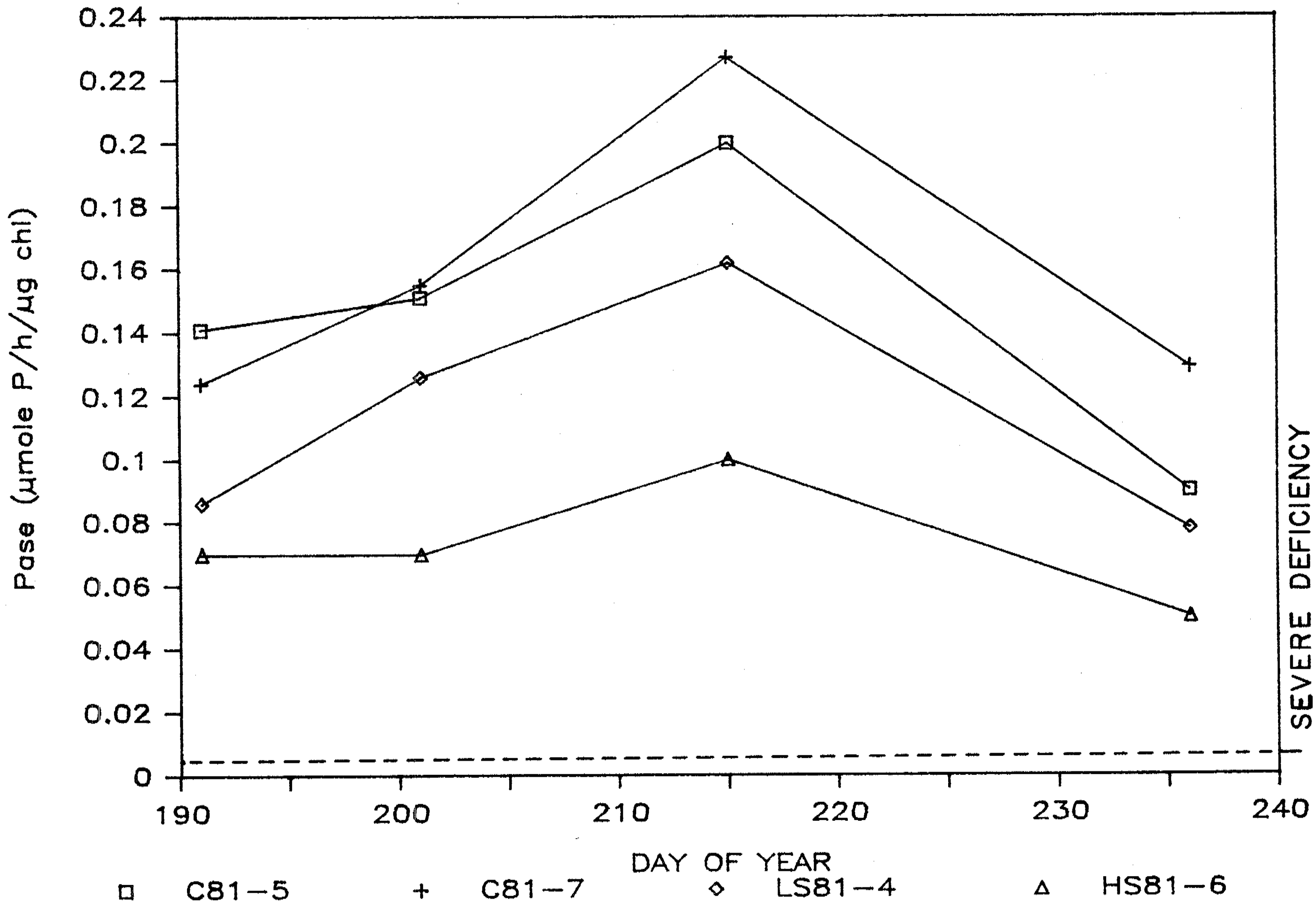
Sediment treatments, LS81-4 and HS81-6, and the controls, C81-5 and C81-7 were severely P deficient throughout the summer according to the alkaline phosphatase and P debt data (Figs. 20 and 21). The mean sediment limnocorral values, however, were about 25 and 50% less (for LS81-4 and HS81-6 respectively) than the controls (Table 11). The P/C and N/P ratios indicated P deficiency in C81-5, C81-7, and LS81-4 but no deficiency in HS81- 6 (Fig. 22 and 23). These ratios underestimate P deficiency in the sediment treatments because of the large particulate P contribution due to detritus (Appendix 2).

In 1982 the control (C82-6) and the screen (SC82-2) limmnocorrals were P deficient throughout the summer according to alkaline phosphatase activity and the N/P and P/C ratios (Table 11 and Figs. 24 to 26). The phosphatase activity in the sediment limnocorral (HS82-7) indicated there was no P deficiency after July 14 (day 196; Fig. 24). In both 1981 and 1982 the lake was less P deficient than the control (Figs. 26 to 28).

Indicators of deficiency not specific to P or N: Chlor/C and ATP/C

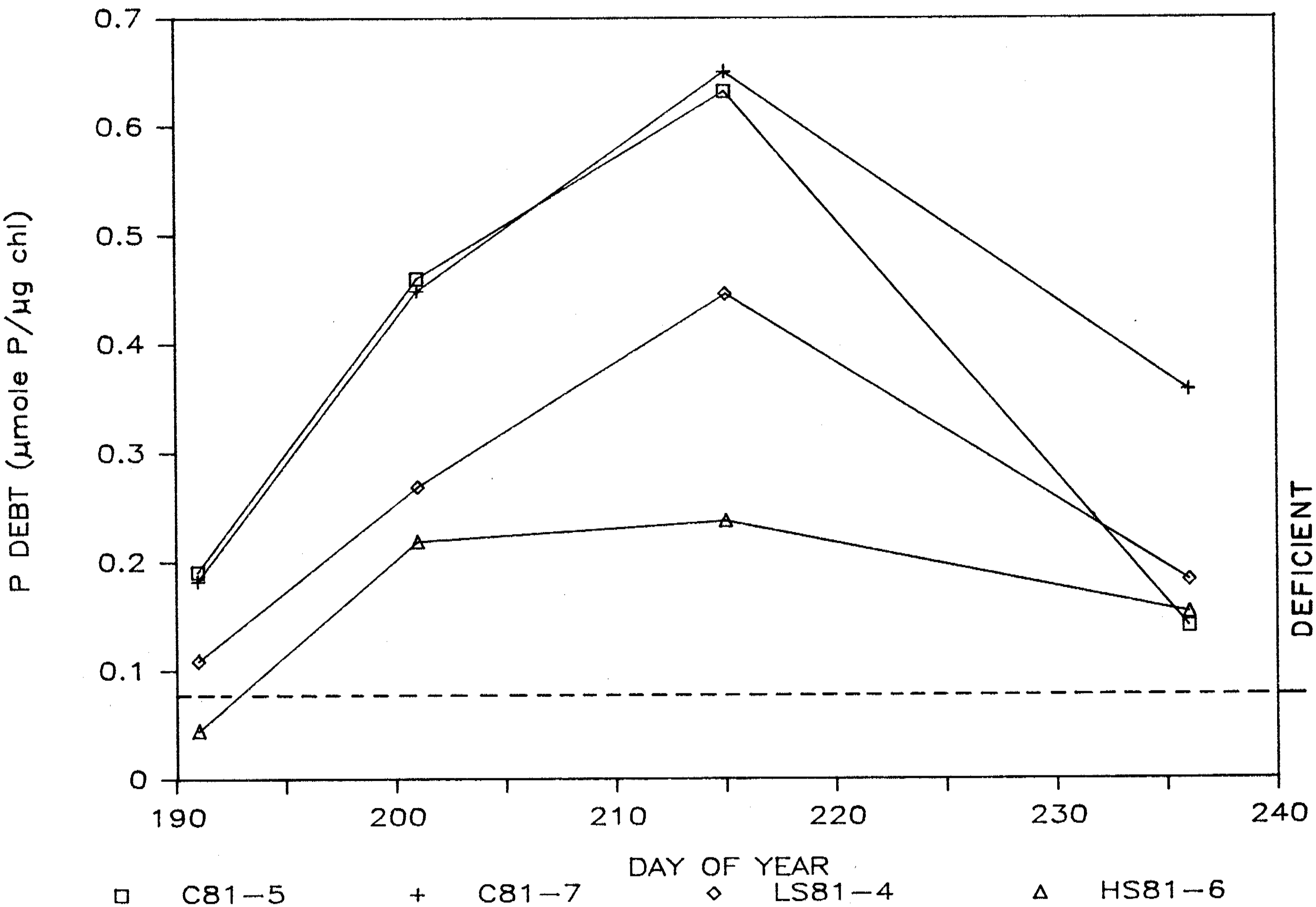
The sediment and control limnocorrals for both years had chlor/C ratios less than 10, which is a general indication of deficiency (Table 11). The means for the sediment limnocorrals were not as low as for the controls. This is probably due to the higher chlorophyll content associated with low light environments. The ATP/C ratios in the controls, screen and P+N limnocorrals were also in the deficient range.

FIGURE 20. Seasonal pattern of alkaline phosphatase activity (Pase) normalized to chlorophyll a (chl) in the 1981 sediment and control limnocorrals.. The broken horizontal line indicates the occurrence of severe P deficiency in algae as given by Healey and Hendzel (1980). C = control, LS = low sediment, HS = high sediment. Day 190 is July 9 and day 240 is August 28. All limnocorrals had plastic bottoms.



Pase (µmole P/h/µg chl)
0.24
0.22
0.2
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
190
200
210
220
230
240
DAY OF YEAR
SEVERE DEFICIENCY
C81–5
C81–7
LS81–4
HS81–6

FIGURE 21. Seasonal pattern of P debt normalized to chlorophyll a (chl) in the 1981 sediment and control limnocorrals. The broken horizontal line indicates the occurrence of P deficiency in algae as given by Healey and Hendzel (1980). C = control, LS = low sediment, HS = high sediment. Day 190 is July 9 and day 240 is August 28. All limnocorrals had plastic bottoms.



0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
P DEBT (μmole P/μg chl)
DEFICIENT
190
200
210
220
230
240
DAY OF YEAR
C81−5
C81−7
LS81−4
HS81−6

FIGURE 22. Seasonal pattern of the particulate P/C ratio in the 1981 sediment and control limnocorrals. The broken horizontal lines indicate the occurrence of severe, moderate, and no P deficiency in algae as given by Healey and Hendzel (1980). C = control, LS = low sediment, HS = high sediment. Day 190 is July 9 and day 240 is August 28. All limnocorrals had plastic bottoms.

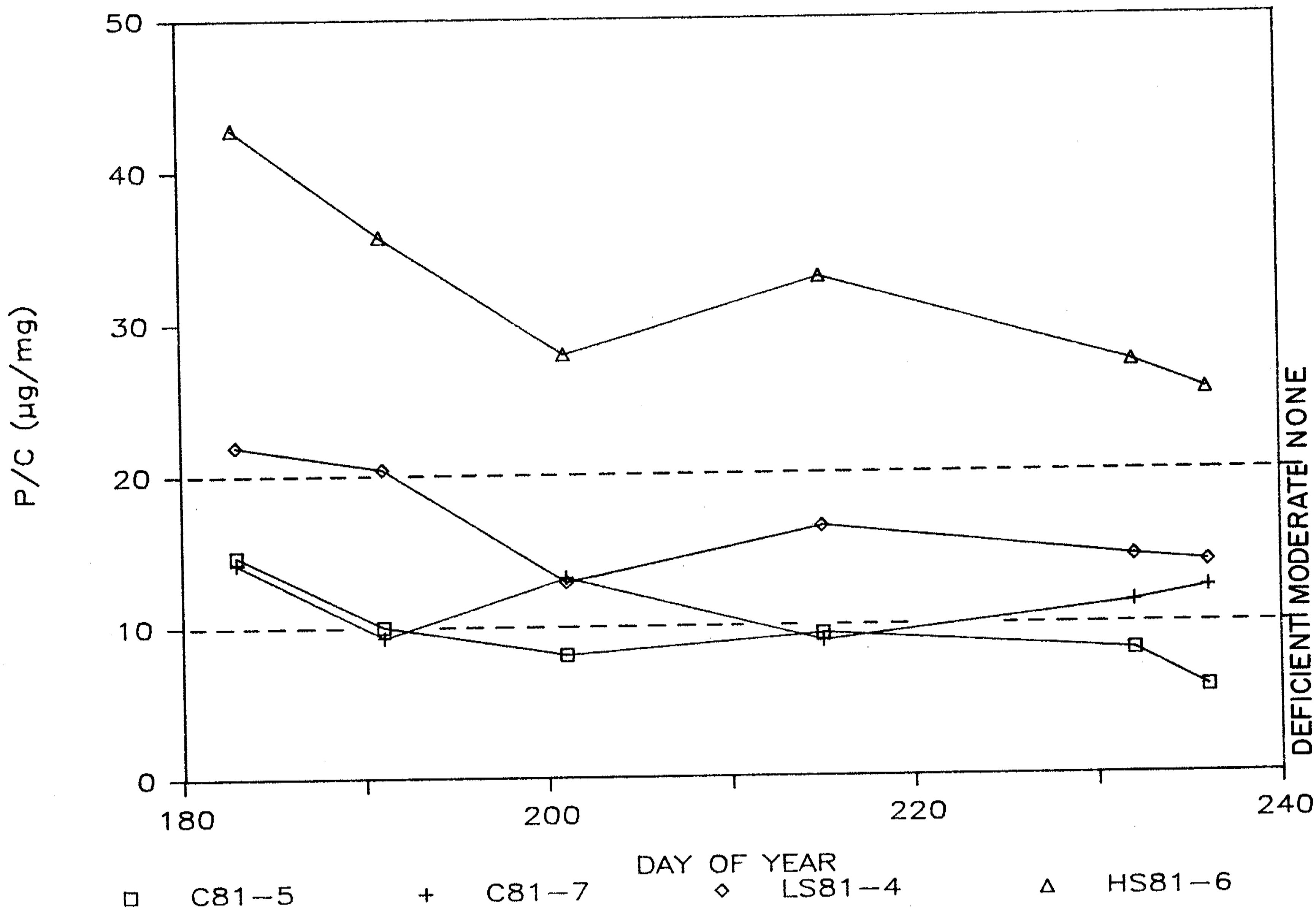
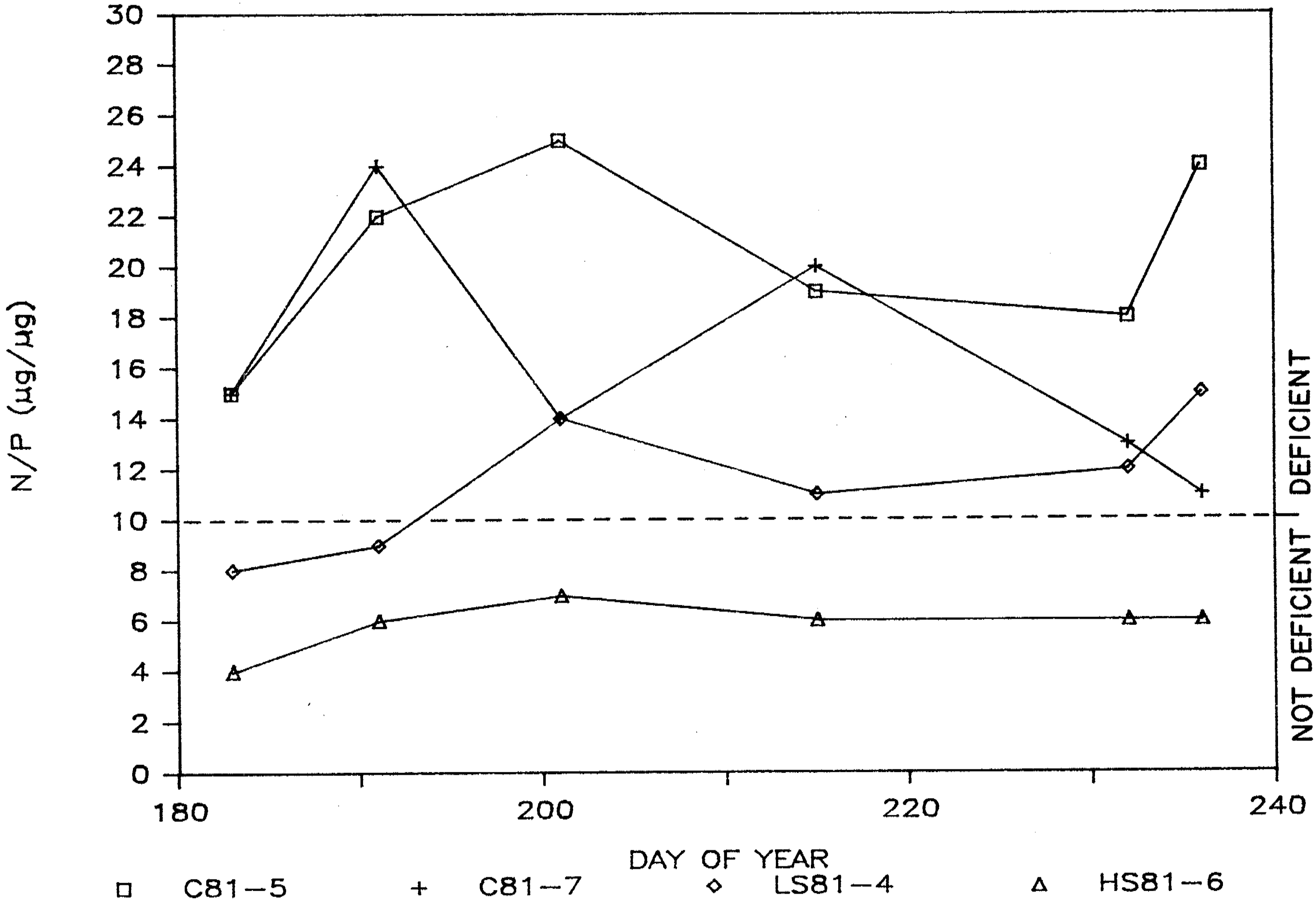

P/C (μg/mg)
50
40
30
20
10
0
180
200
220
240
DAY OF YEAR
DEFICIENT MODERATE NONE
□ C81−5
+ C81−7
◇ LS81−4
△ HS81−6

FIGURE 23. Seasonal pattern of the particulate N/P ratio in the 1981 sediment and control limnocorrals. The broken horizontal line indicates the occurrence of P deficiency in algae as given by Healey and Hendzel (1980). C = control, LS = low sediment, HS = high sediment. Day 190 is July 9 and day 240 is August 28. All limnocorrals had plastic bottoms.



30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
N/P (μg/μg)
180
200
220
240
DAY OF YEAR
DEFICIENT
NOT DEFICIENT
C81–5
C81–7
LS81–4
HS81–6

FIGURE 24. Seasonal pattern of alkaline phosphatase activity (Pase) normalized to chlorophyll a (chl) in the 1982 sediment limnocorral experiments. The broken horizontal lines indicates the occurrence of severe, moderate, and no P deficiency in algae as given by Healey and Hendzel (1980). C = control, HS = high sediment, SC = screen covered, and L = lake. Day 190 is July 9 and day 240 is August 28. All limnocorrals had natural bottoms.

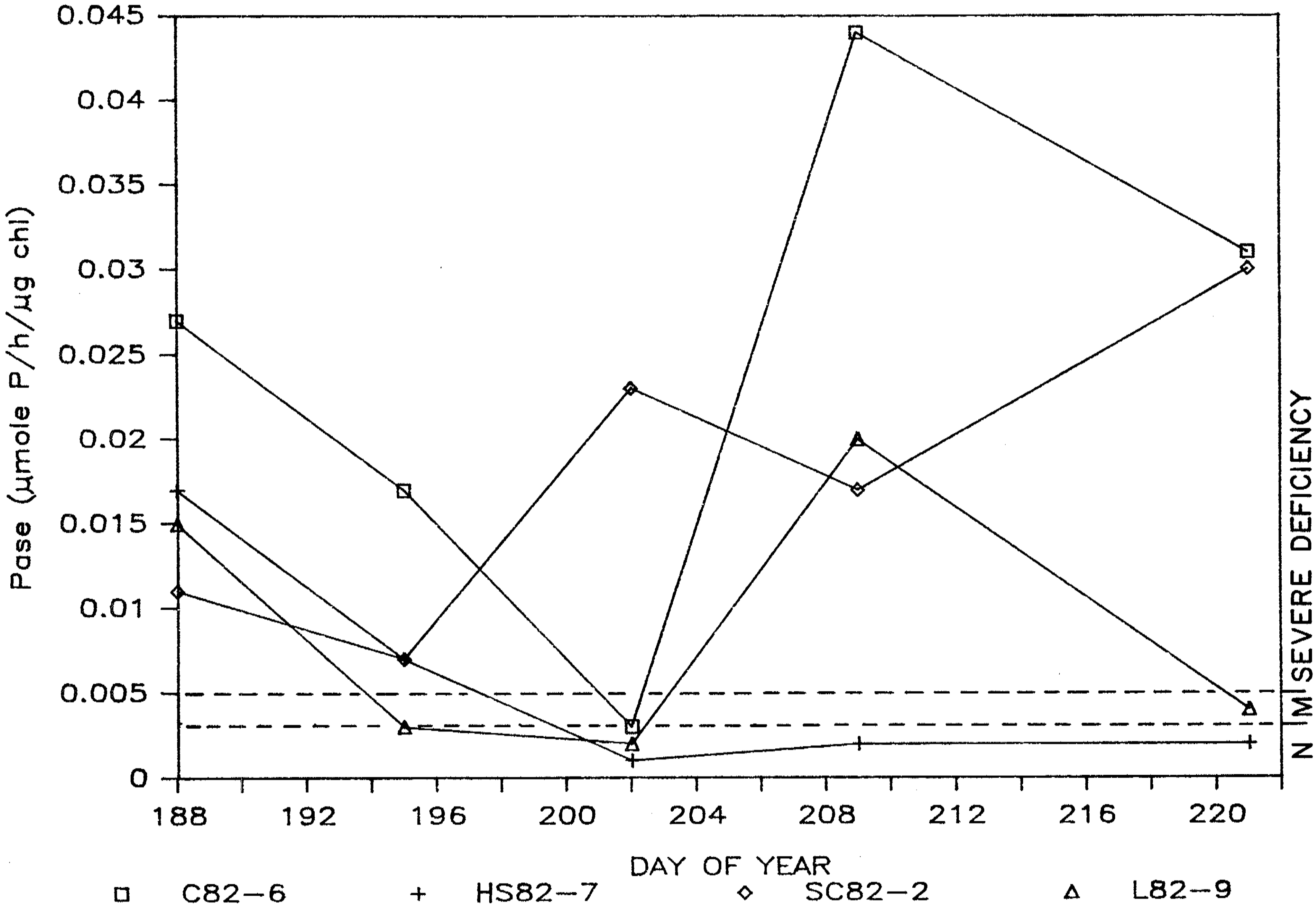
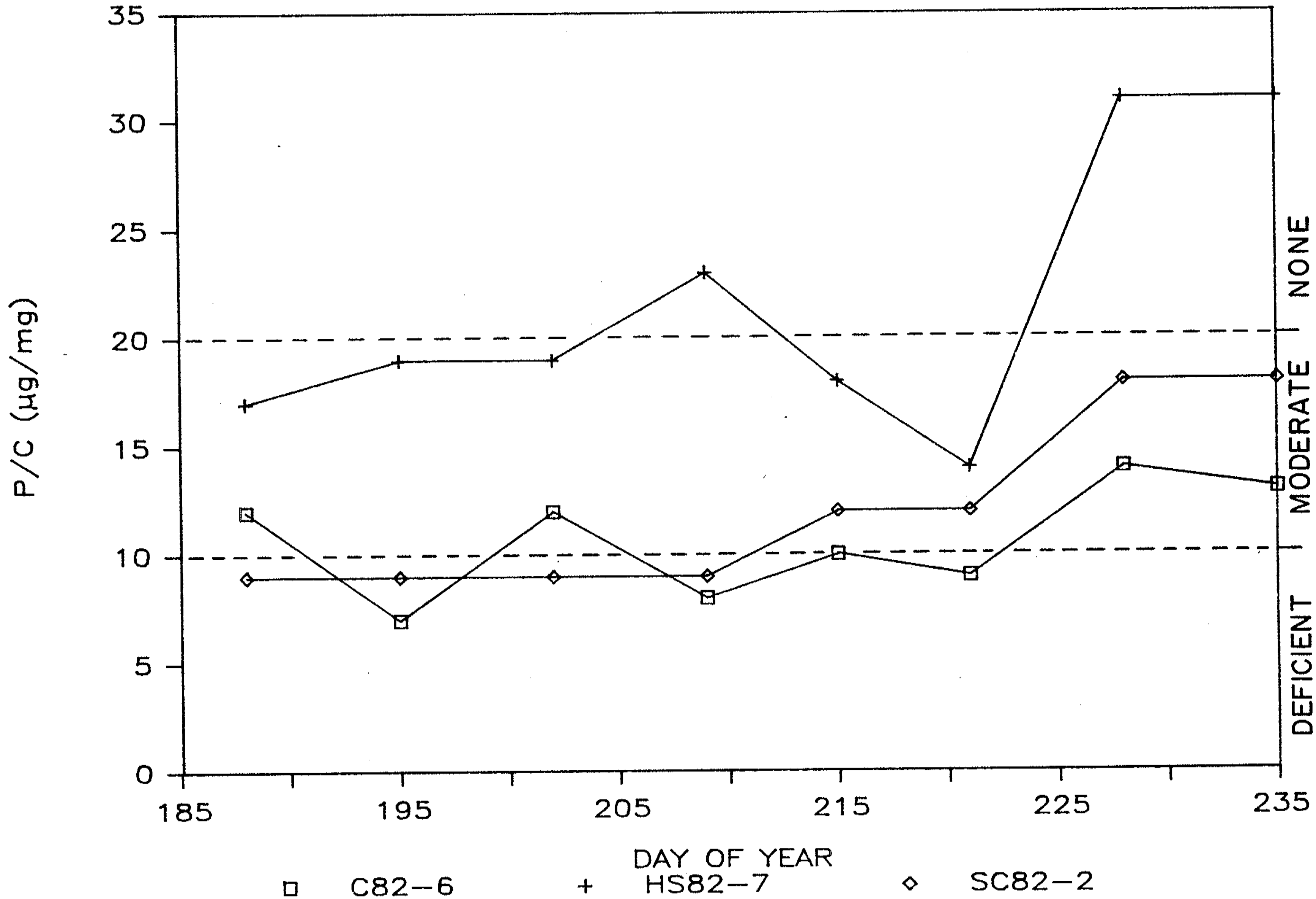

Pase (µmole P/h/µg chl)
0.045
0.04
0.035
0.03
0.025
0.02
0.015
0.01
0.005
0
188
192
196
200
204
208
212
216
220
DAY OF YEAR
SEVERE DEFICIENCY
M
N
C82-6
HS82-7
SC82-2
L82-9

FIGURE 25. Seasonal pattern of the particulate P/C ratio in the 1982 sediment limnocorral experiments. The broken horizontal lines indicates the occurrence of severe, moderate, and no P deficiency in algae as given by Healey and Hendzel (1980). C = control, HS = high sediment, and SC = screen covered. Day 190 is July 9 and day 240 is August 28. All limnocorrals had natural bottoms.



P/C (µg/mg)
35
30
25
20
15
10
5
0
185
195
205
215
225
235
DAY OF YEAR
NONE
MODERATE
DEFICIENT
□ C82-6
+ HS82-7
◇ SC82-2

FIGURE 26. Seasonal pattern of the particulate N/P ratio in the 1982 sediment limnocorral experiments. The broken horizontal line indicates the occurrence of P deficiency in algae as given by Healey and Hendzel (1980). C = control, HS = high sediment, and SC = screen covered. Day 190 is July 9 and day 240 is August 28. All limnocorrals had natural bottoms.

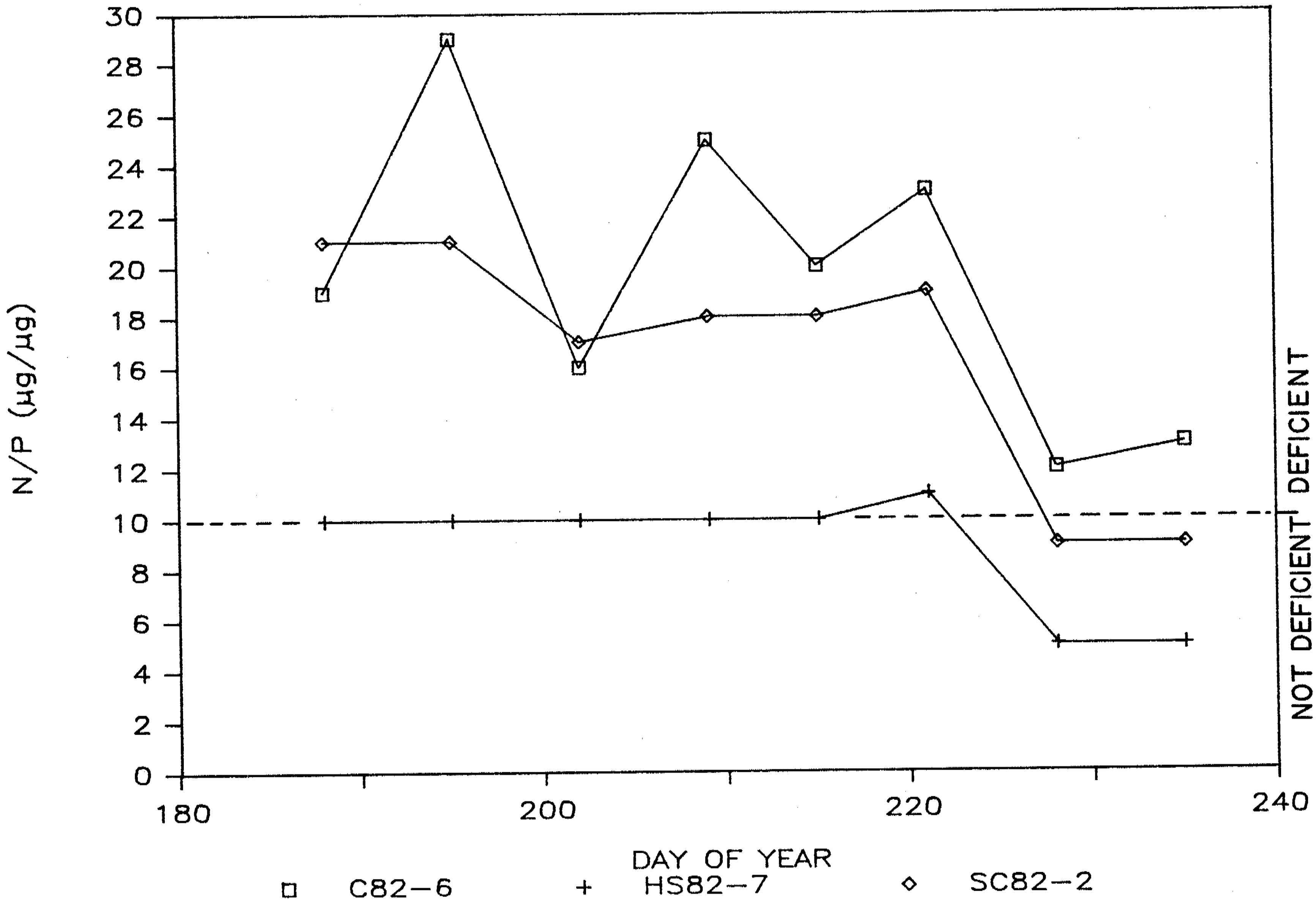

30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
N/P (µg/µg)
180
200
220
240
DAY OF YEAR
C82−6
HS82−7
SC82−2
DEFICIENT
NOT DEFICIENT

FIGURE 27. Seasonal pattern of alkaline phosphatase activity (Pase) normalized to chlorophyll a (chl) in the 1981 P and N limnocorral, control limnocorrals, and lake. The broken horizontal line indicates the occurrence of severe P deficiency in algae as given by Healey and Hendzel (1980). C = control, PN = phosphorus and nitrogen, L = lake. Day 190 is July 9 and day 240 is August 28. All limnocorrals except C81-1 had plastic bottoms.

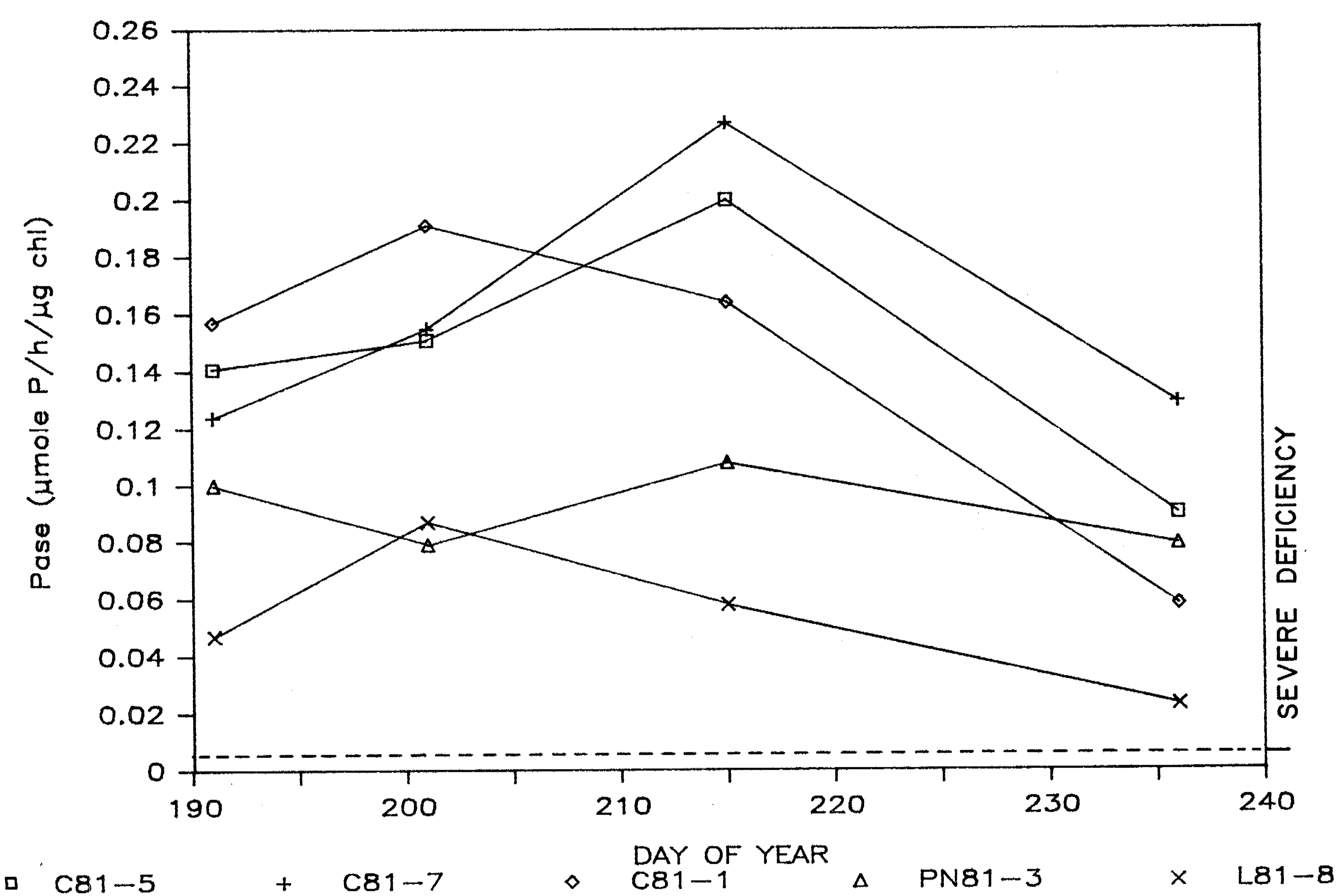
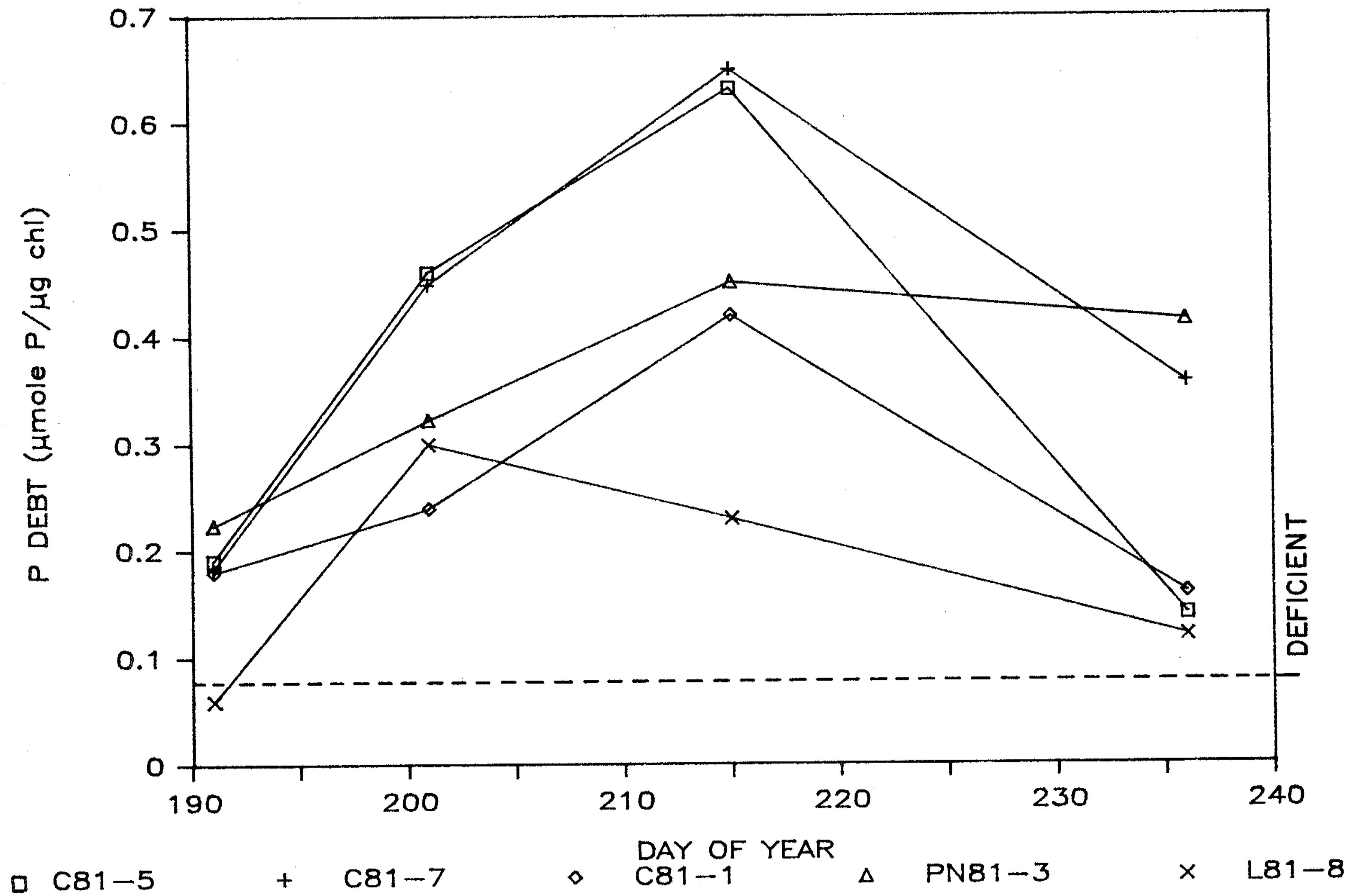

0.26
0.24
0.22
0.2
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Pase (µmole P/h/µg chl)
190
200
210
220
230
240
DAY OF YEAR
SEVERE DEFICIENCY
C81-5
C81-7
C81-1
PN81-3
L81-8

FIGURE 28. Seasonal pattern of P debt normalized to chlorophyll a (chl) in the 1981 P and N limnocorral, control limnocorrals, and lake. The broken horizontal line indicates the occurrence of P deficiency in algae as given by Healey and Hendzel (1980). C = control, PN = phosphorus and nitrogen, L = lake. Day 190 is July 9 and day 240 is August 28. All limnocorrals except C81-1 had plastic bottoms.



P DEBT (µmole P/µg chl)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
190
200
210
220
230
240
DAY OF YEAR
DEFICIENT
□ C81-5
+ C81-7
◇ C81-1
△ PN81-3
× L81-8

Each year the lake had the highest mean ATP/C ratio.

DISCUSSION

Sediment as a nutrient source

The type of sediment added to the limnocorrals was a glacial-lacustrine, silty clay originally deposited in glacial Lake Agassiz 12,000 years ago. The sediments are mainly inorganic, very fine grained and greyish in colour. There has been little opportunity for these permanently frozen sediments to become enriched in organic matter. The N:P ratio in these sediments is low (about 1.0 by weight) relative to the ratio of these nutrients in organic matter. For example, Healey (1975) reports a wide range of N:P ratios in algal cultures, depending on the degree of nutrient deficiency, but none below 2.0. Because the N:P ratio in the sediments is low and because there is little history of nitrogen limitation in Southern Indian Lake (Guildford 1978, Healey and Hendzel 1980), it was expected that P associated with the sediments would be more likely to affect the nutrient status of the algae than N.

Williams et al. (1980) found a good correlation between NaOH extractable P in a variety of sediments from in and around Lake Erie and algal growth in cultures where the sediments were the sole source of P. Fluvial sediments and sediments taken from the lake itself had relatively high proportions of NaOH extractable P (20-37%) and could support growth of P starved *Scenedesmus quadricauda*. However sediments from eroding bluffs on the north shore of Lake Erie contained only 5% NaOH extractable P and this was not adequate to sustain algal growth. The SIL shoreline sediment added to the sediment limnocorrals appears similar to the Lake Erie bluff sediment. Both have a high proportion of clay and contain about 0.6 mg g^{-1} dry weight total P. Because 5% of the bluff sediment total P was inadequate to support algal growth (even though total sediment concentrations in Williams experiments were greater than in the SIL limnocorrals), it is unlikely that the 2% readily available P (based on distilled water extractions) from SIL sediments would have much impact on algal nutrient status even if the 2% is an underestimate. Kelly et al. (1978) measured 30-400% increases in total P in five lakes in Nova Scotia during the construction phase of a hydroelectric project. However, in all the lakes chlorophyll decreased. Kelly suggested that chlorophyll decreased because increased suspended sediments reduced light penetration.

Reduction of light by sediments

I_{24} values in the sediment limnocorrals were about half those of the controls. Light reduction in the sediment limnocorrals was clearly caused by the addition of sediment. I_{24} is a function of depth and k. Depth in the limnocorrals was fairly similar (3.2 m +/- 0.5 m); therefore I_{24} was primarily controlled by k. In the sediment treatment limnocorrals, k varied directly with TSS (Fig. 6). Partitioning of k revealed that over 50% of k was due to light scattering in the sediment limnocorrals. Partitioning also showed that the lake stations were less transparent than the controls because of suspended sediments. This was due in part to the restricted water circulation in the limnocorrals. Although the limnocorrals were well mixed vertically, there was no new sediment-laden water introduced to the control limnocorrals to replace sedimentation losses. In 1981, all but C81-1 and LM81-2 had plastic bottoms so there was no mixing with the lake bottom sediments. PN81-3 was also less transparent than the controls; however, in this case high chlorophyll concentrations were responsible.

To determine if the low I_{24} values found in the sediment limnocorrals might be limiting algal growth, light levels in the sediment limnocorrals were compared to light intensities used to create light limitation for some species of algae in the laboratory (Table 12). The lowest mean I_{24} value in the sediment-treated limnocorrals (7.5 E m^{-2} d^{-1}) would have been light limiting to some species but not to others.

Biomass indicators

It is difficult to measure accurately algal biomass in natural samples. Chlorophyll a, suspended carbon and nitrogen, and ATP were measured as biomass indicators for the limnocorral experiments. Suspended C, N and chlorophyll a are relatively easy to measure; however, they do not distinguish between living and dead material (Wetzel 1975, Hallegraeff 1977). Chlorophyll a is found only in photosynthetic organisms; however, laboratory experiments show that the chlorophyll a content of cells can be quite variable depending on environmental conditions such as light intensity (Rhee and Gotham 1981b, Zevenboom 1980), temperature (Rhee and Gotham 1981a) and nutrient status (Eppley and Renger 1974, Healey 1985). In the limnocorral experiments there were wide ranges of light intensities and nutrient status; therefore, the chlorophyll data must be interpreted with this in mind.

A major concern with the suspended C analyses was that the large quantities of sediment added to the three sediment limnocorrals would contain large enough amounts of detrital carbon to mask changes in

TABLE 12. Some light intensities below which light is limiting in laboratory cultures.

Species	Light ($E\ m^{-2}\ d^{-1}$)	Temperature	Reference
Thalassiosira fluvatilis	8.99	20	Laws and Bannister (1980)
Ceratium furca	2.29	20	Meeson and Sweeney (1982)
" "	1.27	10	"
Gonyaulax polyedra	2.86	20	"
" "	1.53	10	"
Synura sphagnicola	4.75	5-20	Healey (1983)
Phaeodactylum tricornutum	10.48	23	Fawley (1984)
Synechococcus linearis	10.20	22	Healey (1985)

living carbon. A comparison of mean chlorophyll/C ratios from net and seston samples from sediment limnocorrals (LS81-4 and HS81-6) showed the seston samples had no more suspended C relative to chlorophyll than the net samples (Table 13). It was expected that if detrital carbon was abnormally high in the sediment limnocorrals, the chlorophyll/C ratios in the seston samples would be lower than in the net samples. A similar comparison by Healey and Hendzel (1980) on samples from SIL gave the same results.

ATP begins to breakdown immediately when a cell dies, so it should be a good estimator of living matter in a natural water sample. The procedure for ATP extraction and measurement is more complex than that for suspended C and chlorophyll a and the samples must be extracted quickly and skillfully to ensure ATP is not lost. Because all living matter contains ATP, the estimate will include bacteria and small zooplankton as well as photosynthetic organisms. The ATP content of cells has been shown to vary significantly with nutrient status especially P deficiency (Sakshaug 1980, Healey and Hendzel 1980). Experiments described in Appendix 1 showed that, in natural water samples and in a uni-algal culture, high concentrations of suspended sediment interfered wth the extraction of ATP resulting in significant underestimation of ATP. For these reasons, it was decided not to use the ATP data (given in Appendix 7) to estimate biomass. Data from samples that did not contain high concentrations of suspended sediments were used in normalizing the nutrient status indicators alkaline phosphatase, P debt and N debt. In the sediment limnocorrals nutrient status indicators were normalized to chlorophyll a. The biomass response in the limnocorral experiments must be assessed using chlorophyll a and

TABLE 13. Mean chlorophyll/carbon ratios (ug mg^{-1}) in seston and net samples in 1981. Net plankton are >10 um.

Limnocorral	Treatment	Chlorophyll/carbon Seston	Net	Bottom type
C81-1	control	5.4	6.9	natural
LM81-2	moss-peat (52 Kg)	5.4	6.9	natural
C81-5	control	4.6	5.1	plastic
C81-7	control	4.3	4.0	plastic
LS81-4	sediment (33 Kg)	5.7	7.1	plastic
HS81-6	sediment (52 Kg)	5.9	5.4	plastic
PN81-3	P&N	6.0	5.4	plastic
L81-8	lake	5.7	6.4	

suspended C results. The suspended N data were very similar to the suspended C results.

It was expected that, if the SIL shoreline sediments added to the limnocorrals were a readily available source of P, the P might be apparent as increased algal biomass. P added to PN81-3 caused a three fold increase in suspended C and chlorophyll above the control limnocorrals. It is not clear that there was any significant biomass increase in response to the sediment addition. Based on the first years experiments it appeared that the lower concentration of sediment (LS81-4) may have stimulated biomass while the higher sediment concentration (HS81-6) decreased biomass. In 1982 the high sediment concentration (HS82-7) increased biomass. HS81-6 and HS82-7 had the same weight of sediment added but the resulting light environments were different because the 1982 limnocorrals were shallower than those in 1981. If the chlorophyll a increases in LS81-4 and HS82-7 were solely in response to reduced light levels rather than available P, then screen covered SC82-2, designed to have the same mean water column light intensity as HS82-7, should show similiar chlorophyll a values. SC82-2 had 23% and HS82-7 had 46% more chlorophyll a than the control. This suggests that chlorophyll in HS82-7 increased due to the combined effect of decreased light and increased P from the sediments.

It was thought that the fine- grained sediments might increase bacterial biomass as a result of increased surface area. The results of two sets of samples showed that except for PN81-3 the bacterial numbers were not significantly different in any of the plastic bottomed limnocorrals.

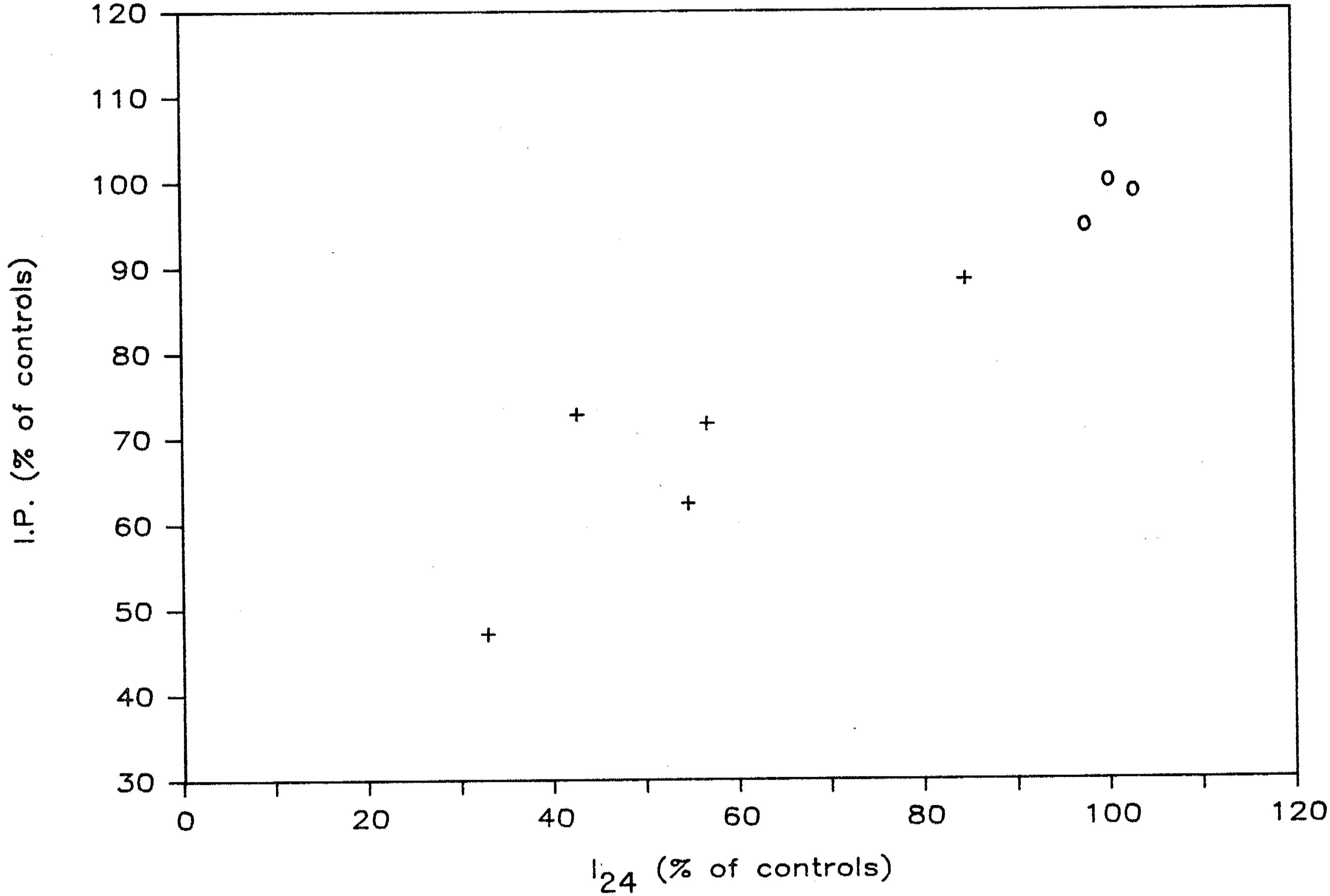
Primary Productivity

Integral primary productivity was 25 to 50% lower in the sediment limnocorrals than in the controls. This appears to be the result of lower mean water column light intensity (I_{24}), caused by the sediment, rather than any physiological interaction between the sediment and the algae. This can be illustrated in two ways. Firstly, the screen-covered limnocorral (SC82-2), which was designed to have the same I_{24} as HS82-7 but without sediment addition, had similar integral production to HS82-7 (Fig. 17) during the first half of the season until the screen-covered limnocorral became P deficient. Secondly, integral production which is dependent on I_{24}, alpha^B, and P_m^B varied consistently with I_{24} in the sediment limnocorrals but not with the physiological parameters, alpha^B or P_m^B (Fig. 29).

The relationship between I_{24} and integral productiviy indicates that the algae in the sediment limnocorrals were light limited to varying degrees with HS81-6 being the most light limited. HS81-6 was the only limnocorral with alpha^B and P_m^B values greater than the control. This may be an indication of adaptation to lower light. Prézelin (1981) and Falkowski (1980) give examples of algae that demonstrated higher rates of light limited photosynthesis (alpha^B) and/or light saturated production (P_m^B) when moved from high to lower light.

The large overall difference in integral production between 1981 and 1982 can be explained by the decrease in alpha^B. However it is not clear why alpha^B values were so much lower in 1982.

FIGURE 29. The relatioship between daily integral primary productivity (I.P.) and mean daily water column light intensity (I_{24}) in the sediment, screen covered, and control limnocorrals from both 1981 and 1982. The data are time weighted means expressed as a percent of the appropriate controls in order to intercompare the different years. Individual control limnocorral values are expressed as a percent of the mean of controls for each year in order to show the range of variability between controls. The control limnocorrals are denoted by the symbol "O".


I.P. (% of controls)
120
110
100
90
80
70
60
50
40
30
0
20
40
60
80
100
120
I_{24} (% of controls)

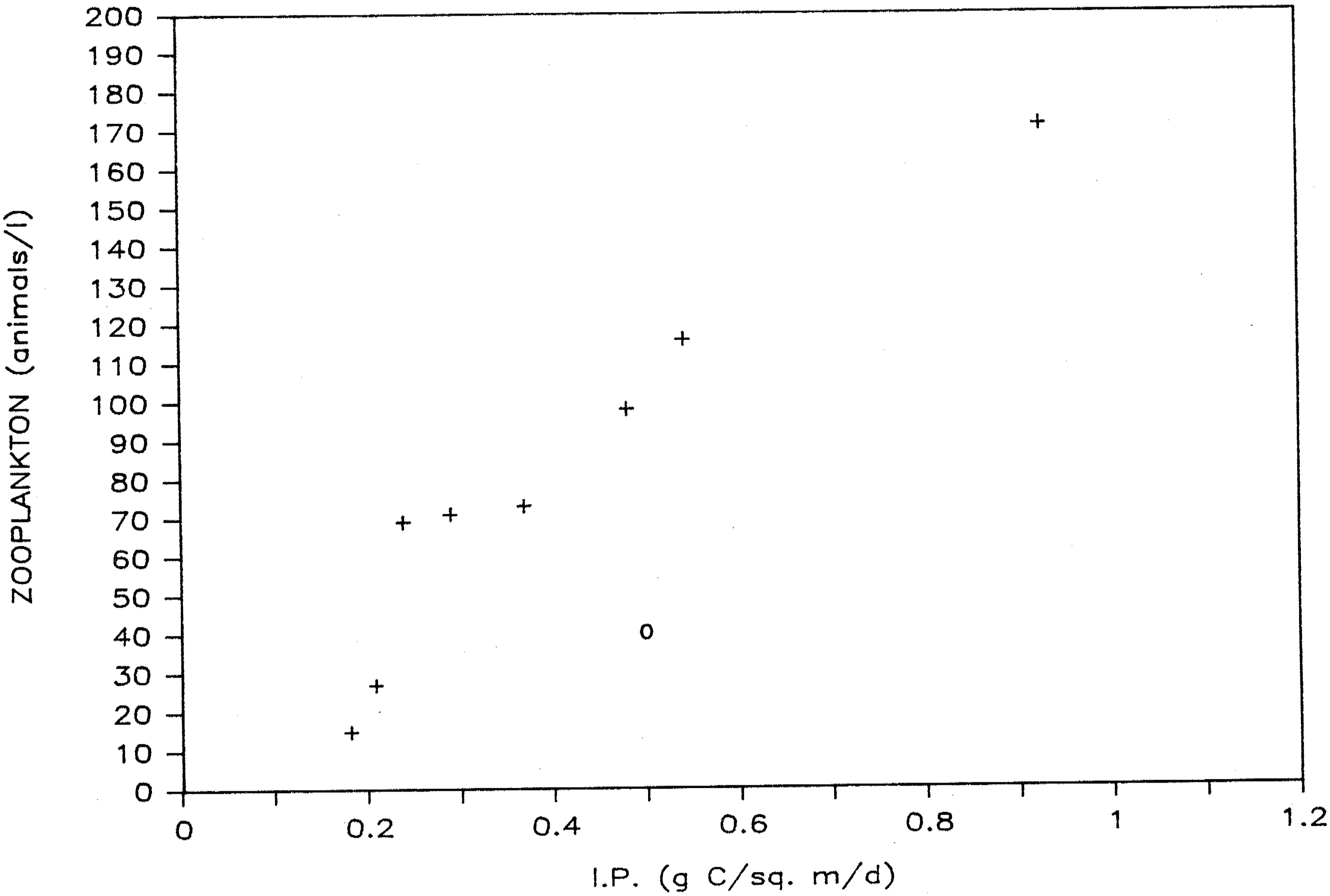
Although light reduction resulted in significantly less integral production in LS81-4, HS81-6, HS82-7 and SC82-2 compared to the controls, there was no corresponding decrease in biomass except in HS81-6. As discussed previously, mean chlorophyll a and suspended carbon values in the sediment limnocorrals were not remarkably different from the controls. One possible explanation for this descrepancy between production and biomass is that higher rates of zooplankton grazing in the controls accounted for the lower biomass concentrations found there. There is an excellent correlation between integral productivity and zooplankton abundance in sediment and control limnocorrals (Fig. 30).

Loss rates of biomass, caused by sedimentation, might also be accelerated in the control limnocorrals if the algae are in poor condition due to nutrient depletion. Titman and Kilham (1976) found algae sank faster when nutrient poor. The SIL control limnocorrals were definitely more nutrient-limited than the sediment limnocorrals.

Nutrient Status

Nitrogen did not appear to be a limiting nutrient in either the control or sediment limnocorrals at any time during the summers of 1981 or 1982. Only when PN81-3 was enriched with P alone was there a suggestion that N might be limiting. However, N deficiency did not replace P deficiency. PN81-3 remained severely P deficient throughout the season. Nitrogen fixation by blue-green algae may have prevented severe N limitaton. N_2 fixers were present before the N treatments were stopped and there was a doubling in biomass of N_2 fixers after N treatments ended (Kling, personal communication).

FIGURE 30. The relationship between daily integral primary productivity (I.P.) and number of zooplankton in the sediment, screen covered, control and P and N limnocorrals from 1981 and 1982. The data are mean values for each year. The control limnocorral C81-1 (denoted by the symbol "o") had an unusually low number of zooplankton. This may have been due to the abnormally high number of fish in this limnocorral (Hecky unpublished data).


ZOOPLANKTON (animals/l)
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
0
0.2
0.4
0.6
0.8
1
1.2
I.P. (g C/sq. m/d)

The results show that in general, P was the limiting nutrient in the limnocorrals. This is not surprising since P has been shown to be the nutrient most likely to be limiting in lakes (Schindler 1976, Healey and Hendzel 1980). Even the P&N enrichment limnocorral remained P deficient although to a lesser degree than the controls.

The P nutrient status indicators show that shoreline sediment can reduce P deficiency. There was no P deficiency in HS82-7. In LS81-4 and HS81-6, although P deficiency was still present, it was less than that in the controls; and the limnocorral with the higher sediment concentration was less P deficient than the low sediment limnocorral. It is not clear from the results whether P deficiency was lower because P was made available from the sediments or because the demand for P was lower due to decreased light levels and the resulting lower rates of primary productivity or both.

The sediment extraction experiment discussed previously showed that about 2% of total sediment P could be extracted in distilled water. The mean SRP data from the sediment limnocorrals (Table 14) also indicate that a small amount of sediment P is readily extractable. If 2% of total sediment P was released each time sediment was added to HS81-6 the PO_4 concenration in the limnocorral would increase by about 0.007 umole L^{-1}. The SRP data show the sediment limnocorrals have 0.01-0.02 umole L^{-1} more SRP than the control. These changes in P concentration are quite small and I would not expect a significant growth response by the algae to these changes based on growth rates of P limited algae in the literature (Rhee 1973, Tilman and Kilham 1976). In fact there was no significant increase in biomass in the sediment limnocorrals, productivity was less than the controls and, although reduced, P

TABLE 14. Mean SRP and TDP for 1981. Analyses were done at SIL chemistry lab (Hecky unpublished data).

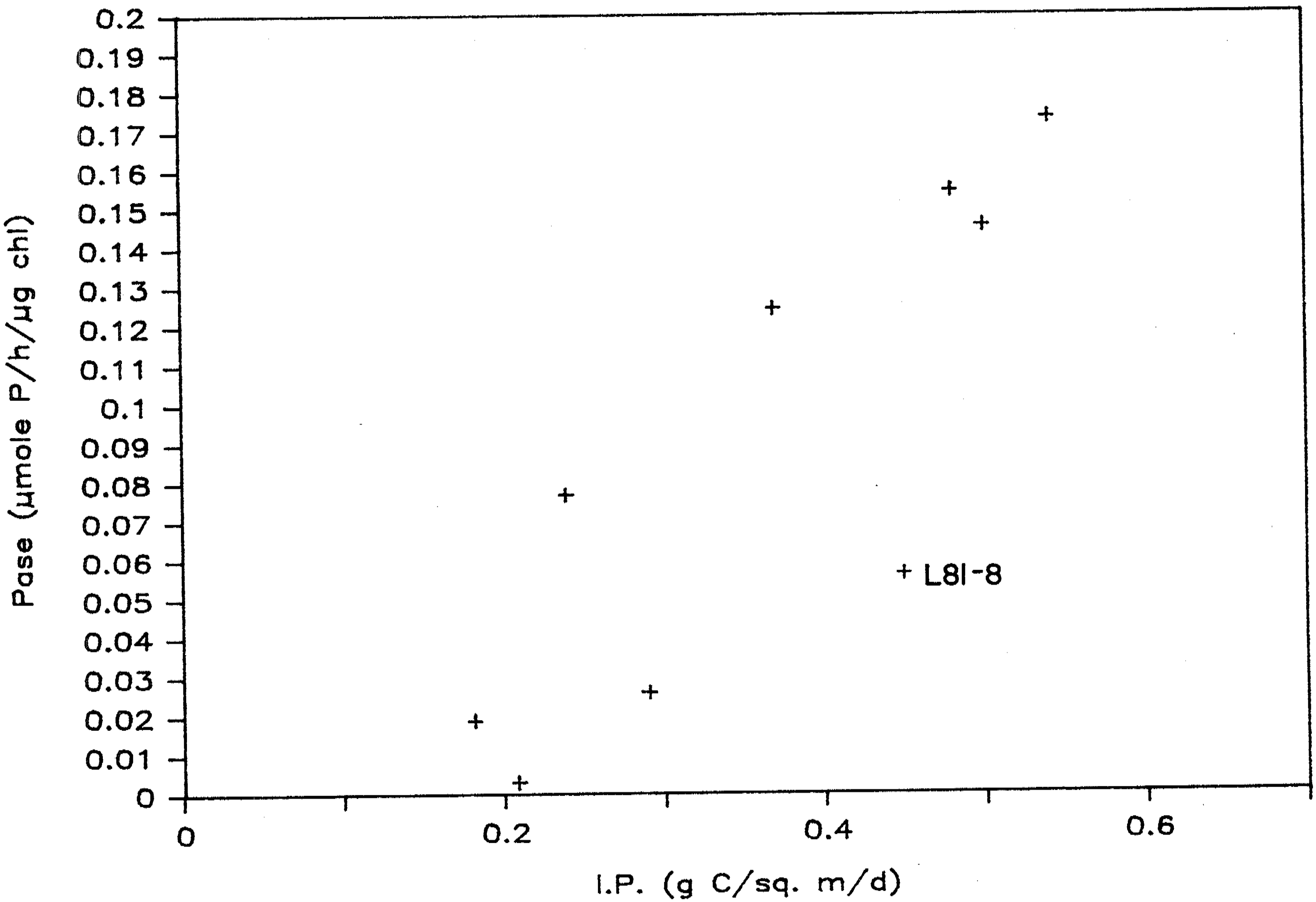
Limnocorral	Treatment	SRP (umole L^{-1})	TDP (umole L^{-1})
C81-1	control	0.02	0.11
LM81-2	moss-peat (63 Kg)	0.12	0.25
C81-5	control	0.03	0.09
C81-7	control	0.02	0.10
LS81-4	sediment (33 Kg)	0.04	0.12
HS81-6	sediment (52 Kg)	0.04	0.13
PN81-3	P&N	0.03	0.11
L81-8	lake	0.03	0.13

deficiency was still present in 1981. Therefore it seemed that the P released from the sediments either was not in a form the algae could use or was in insufficient amount to have a detectable effect on the algae. The culture experiments of Williams et al. (1980) showed P starved Scenedesmus did not grow appreciably with shoreline sediments as a sole P source even when added at greater concentrations than those used in the limnocorral.

In 1982 the screen limnocorral experiment was especially designed to determine whether the sediments relieved P deficiency by releasing P or by reducing light and thus P demand. The nutrient status results support the hypothesis that P was released. Both limnocorrals had similar mean light intensities yet the screen limnocorral remained P deficient. It should be noted however that the degree of P deficiency experienced by all the limnocorrals in 1982 was much lower than 1981. So, although the screen limnocorral was in the P deficient range, neither the screen limnocorral nor the control was nearly as P deficient as any of the 1981 limnocorrals. Thus only a small amount of P would be required to relieve P deficiency.

The major influence of the sediments on nutrient status was through light reduction. The decrease in light intensity due to sediment addition caused a decrease in integral productivity (Fig. 29); and, as integral production decreased so did P deficiency (Fig. 31). Rather than the sediments reducing P deficiency by releasing P, the sediments reduced light which reduced integral production so there was less P demand and therefore less P deficiency.

FIGURE 31. The relationship between daily integral primary productivity (I.P.) and alkaline phosphatase activity (Pase) in the sediment,screen covered, and control limnocorrals from 1981 and 1982. The data are time weighted mean values for each year. The lake station (L81-1) which fell well outside the relationship is noted.



0.2
0.19
0.18
0.17
0.16
0.15
0.14
0.13
0.12
0.11
0.1
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
Pase (µmole P/h/µg chl)
L8I-8
0
0.2
0.4
0.6
I.P. (g C/sq. m/d)

Interactions of light and nutrients

The productivity data showed that in all three sediment limnocorrals and in the screen limnocorral, I_{24} was well below Ik and productivity was light limited to varying degrees. Since P deficiency was reported in 3 of these 4 limnocorrals it appears that two factors, light and a nutrient (P), were limiting a population simultaneously. Rhee and Gotham (1981a) and Healey (1985) have shown in laboratory cultures that a single species can be both light and nutrient limited over a narrow range of light intensities and nutrient concentrations because, to a degree, a physical factor can compensate for a nutrient and vice-versa. In the limnocorrals this apparent simultaneous limitation may also have been a case of different species being limited by different factors such as described by Titman (1976).

The major effect of shoreline sediments added to the limnocorrals was to reduce light resulting in lower levels of integral productivity in the sediment limnocorrals and a reduced demand for P. Although productivity was higher in the controls, biomass was not much higher than the sediment limnocorrals. This descrepancy is probably due in part to zooplankton grazing. Based on the low productivity and low zooplankton numbers in the sediment limnocorrals one could speculate that increased sediment concentrations could cause significant decreases in overall productivity of similar systems.

MOSS-PEAT LIMNOCORRALS

RESULTS

Physical-chemical response to moss-peat additions

The main physical change observed after the addition of moss-peat material was in water color. The water became dark brown as a result of leached dissolved humic matter (DHM). Absorbance at 445 nm increased in proportion to the weight of moss-peat material added to the limnocorrals (Table 15) The increase was not a gradual change over time. It rose within 10 days of the moss-peat additions and remained higher throughout each summer (Figs. 32 and 33).

Increased light absorption by DHM usually resulted in slightly higher light extinction coefficients (k) in the moss-peat limnocorrals (Table 15). However, compared to the k values in the sediment limnocorrals (Table 6) these increases were small.

The C:N:P weight ratio for the moss-peat material added to the limnocorrals was approximately 960:10:1 (based on analyses in Appendix 8). The total weight of moss-peat material and individual nutrients added to the three limnocorrals is given in Table 5. Only about 2% of total carbon was carbonate. The moss-peat added much more organic carbon and nitrogen (Table 5) than the two other types of limnocorral treatment (fine-grained sediments and P and N enrichment). Two months after the moss-peat addition to LM81-2, an Eckman dredge sample of the moss-peat material recovered from the bottom of that limnocorral was analyzed for C, N and P (Appendix 9). The organic carbon content decreased about 20% while the N and P increased.

TABLE 15. Mean values for selected physical and chemical parameters measured in the moss-peat and control limnocorrals in 1981 and 1982. Fe, TDN, and TDP analyses were done at the Freshwater Institute analytical lab.

Limnocorral	Treatment	A_{455} (nm)	k (m^{-1})	Fe (umole L^{-1})	TDN (umole L^{-1})	TDP (umole L^{-1})	pH
C81-1	control	0.045	1.03	0.7	22.6	0.23	8.09
LM81-2	moss-peat (63 Kg)	0.070	1.10	1.5	26.0	0.42	7.51
OC82-5	control (1 yr old)	0.055	0.96	0.7	21.8	0.29	7.70
C82-6	control	0.062	1.13	1.1	22.6	0.32	7.99
LM82-3	moss-peat (52 Kg)	0.079	1.08	1.1	24.2	0.52	7.52
HM82-4	moss-peat (104 Kg)	0.100	1.29	1.1	27.5	0.55	7.15
OM82-8	moss-peat (1 yr old)	0.055	0.97	1.5	23.7	0.36	8.02
FM82-1	moss-peat (flooded 1976)	0.073	1.15	1.8	24.3	0.36	7.86

FIGURE 32. Seasonal pattern of absorbance at 445 nm in the 1981 moss-peat and control limnocorrals. C = control and LM = low moss. Day 170 is June 19 and day 230 is August 18.

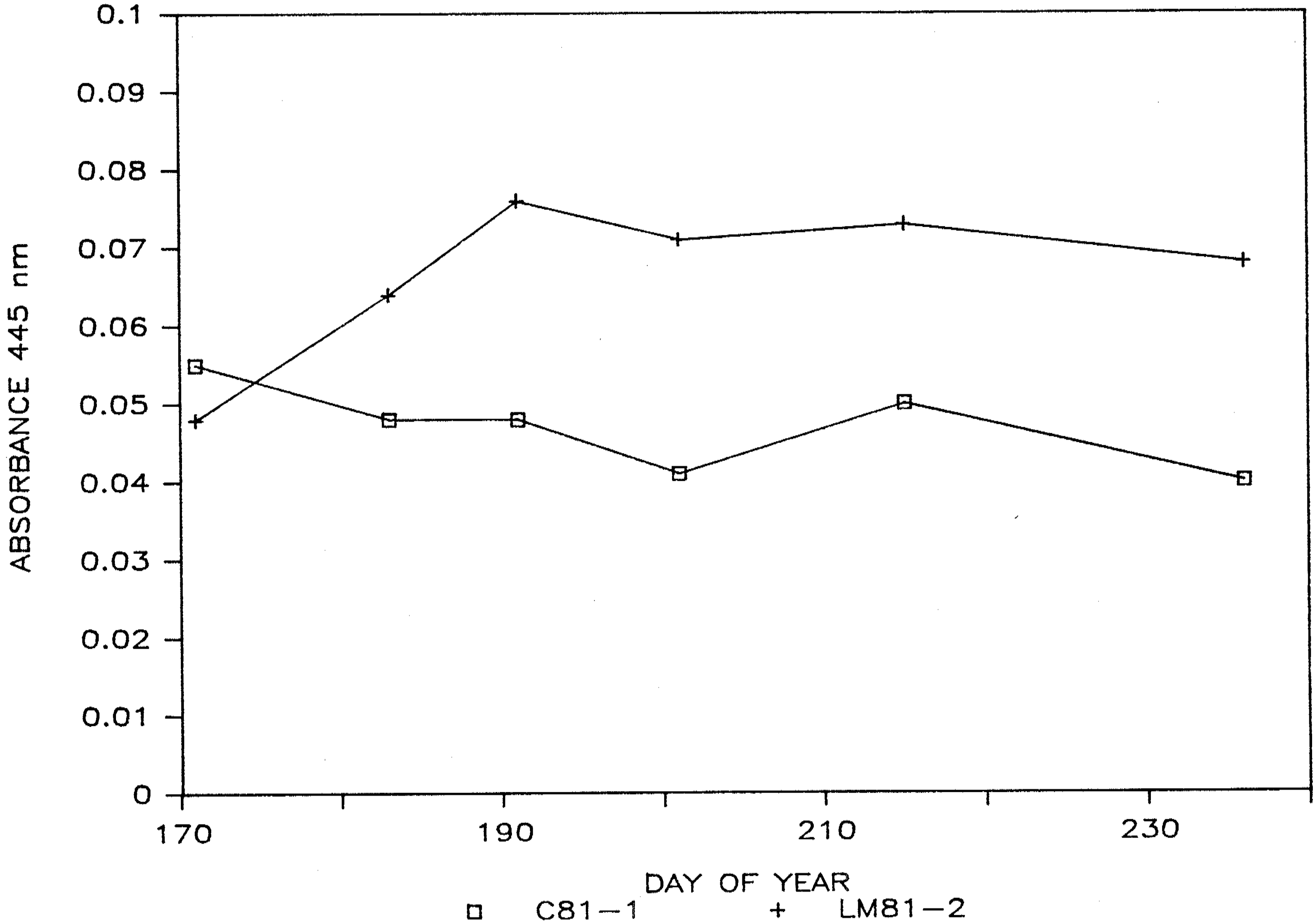
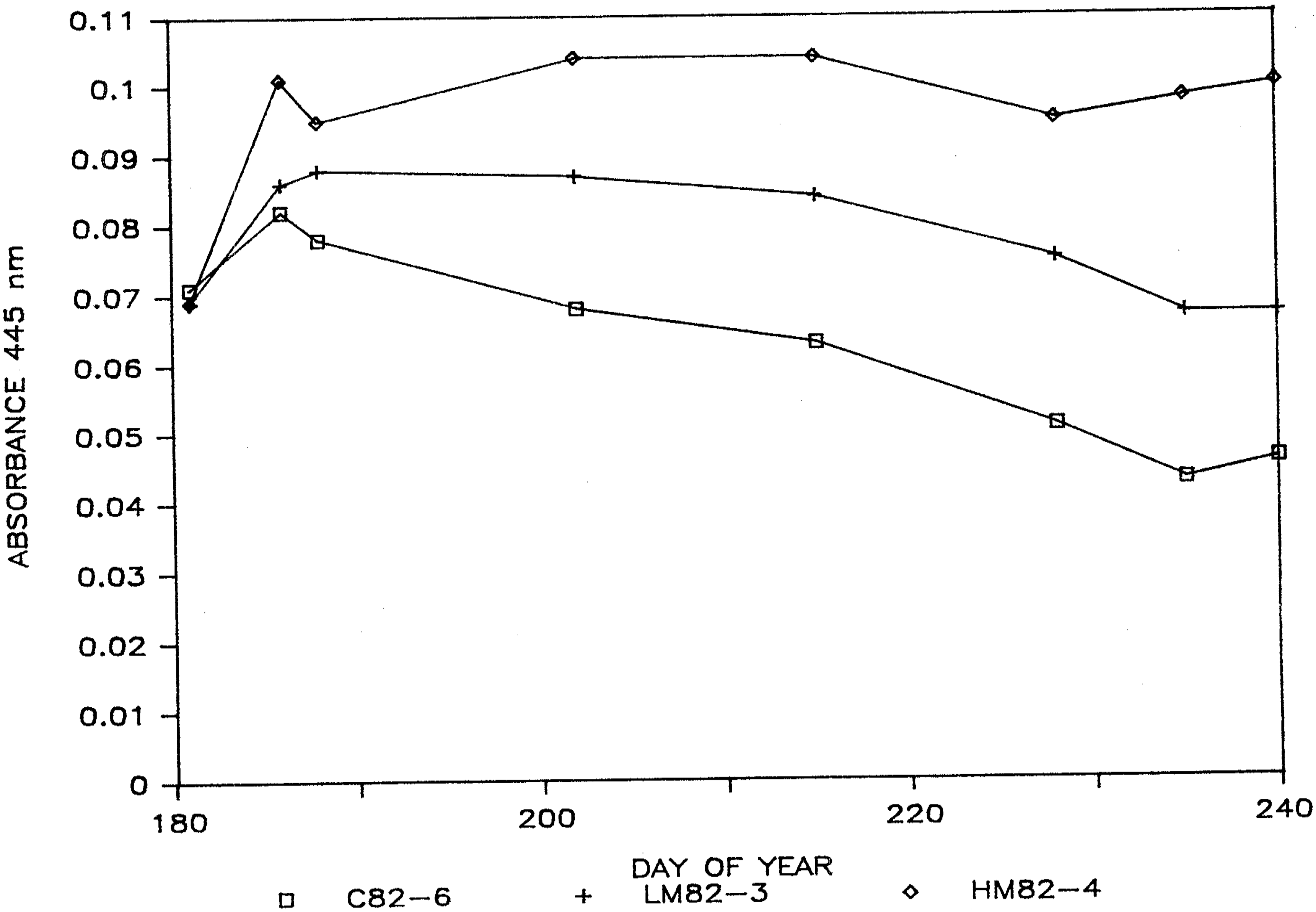

0.1
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
ABSORBANCE 445 nm
170
190
210
230
DAY OF YEAR
C81−1
LM81−2

FIGURE 33. Seasonal pattern of absorbance at 445 nm in the 1982 moss-peat and control limnocorrals. C = control and LM = low moss, and HM = high moss. Day 180 is June 29 and day 240 is August 28.


0.11
0.1
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
ABSORBANCE 445 nm
180
200
220
240
DAY OF YEAR
C82-6
LM82-3
HM82-4

In the first few days immediately following the moss-peat additions, pieces of vegetation floated at the surface of the limnocorrals. After a week most of the material disappeared, and the total suspended solids data (Fig. 34) indicated that the moss-peat limnocorral (LM81-2) did not contain an unusually high load of suspended material greater than 1 um.

The moss-peat limnocorrals contained more dissolved N and P than the controls (Table 15). These nutrients tended to increase over the summer (Figs. 35 to 38). About 50% of the TDP in the moss-peat limnocorral LM81-2 was SRP. In the control (C81-1) SRP was usually below the limit of detection (Table 14).

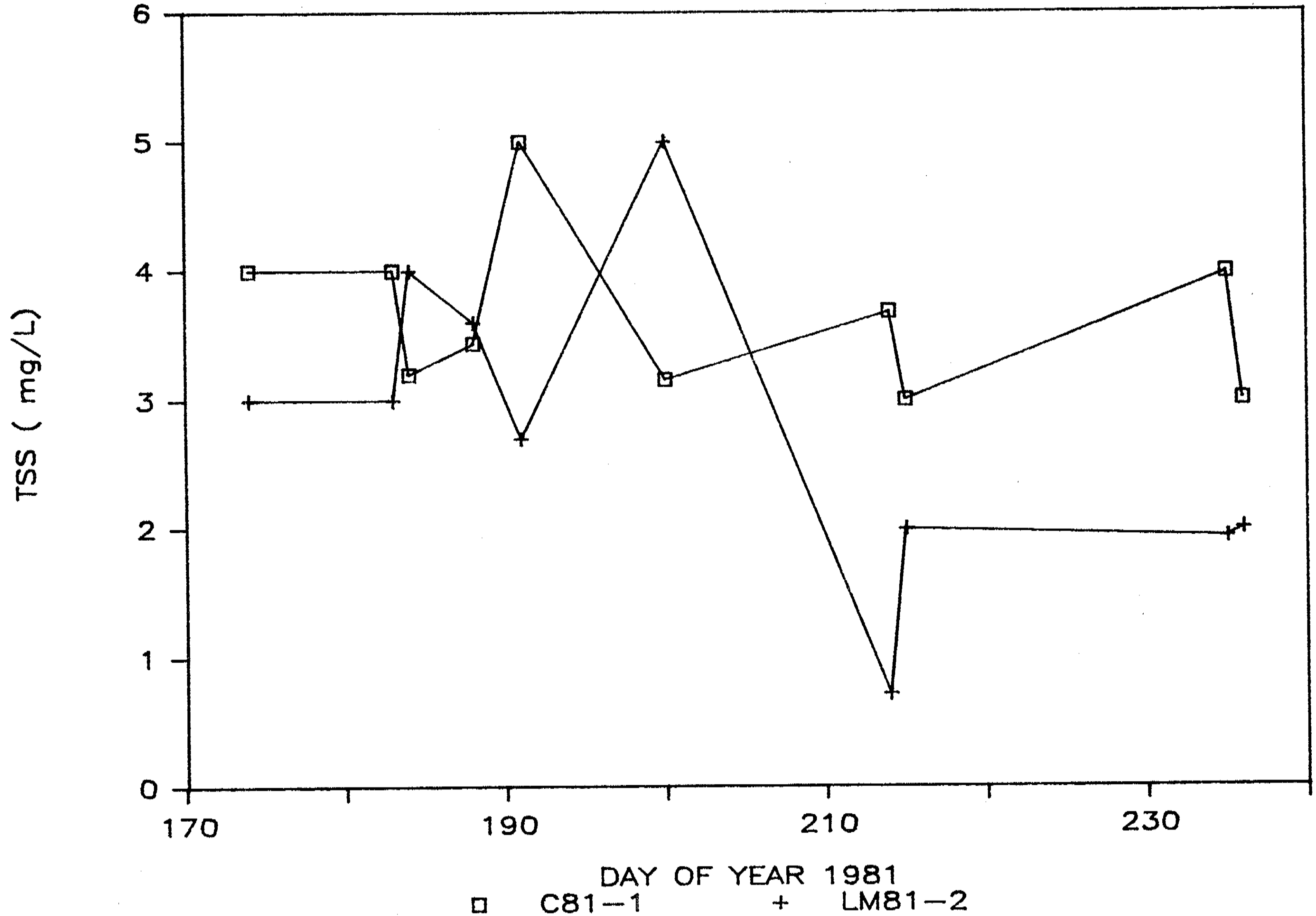
In 1981 the total Fe concentration in moss-peat limnocorral LM81-2 was double that in the control (Table 14). In 1982 there was no difference in total Fe concentration between the comparable limnocorral LM82-3 and control.

One year after the moss-peat addition, A_{445}, TDN and TDP in the limnocorral (OM82-8) containing the one year old moss were similar to the controls (Table 15). However, total Fe remained high. In the limnocorral situated over flooded shoreline (FM82-1), A_{445} and total Fe were above the controls.

<u>Biomass response to moss-peat addition</u>

Chlorophyll a and suspended carbon were used to estimate algal biomass in the moss-peat limnocorrals. As discussed in the section on sediment algal interactions there are several disadvantages to using suspended C and chlorophyll to estimate algal biomass. With respect to the moss-peat limnocorrals in particular there was concern that the

FIGURE 34. Seasonal pattern of total suspended solids (TSS) in the 1981 control and moss-peat limnocorrals. C = control and LM = low moss. Day 170 is June 19 and day 230 is August 18.



TSS (mg/L)
0
1
2
3
4
5
6
170
190
210
230
DAY OF YEAR 1981
C81-1
LM81-2

FIGURE 35. Seasonal pattern of total dissolved nitrogen (TDN) in the 1981 control and moss-peat limnocorrals. C = control and LM = low moss. Day 170 is June 19 and day 230 is August 18.

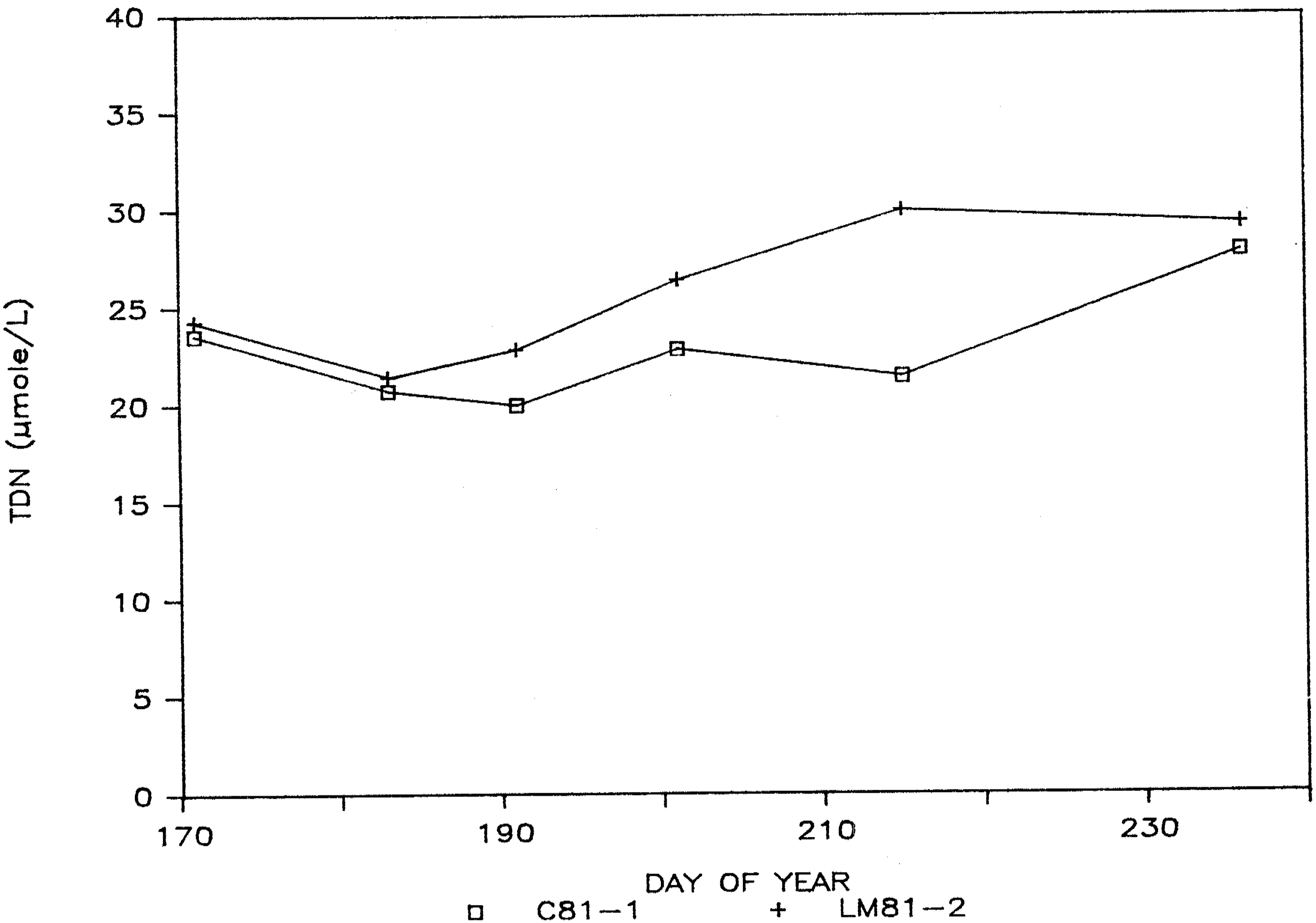

40
35
30
25
20
15
10
5
0
TDN (µmole/L)
170
190
210
230
DAY OF YEAR
C81−1
LM81−2

FIGURE 36. Seasonal pattern of total dissolved phosphorus (TDP) in the 1981 control and moss-peat limnocorrals. C = control and LM = low moss. Day 170 is June 19 and day 230 is August 18. TDP analyses were done at the Freshwater Institute analytical chemistry lab.

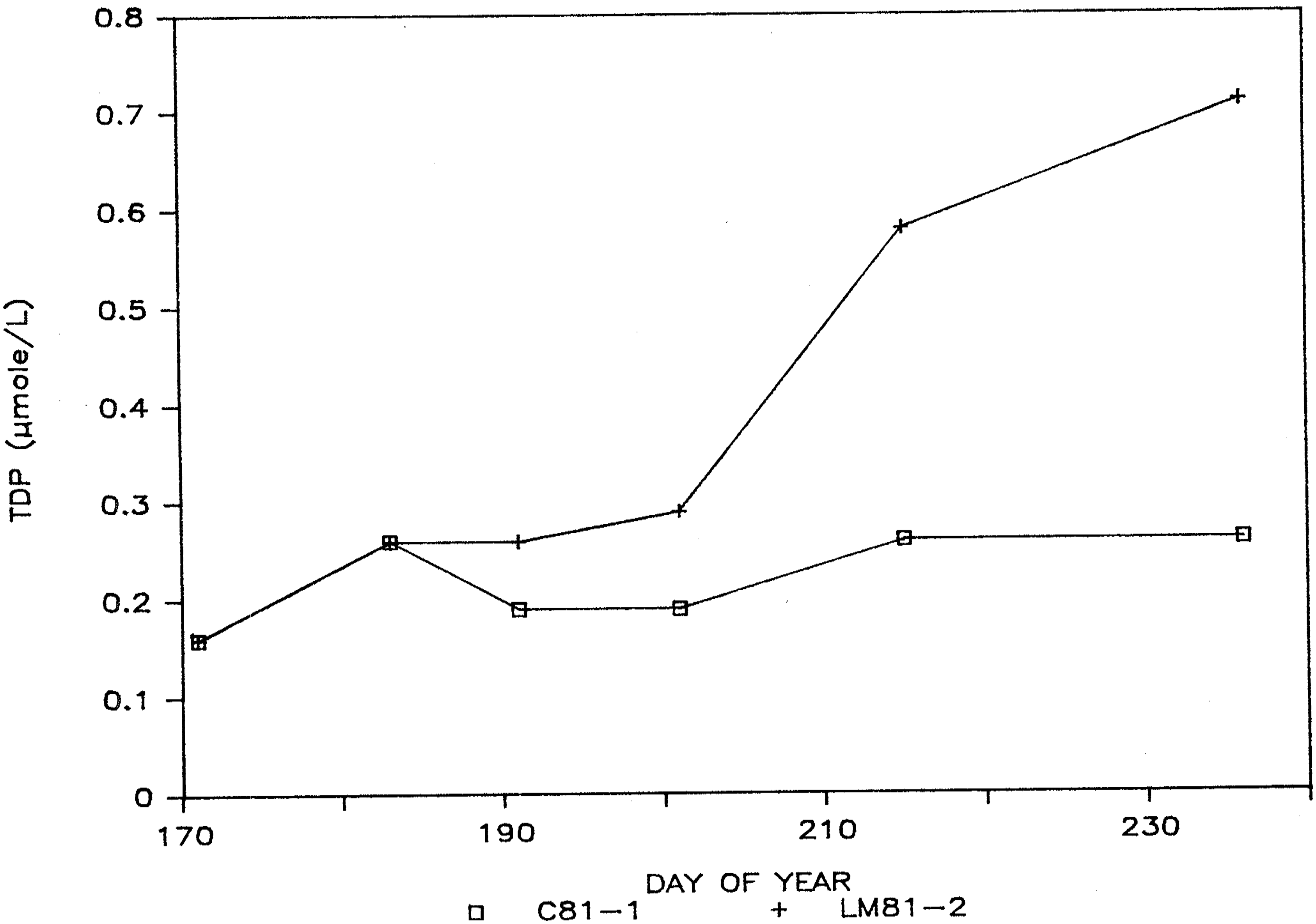

TDP (µmole/L)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
170
190
210
230
DAY OF YEAR
C81−1
LM81−2

FIGURE 37. Seasonal pattern of total dissolved nitrogen (TDN) in the 1982 control and moss-peat limnocorrals. C = control, LM = low moss, and HM = high moss. Day 180 is June 29 and day 240 is August 28.

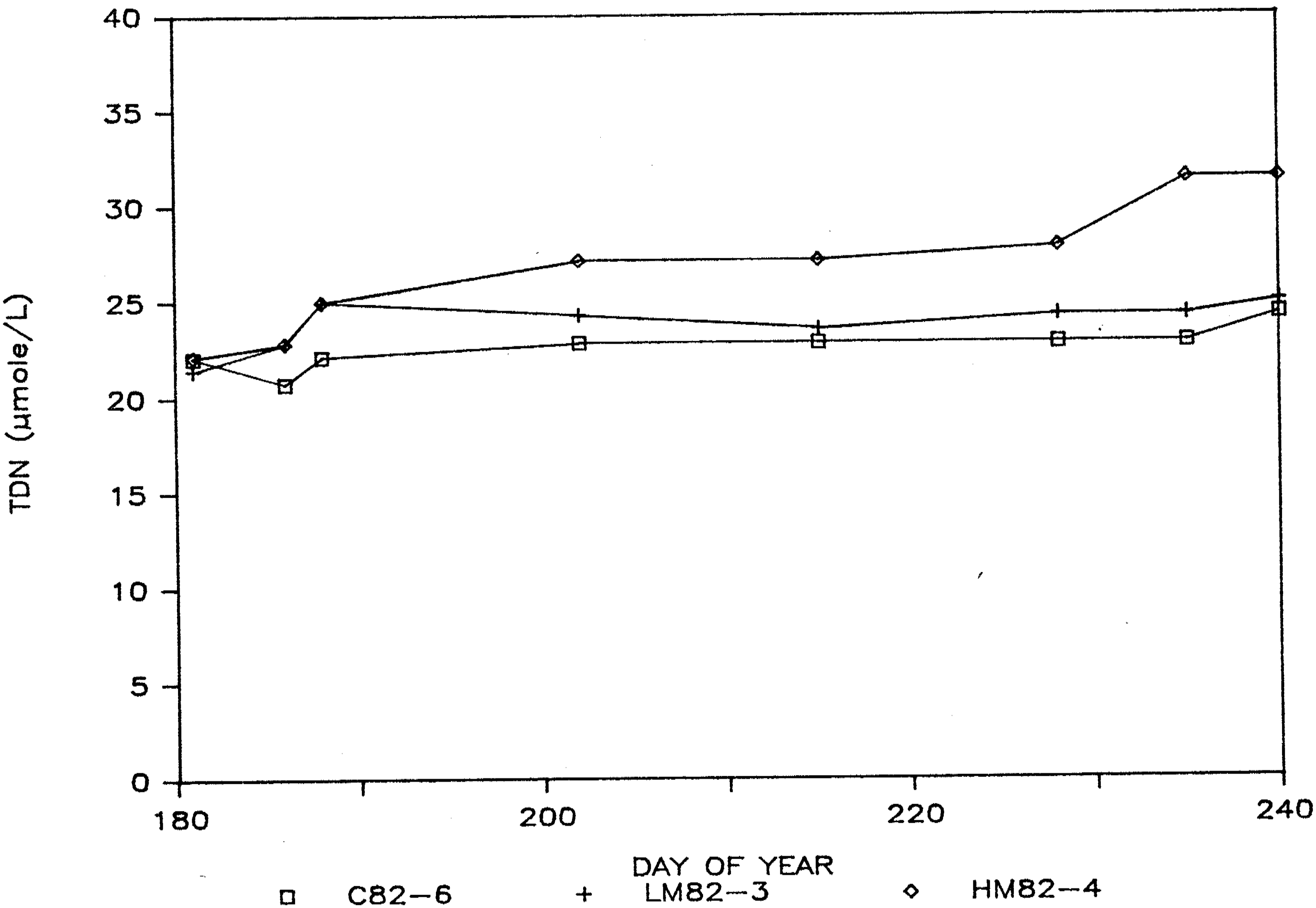
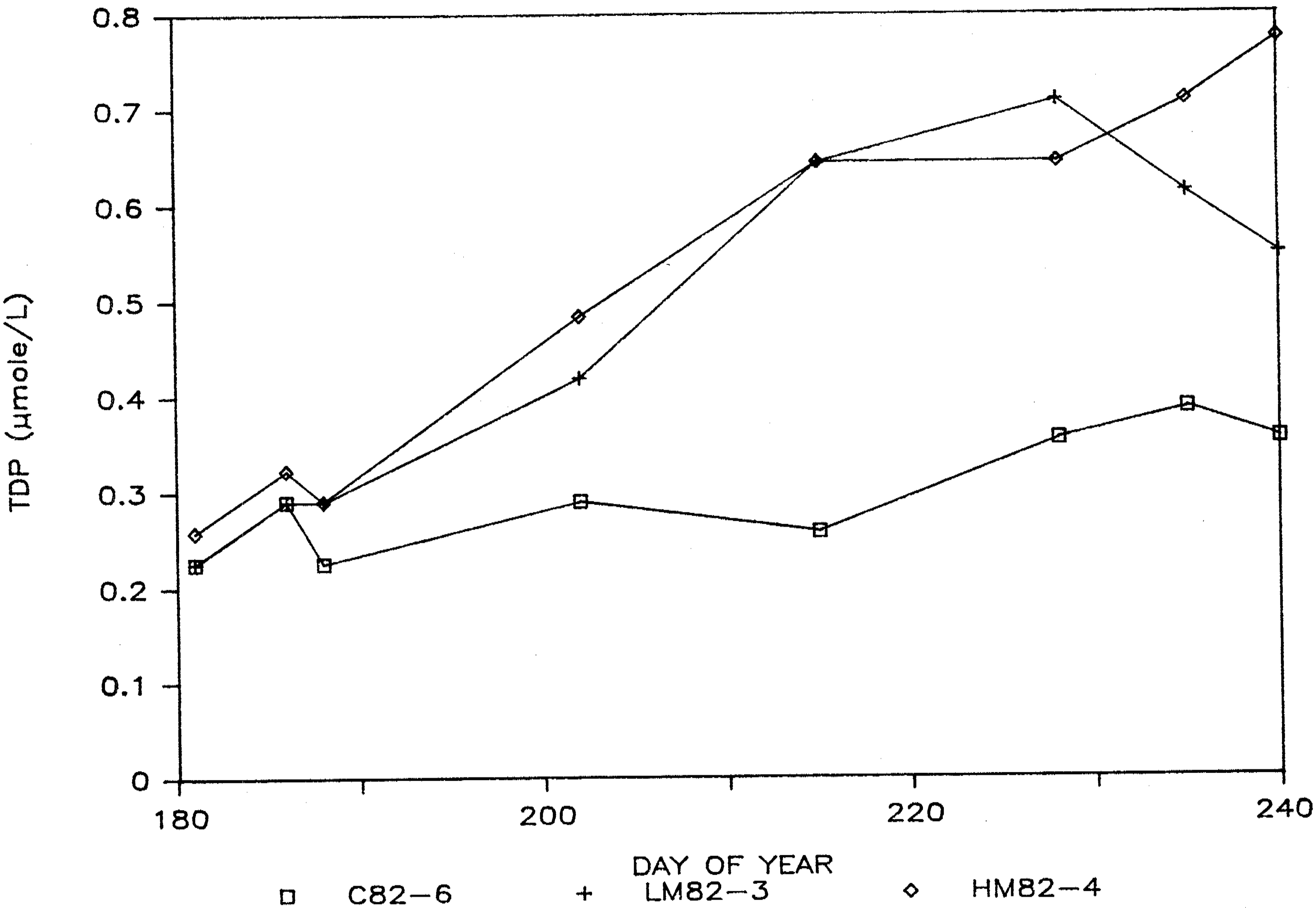

TDN (µmole/L)
DAY OF YEAR
C82–6
LM82–3
HM82–4

FIGURE 38. Seasonal pattern of total dissolved phosphorus (TDP) in the 1982 control and moss-peat limnocorrals. C = control, LM = low moss, and HM = high moss. Day 180 is June 29 and day 240 is August 28. TDP analyses were done at the Freshwater Institute analytical chemistry lab.


TDP (µmole/L)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
180
200
220
240
DAY OF YEAR
C82−6
LM82−3
HM82−4

large quantity of organic carbon added as moss-peat material would distort the suspended carbon measurements. If the moss-peat limnocorral contained significant amounts of detrital carbon smaller than 10 um, one would expect the chl/C ratio in the seston sample to be lower than the chl/C ratio in the net sample which retains particles greater than 10 um. The ratio in the seston sample was less than the net sample (Table 13); however, the mean ratios in the comparable control limnocorral were the same as in the moss-peat limnocorral. This suggests differences in chl/C ratios between seston and net samples are unrelated to the moss-peat material. Even when the weight of moss-peat added to the limnocorral was doubled (HM82-4), the chl/C ratio remained greater than the control (Table 16). In the shallowest limnocorral situated over flooded moss-peat vegetation (FM82-1), there was evidence that a significant portion of the suspended C was detritus. The chl/C ratio for FM82-1) was less than half the control (Table 16).

Because of its sensitivity to P deficiency, ATP was not used as a biomass indicator but was used to normalize P deficiency indicators.

Initially chlorophyll a and suspended C were stimulated by moss-peat material. With the lower addition of organic material (LM81-2 and LM82-3) this phase lasted only a few weeks (Figs. 39 to 42). Mean chlorophyll and suspended C in LM81-2 and LM82-3 were 30% lower than their controls (Table 16). In HM82-4 which had twice as much moss-peat as LM81-2 and LM82-3, the phase of stimulation lasted longer and mean chlorophyll and C are almost double the control. However, by the end of the experiment, chlorophyll and C in HM82-4 were similar to the control. The inhibitory effect of the 1981 moss addition on chlorophyll and carbon was not evident after 1 year. OM82-8 which was LM81-2 in 1981

TABLE 16. Chlorophyll a and suspended carbon data for the moss-peat and control limnocorrals in 1981 and 1982. The data are time weighted means for July 10 to August 24,1981 (days 191-236) and July 7 to August 9, 1982 (days 188-221). The experimental limnocorral data are expressed as a percent of the appropriate controls.

Limnocorral	Treatment	Chlorophyll a		Suspended carbon		Chl/C
		ug L^{-1}	%	ug L^{-1}	%	ug mg^{-1}
C81-1	control	3.9		719		5.4
LM81-2	moss-peat (63 Kg)	2.7	69	496	69	5.4
OC82-5	control (1 yr old)	2.1		885		2.4
C82-6	control	2.2		909		2.4
LM82-3	moss-peat (52 Kg)	1.6	73	645	71	2.5
HM82-4	moss-peat (104 Kg)	4.4	200	1442	159	3.1
OM82-8	moss-peat (63 Kg) (1 yr old)	2.5	119	913	103	2.7
FM82-1	moss-peat (attached)	2.1	96	1261	139	1.7

FIGURE 39. Seasonal pattern of chlorophyll a in the 1981 control and moss-peat limnocorrals. C = control and LM = low moss. Day 170 is June 19 and day 230 is August 18.

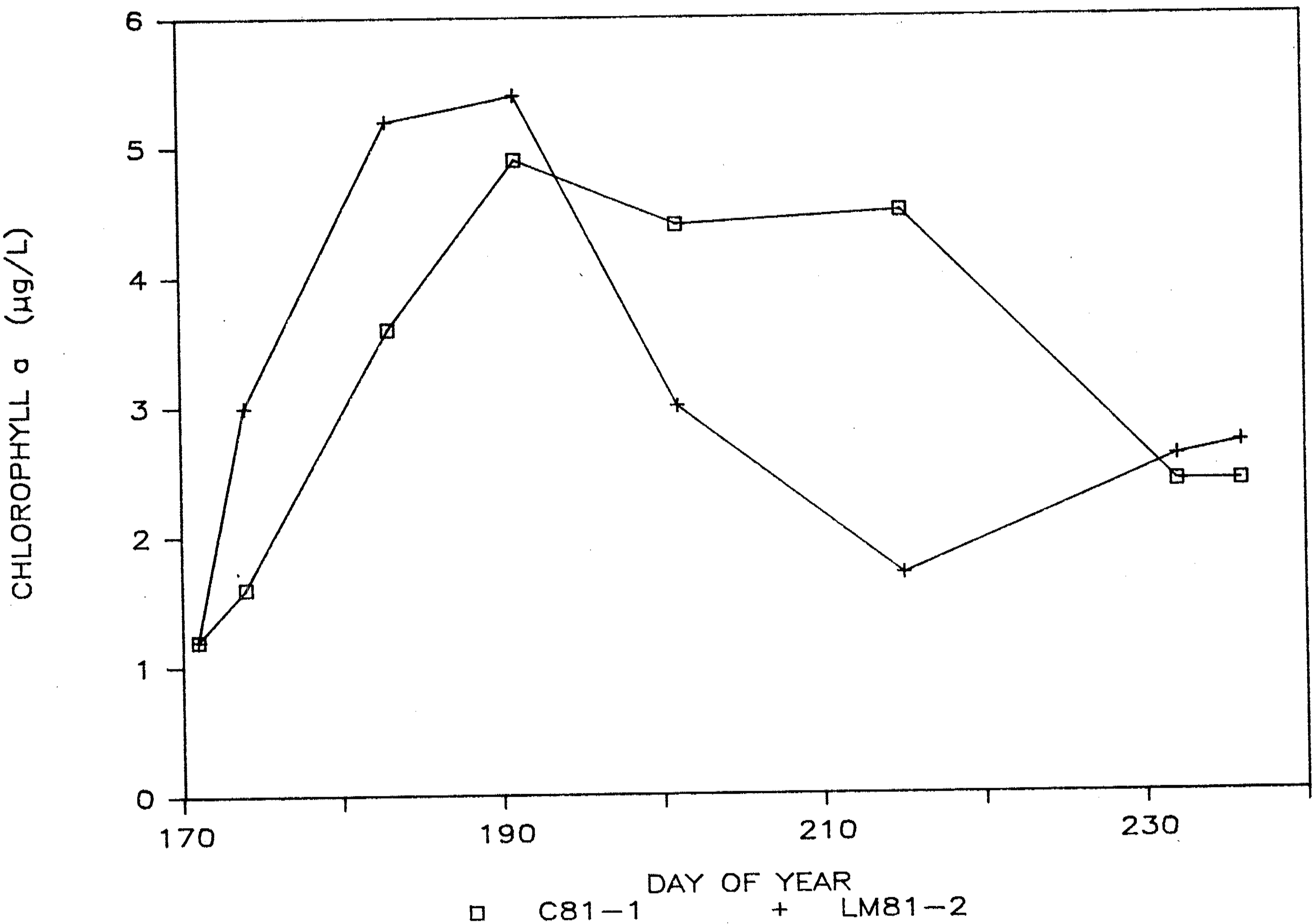

6
5
4
3
2
1
0
CHLOROPHYLL a (µg/L)
170
190
210
230
DAY OF YEAR
□ C81-1
+ LM81-2

FIGURE 40. Seasonal pattern of suspended carbon in the 1981 control and moss-peat limnocorrals. C = control and LM = low moss. Day 170 is June 19 and day 230 is August 18.

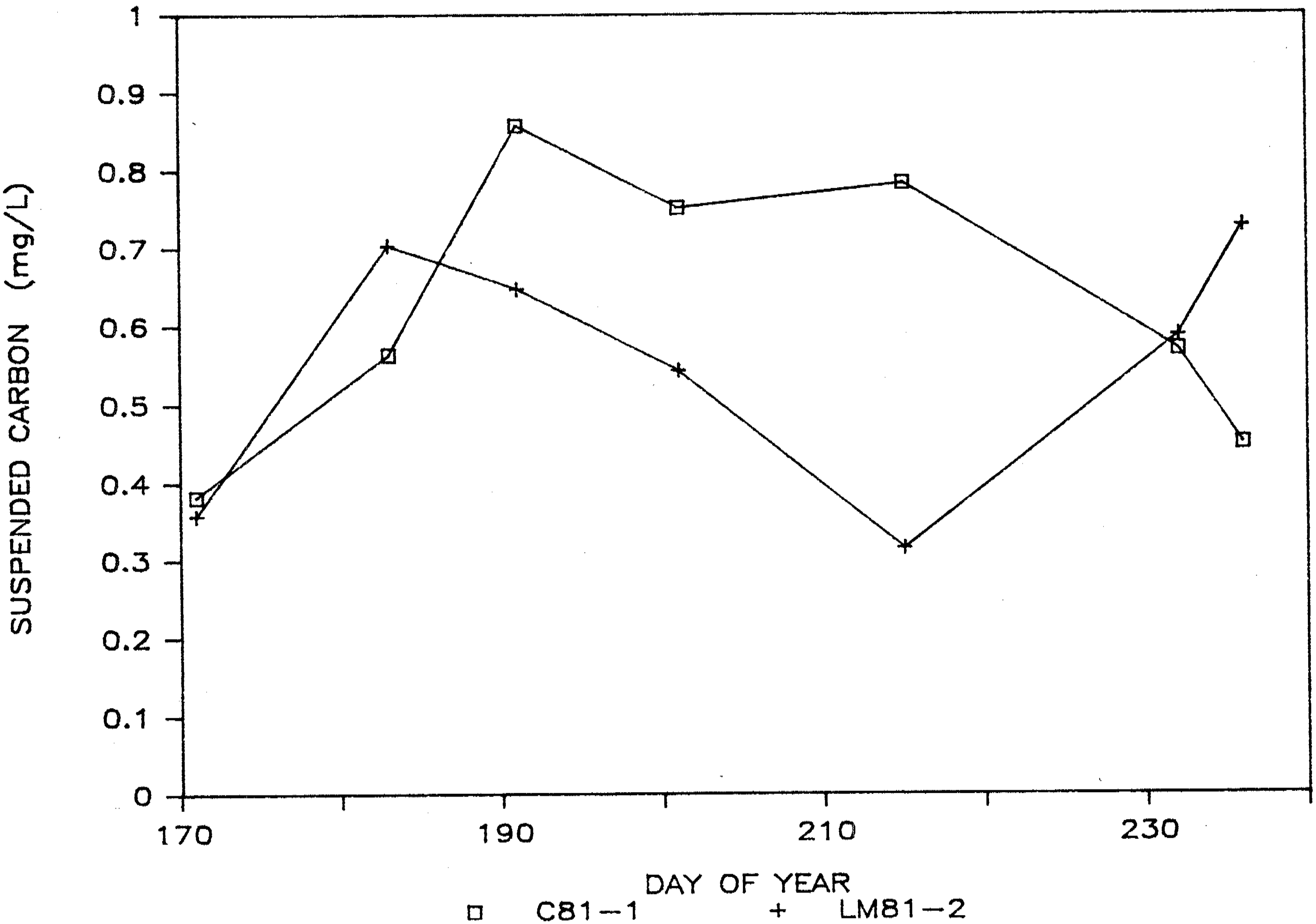
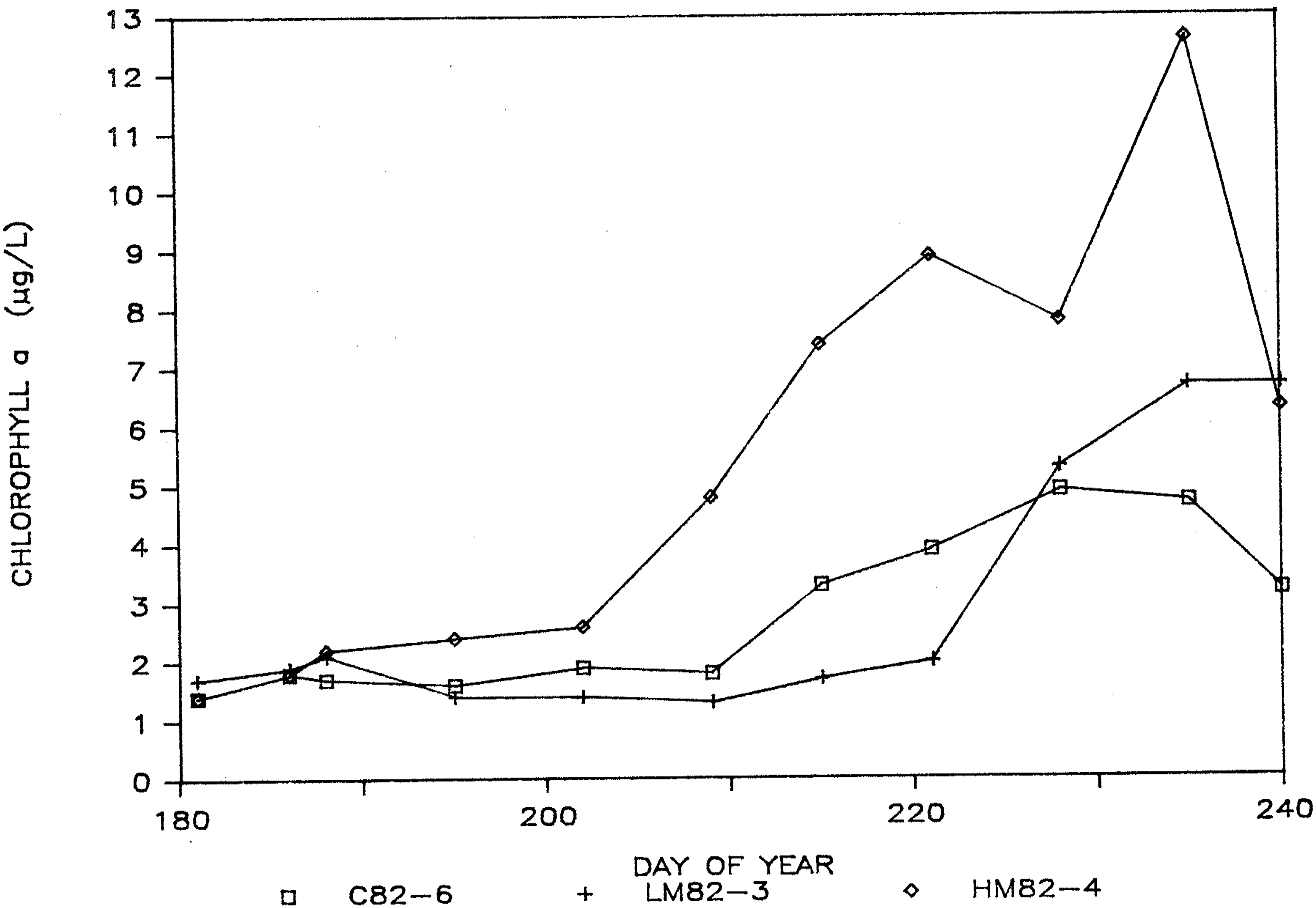
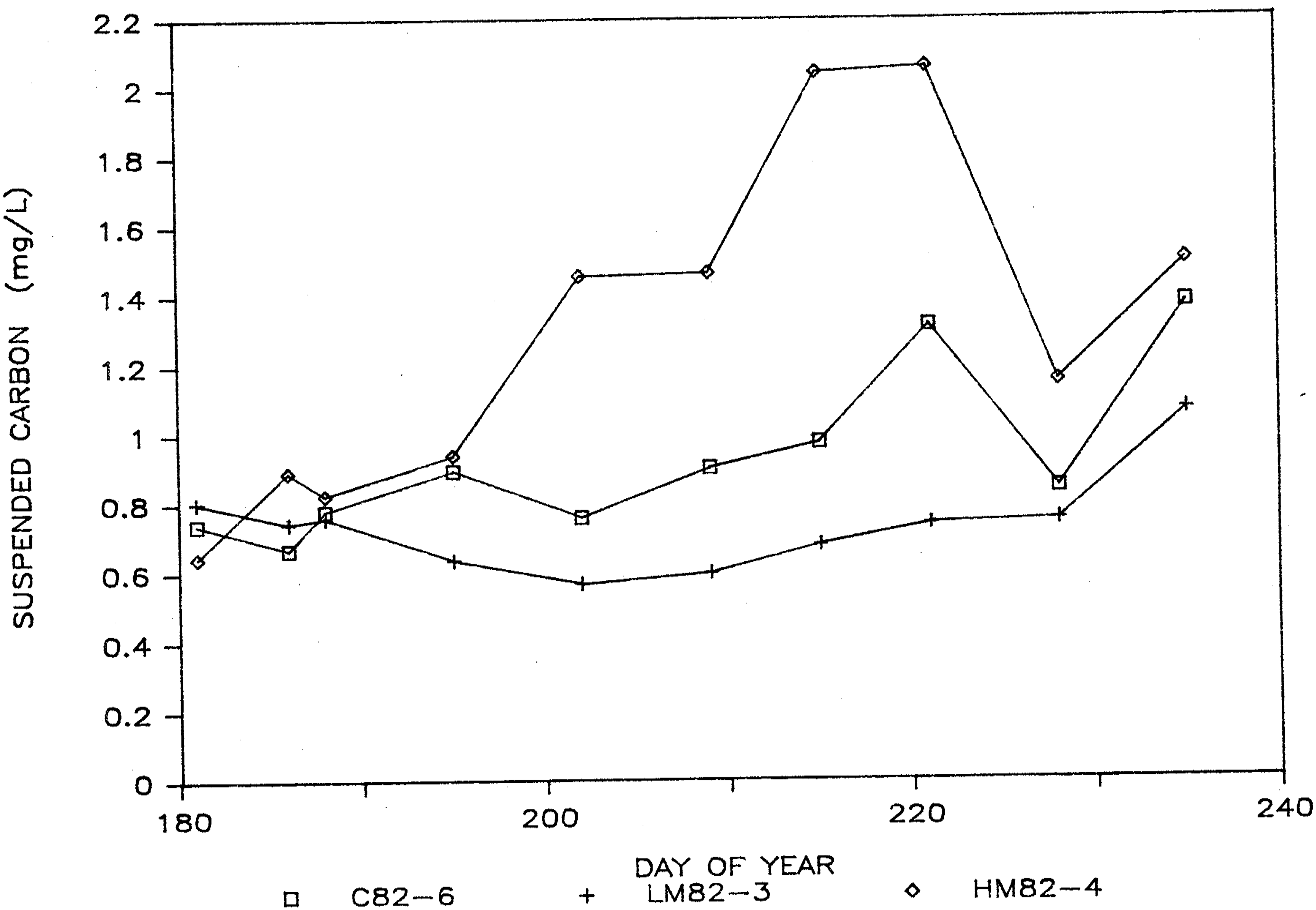

SUSPENDED CARBON (mg/L)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
170
190
210
230
DAY OF YEAR
C81−1
+ LM81−2

FIGURE 41. Seasonal pattern of chlorophyll a in the 1982 control and moss-peat limnocorrals. C = control, LM = low moss, and HM = high moss. Day 180 is June 29 and day 240 is August 28.



CHLOROPHYLL a (µg/L)
13
12
11
10
9
8
7
6
5
4
3
2
1
0
180
200
220
240
DAY OF YEAR
C82-6
LM82-3
HM82-4

FIGURE 42. Seasonal pattern of suspended carbon in the 1982 control and moss-peat limnocorrals. C = control, LM = low moss, and HM = high moss. Day 180 is June 29 and day 240 is August 28.


2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
SUSPENDED CARBON (mg/L)
180
200
220
240
DAY OF YEAR
C82-6
LM82-3
HM82-4

had as much suspended C as the control and 60% more chlorophyll a.

In the limnocorral FM82-1 which was situated over actual attached moss vegetation that was flooded in 1976, the mean chlorophyll value was the same as the control indicating that six year old attached moss neither stimulated or inhibited the accumulation of chlorophyll. Suspended C in this limnocorral was 40% greater than in the control; but, as mentioned previously this was probably because of contamination by detrital carbon due to the shallow depth.

Bacteria

Mean oxygen concentrations in the moss-peat limnocorrals were consistently lower than in the controls (Table 17). This indicates a higher rate of oxygen consumption and probably more bacterial activity in the moss-peat limnocorrals. Two sets of water samples were counted for bacteria (Table 8). There was essentially no difference between the moss-peat treatment and the control. It is possible that more bacteria were present in the moss-peat limnocorrals, but they were not sampled because they were growing on the organic material at the bottom of the limnocorral. Alternatively bacterial activity may have been higher in the moss-peat limnocorrals, but bacterial numbers were depressed by the greater number of zooplankton grazing there (Table 17).

Zooplankton

Moss-peat clearly stimulated zooplankton numbers (Table 17). After 1 year the moss-peat limnocorral OM82-8, which was moss-peat LM81-2 the previous year, still had about twice as many zooplankton as the control. The moss vegetation flooded in 1976 (FM82-1) did not stimulate

TABLE 17. Mean oxygen concentrations (expressed as a percentage of atmospheric saturation) and mean zooplankton numbers for the moss-peat and control limnocorrals in 1981 and 1982. C. Anema analyzed the oxygen, and D. Ramsey counted the zooplankton. All limnocorrals had natural bottoms.

Limnocorral	Treatment	Oxygen %	Zooplankton animals L^{-1}
C81-1	control	99	39
LM81-2	moss-peat (63 Kg)	81	173
OC82-5	control (1 yr old)	92	61
C82-6	control	91	71
LM82-3	moss-peat (52 Kg)	82	93
HM82-4	moss-peat (104 Kg)	71	207
OM82-8	moss-peat (63 Kg, 1 yr old)	91	125
FM82-1	moss-peat (flooded 1976)	87	72

zooplankton numbers in 1982.

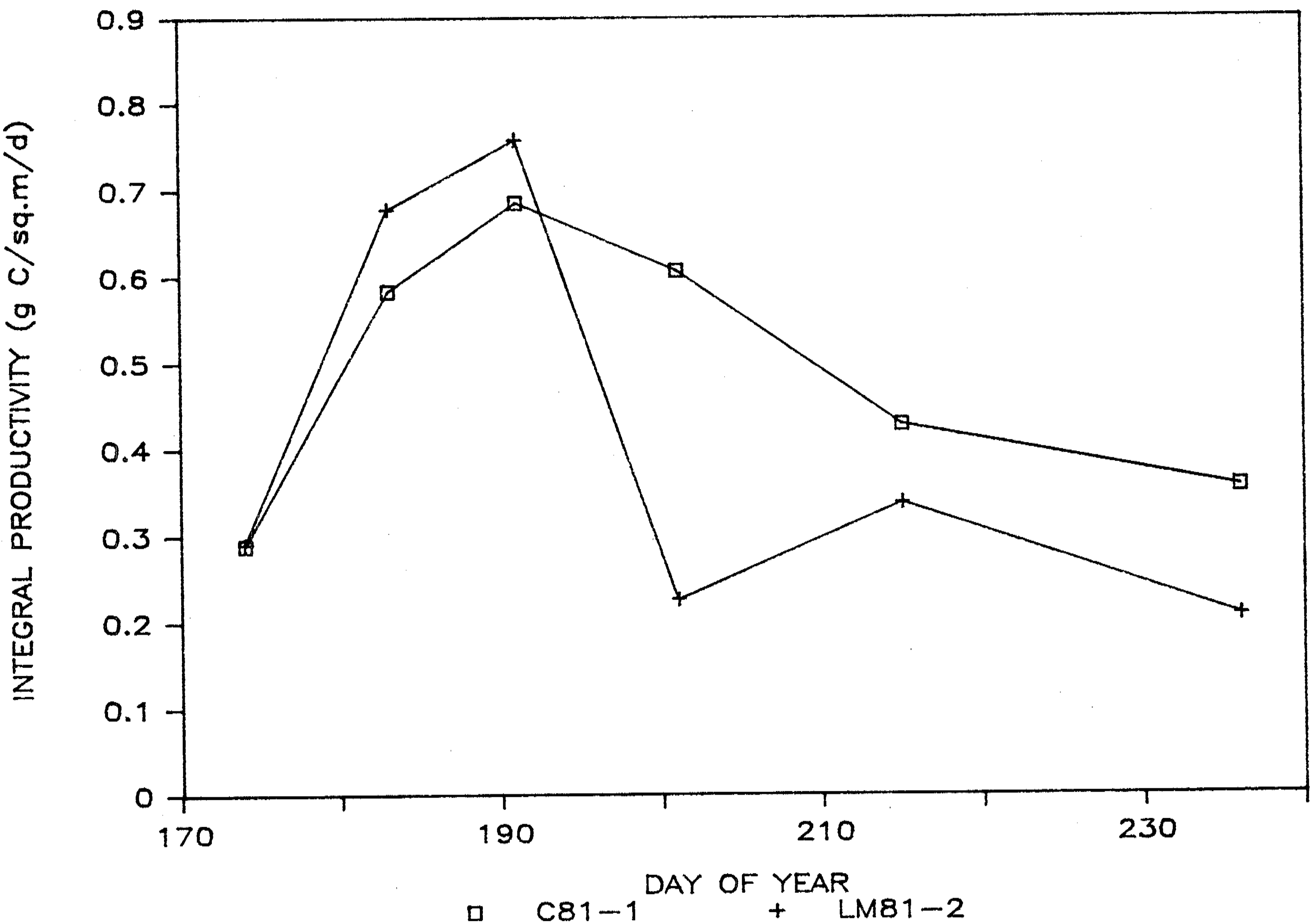
Primary Productivity

Mean integral production was 20-30% lower in the moss-peat limnocorrals (LM81-2 and LM82-3) than in their controls (Table 18). This appears to be the result of two factors: a requirement for higher light intensities (I_k) and lower availability of light (I_{24}). The moss-peat treatment did not inhibit production immediately (Figs. 43 and 44). For about a month integral production was the same or higher than the controls. This was followed by a 30-60% decrease below the levels of the controls.

OM82-8 is the former moss-peat LM81-2 and C82-5 the former control C81-1. After 1 year it appeared that the moss-peat in the bottom of the limnocorral had no inhibitory effect on primary productivity (Table 18). In fact the mean data indicate that the one year old moss-peat material might stimulate productivity. However the comparison between the one year old control and one year old treated limnocorral may not be appropriate because the one year old control limnocorral had much heavier periphyton wall growth than the one year old moss-peat limnocorral. When the one year old moss-peat limnocorral is compared to the new 1982 control (C82-6) there is no difference in integral production.

Only two sets of production measurements were made on FM82-1, the limnocorral that was situated over actual flooded shoreline. It is difficult to compare this limnocorral to the control or other moss-peat limnocorrals because it is almost 1 m shallower and the moss-peat vegetation is attached to the bottom which has been subjected to

FIGURE 43. Seasonal pattern of daily integral primary productivity in the 1981 control and moss-peat limnocorrals. C = control and LM = low moss. Day 170 is June 19 and day 230 is August 18.



0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
INTEGRAL PRODUCTIVITY (g C/sq.m/d)
170
190
210
230
DAY OF YEAR
C81-1
LM81-2

FIGURE 44. Seasonal pattern of daily integral primary productivity in the 1982 control and moss-peat limnocorrals. C = control and LM = low moss. Day 180 is June 29 and day 220 is August 8.

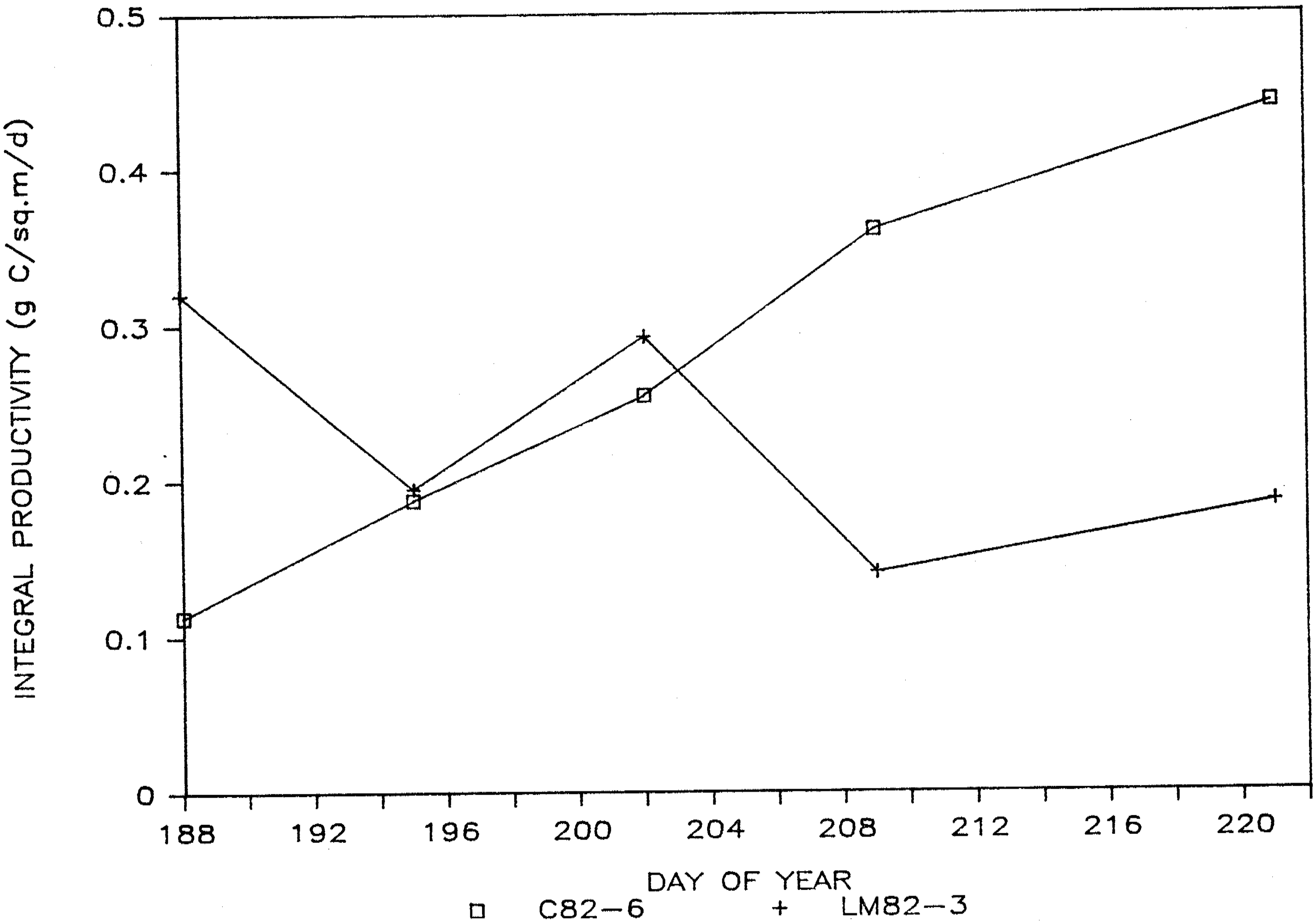

INTEGRAL PRODUCTIVITY (g C/sq.m/d)
0.5
0.4
0.3
0.2
0.1
0
188
192
196
200
204
208
212
216
220
DAY OF YEAR
C82-6
LM82-3

TABLE 18. Seasonal means of relevant parameters of primary productivity for moss-peat and control limnocorrals in 1981 and 1982. The data are means for July 10 to August 24, 1981 (days 191-236) and July 7 to August 9, 1982 (days 188-221). The experimental limnocorral data are expressed as a per cent of the appropriate controls. Individual controls are expressed as a per cent of the mean of the controls for each year in order to show the range of variability between the controls. Symbols are explained below.

Limnocorral	Treatment	I.P.	%	I_{24}	%	$Alpha^B$	%	P_m^B	%	I_k	I_{24}/I_k
C81-1	control	500		21.1		7.07		4.80		17.1	1.2
LM81-2	moss-peat (63 Kg)	399	80	16.2	77	5.05	71	4.62	96	20.2	0.8
OC82-5	control (1 yr old	217		19.4		2.71		3.24		18.9	1.0
C82-6	control	290		18.7		4.24		4.98		19.3	1.0
LM82-3	moss-peat (52 Kg)	212	73	15.1	81	3.83	90	4.56	92	23.3	0.6
OM82-8	moss-peat (63 Kg) (1 yr old)	296	136	19.8	102	3.45	127	4.44	137	20.4	1.0

I.P. is the daily rate of primary productivity (mg C m^{-2} d^{-1})

I_{24} is the mean water column light intensity during 24 hours (E m^{-2} d^{-1})

$Alpha^B$ is the initial slope of the primary productivity irradiance curve in the incubator expressed per unit of chlorophyll (mg C E^{-1} m^2 mg Chl a^{-1})

P_m^B is the maximum rate of primary productivity observed in the incubator expressed per unit of chlorophyll (mg C mg Chl a^{-1} h^{-1})

I_k is irradiance at the onset of light saturation (E m^{-2} d^{-1})

sedimentation for six years. The mean of two production measuremnts indicates that production was low relative to the control (Table 19).

HM82-4 received twice as much moss-peat material as LM82-3. The average of two production measurements shows integral production in HM82-4 was almost double that in LM82-3 (Table 19). However, the high rate is probably due to the high chlorophyll concentrations in HM82-4. When the light saturated rate of primary productivity is normalized to chlorophyll (P_m^B), the rate is actually lower than P_m^B for LM82-3 (Table 19).

Indicators of nutrient deficiency

There were no positive signs of nitrogen deficiency in any of the moss-peat limnocorrals or the controls. Mean N/C ratios and N debt values are in Table 20.

Moss-peat material reduced the occurrence and severity of P deficiency in the limnocorrals. The means of the P deficiency indicators are given in Table 20. Alkaline phosphatase normalized to ATP shows that the control (C81-1) was severely P deficient while LM81-2, the only moss-peat limnocorral in 1981, was moderately P deficient. P debt/ATP, N/P and P/C ratios indicate no P deficiency in the moss-peat limnocorral but P deficiency in the control C81-1.

In 1982 a similar but less dramatic response was observed. The controls C82-6 and C82-5 were moderately P deficient according to alkaline phosphatase/ATP and P/C and N/P. The two moss-peat limnocorrals created in 1982, LM82-3 and HM82-4, both had no P deficiency according to alkaline phosphatase activity but moderate P deficiency according to the composition ratios, N/P and P/C. The older

TABLE 19. Relevant parameters of primary productivity for moss-peat and control limnocorrals in 1982 based on the two days July 21 and August 9. Headings are as in table 18.

Limnocorral	Treatment	I.P.	%	I_{24}	%	$Alpha^B$	%	P_m^B	%	I_k	I_{24}/I_k
C82-6	control	349		17.4		3.32		4.32		19.9	0.9
LM82-3	moss-peat (52 Kg)	240	69	14.2	82	3.83	115	5.10	118	20.4	0.7
HM82-4	moss-peat (104 Kg)	436	125	16.5	95	2.98	90	3.66	85	19.0	0.9
FM82-1	moss-peat (flooded 1976)	176	50	24.2	140	2.55	77	3.18	74	20.7	1.2
L82-9	lake	226	65	15.4	89	2.89	87	3.54	82	18.9	0.8

TABLE 20. Mean values for various physiological indicators of N and P deficiency in the moss-peat and control limnocorrals in 1981 and 1982. P and N headings indicate parameters indicative of P and N deficiency respectively: general indicators cannot on the basis of present evidence be ascribed with any certainty to either N or P deficiency (Healey and Hendzel 1980). Composition ratios are ug particulate P, N, ATP, or chlorophyll a (chl) mg particulate C^{-1}; ug particulate N ug particulate P^{-1}. Nutrient debts are umoles ammonium or phosphate removed in 24 h darkness ug ATP^{-1}. Negative debt means net release of nutrient. Alkaline phosphatase activity (Pase) is umole o-methyl fluorescein phosphate hydrolyzed h^{-1} ug ATP^{-1}. n.d. = no data.

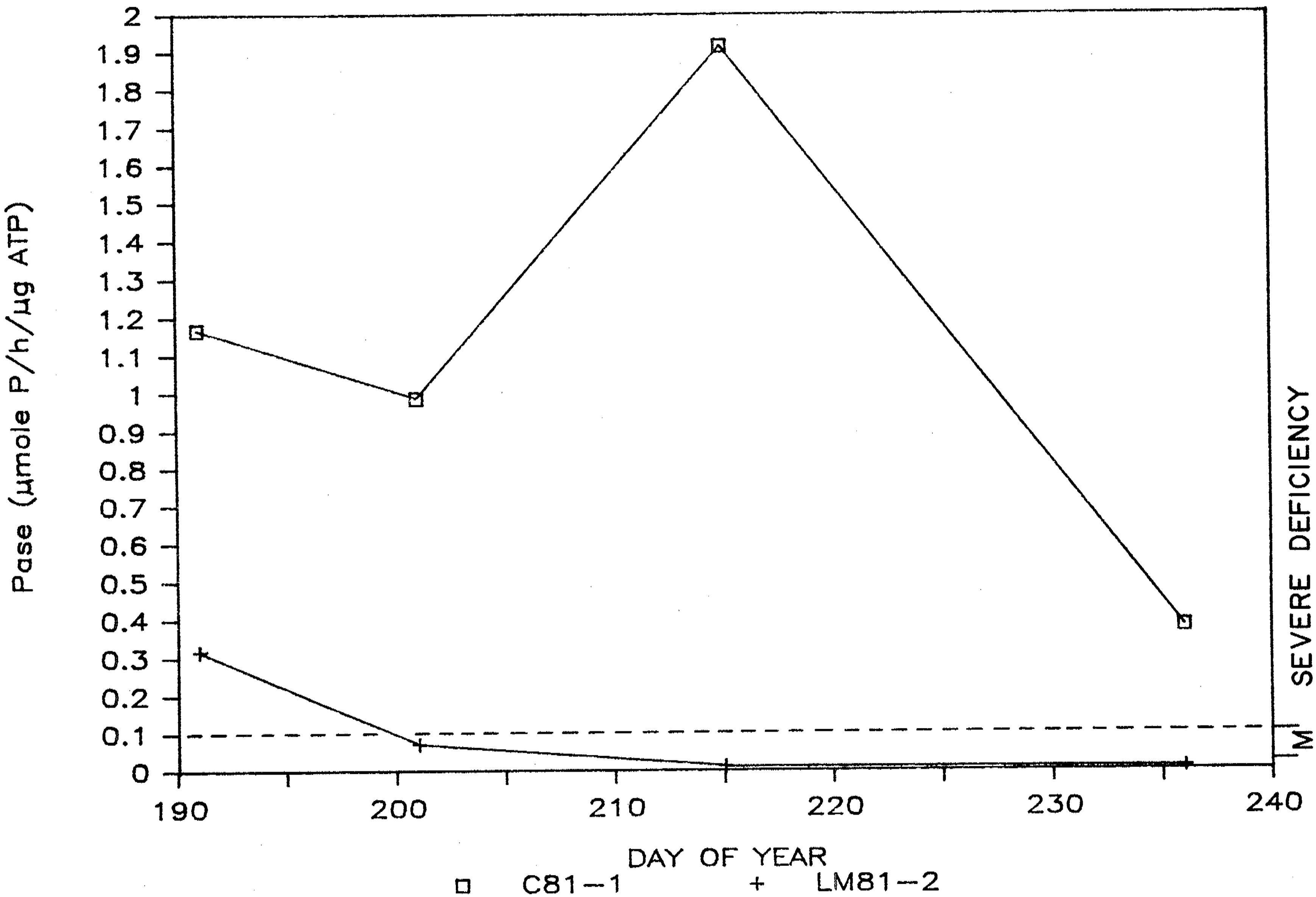
		N		P				GENERAL	
Limnocorral	Treatment	Ndebt[1]	N/C[2]	Pase[3]	Pdebt[4]	P/C[5]	N/P[6]	Chl/C[7]	ATP/C[8]
C81-1	control	0.961	210	1.226	2.635	14	16	5.5	0.77
LM81-2	moss-peat (63 Kg)	-0.259	170	0.061	0.120	27	7	5.8	2.23
OC82-5	control (1 yr old)	n.d.	190	0.047	n.d.	12	17	2.9	0.92
C82-6	control	n.d.	190	0.079	n.d.	11	20	3.0	0.76
LM82-3	moss-peat (52 Kg)	n.d.	200	0.007	n.d.	15	15	3.3	1.33
HM82-4	moss-peat (104 Kg)	n.d.	180	0.004	n.d.	17	13	3.8	1.13
OM82-8	moss-peat (63 Kg) (1 yr old)	n.d.	190	0.083	n.d.	12	17	3.2	0.93
FM82-1	moss-peat (flooded 1976)	n.d.	160	0.122	n.d.	10	17	1.7	0.70

1 >1.000 = N deficiency
2 80-140 = moderate, <80 = severe N deficiency
3 0.02-0.10 = moderate, > 0.10 = severe P deficiency
4 >0.500 = P deficiency
5 10-20 = moderate, <10 = severe P deficiency
6 >10 = P deficiency
7 <10 = deficiency
8 <2.0 = deficiency

moss-peat limnocorrals, FM82-1 and OM82-8, both showed as much or more P deficiency than the controls. There was a tendency for P deficiency to decrease over the summer in the moss-peat limnocorrals (Figs. 45 to 50). The controls tended to become more P deficient throughout the summer.

Ratios for ATP/C less than 2.0 suggest nutrient deficiency (Healey and Hendzel 1979). While only one moss-peat limnocorral had a ratio greater than 2.0, all the new moss-peat limnocorrals had ratios greater than the controls (Table 20). This indicates that the moss-peat limnocorrals were less nutrient deficient than the controls. The relatively high ATP/C ratios in the moss-peat limnocorrals were the result of high ATP concentrations and low suspended C in the moss-peat limnocorrals compared to the controls. The P deficiency indicators discussed previously suggest that ATP levels were high in the moss-peat limnocorrals because there was little or no P deficiency. There is little difference between the moss peat limnocorrals and the controls with respect to the chlorophyll/C ratio. All the ratios are less than 10 which indicates nutrient deficiency.

FIGURE 45. Seasonal pattern of alkaline phosphatase activity (Pase) normalized to ATP in the 1981 moss-peat and control limnocorrals. The broken horizontal line indicates the occurrence of severe P deficiency in algae as given by Healey and Hendzel (1980). The range for moderate P deficiency is denoted by the symbol "M". C = control and LM = low moss. Day 190 is July 9 and day 230 is August 18.



Pase (µmole P/h/µg ATP)
2
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
190
200
210
220
230
240
SEVERE DEFICIENCY
M
DAY OF YEAR
C81—1
LM81—2

FIGURE 46. Seasonal pattern of alkaline phosphatase activity (Pase) normalized to ATP in the 1982 moss-peat and control limnocorrals. The broken horizontal lines indicate the occurrence of severe, moderate, and no P deficiency in algae as given by Healey and Hendzel (1980). C = control, LM = low moss and HM = high moss. Day 188 is July 7 and day 220 is August 8.

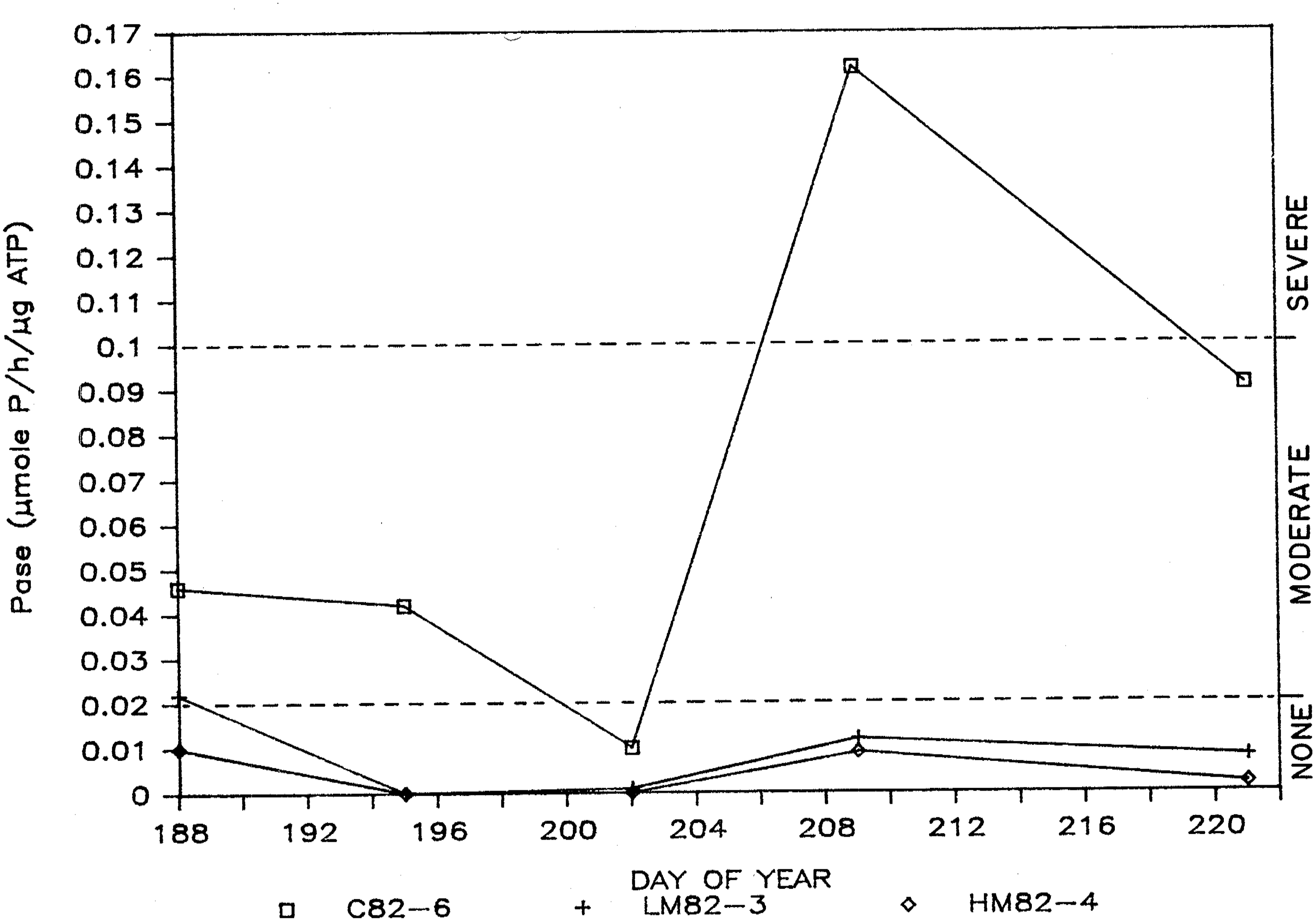

Pase (µmole P/h/µg ATP)
0.17
0.16
0.15
0.14
0.13
0.12
0.11
0.1
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
188
192
196
200
204
208
212
216
220
DAY OF YEAR
SEVERE
MODERATE
NONE
C82–6
LM82–3
HM82–4

FIGURE 47. Seasonal pattern of the particulate P/C ratio in the 1981 moss-peat and control limnocorrals. The broken horizontal lines indicate the occurrence of severe, moderate, and no P deficiency in algae as given by Healey and Hendzel (1980). C = control and LM = low moss. Day 180 is June 29 and day 240 is August 28.

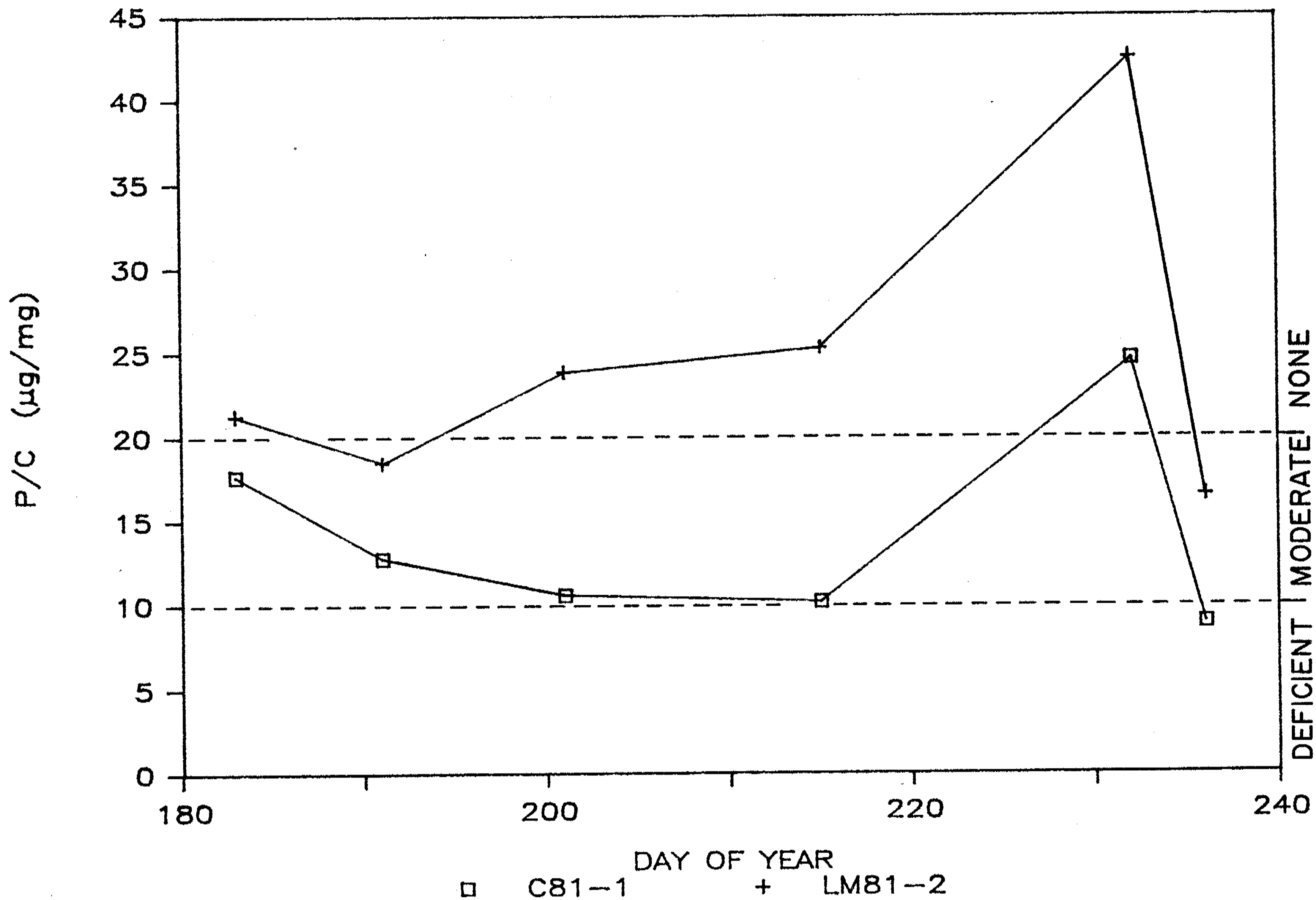

P/C (μg/mg)
45
40
35
30
25
20
15
10
5
0
180
200
220
240
DAY OF YEAR
NONE
MODERATE
DEFICIENT
□ C81-1
+ LM81-2

FIGURE 48. Seasonal pattern of the particulate P/C ratio in the 1982 moss-peat and control limnocorrals. The broken horizontal lines indicate the occurrence of severe, moderate, and no P deficiency in algae as given by Healey and Hendzel (1980). C = control, LM = low moss, and HM = high moss. Day 180 is June 29 and day 240 is August 28.

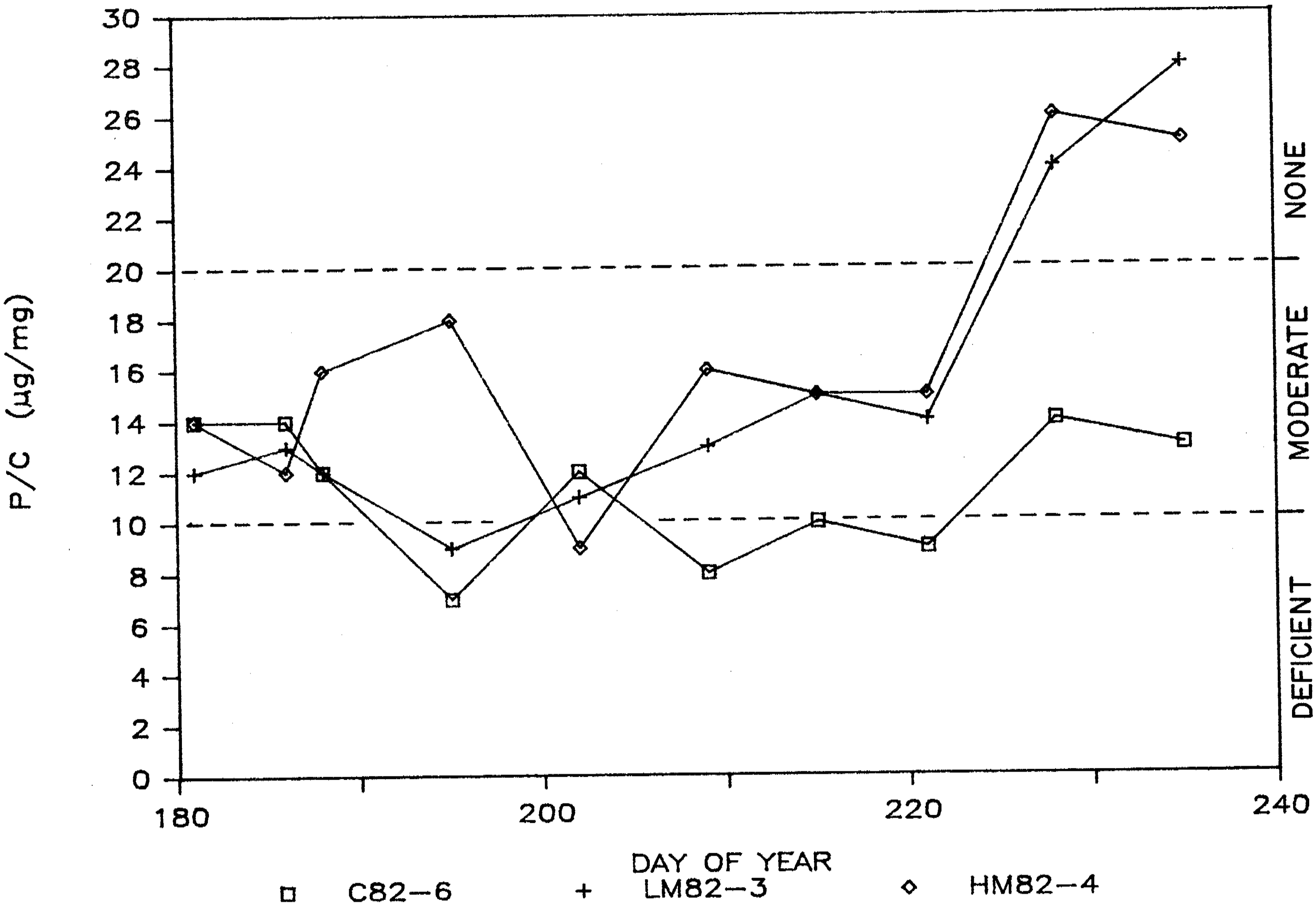

P/C (µg/mg)
DAY OF YEAR
NONE
MODERATE
DEFICIENT
C82–6
LM82–3
HM82–4

FIGURE 49. Seasonal pattern of the particulate N/P ratio on the 1981 moss-peat and control limnocorrals. The broken horizontal line indicates the occurrence of P deficiency in algae as given by Healey and Hendzel (1980). C = control and LM = low moss. Day 180 is June 29 and day 240 is August 28.

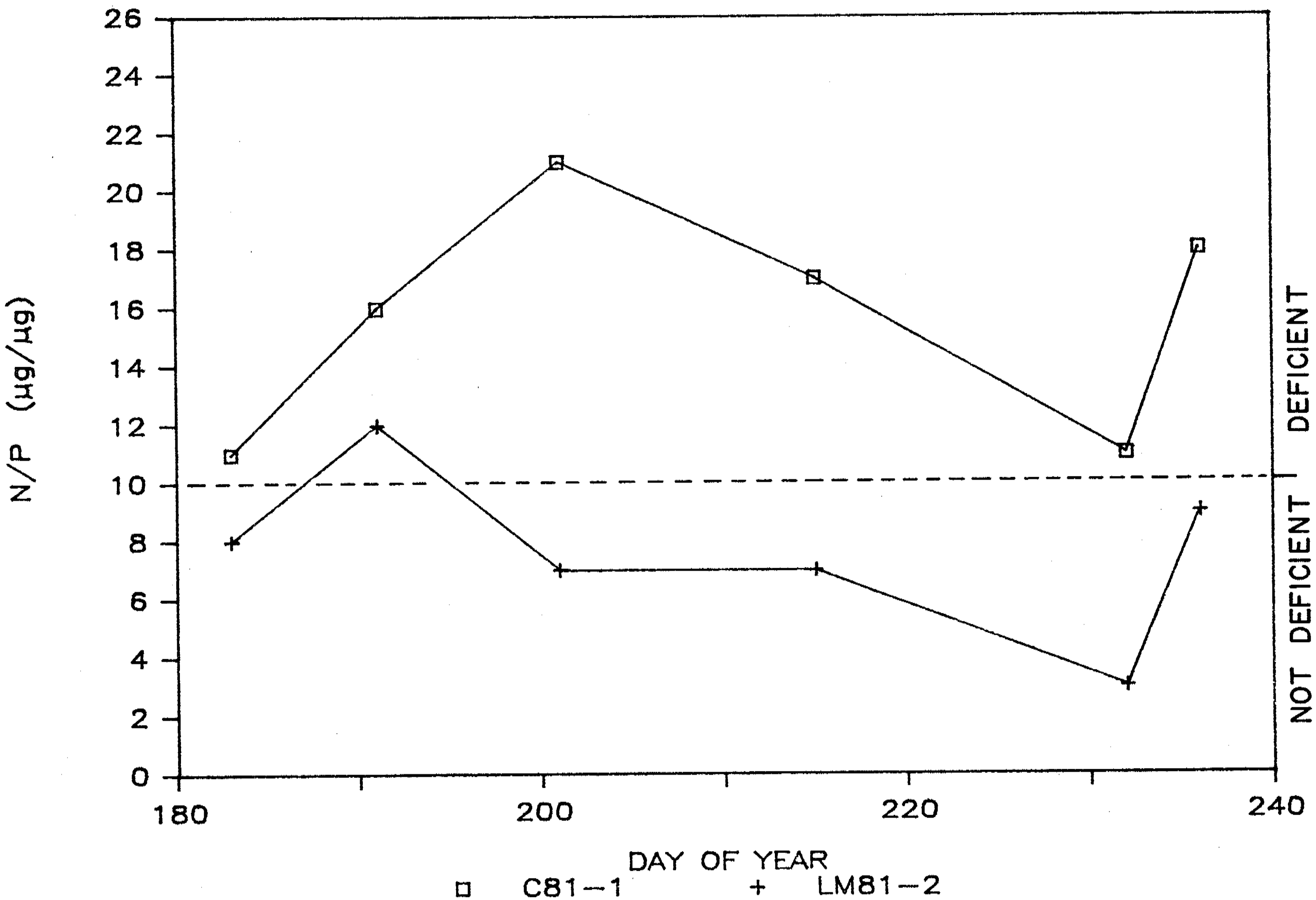
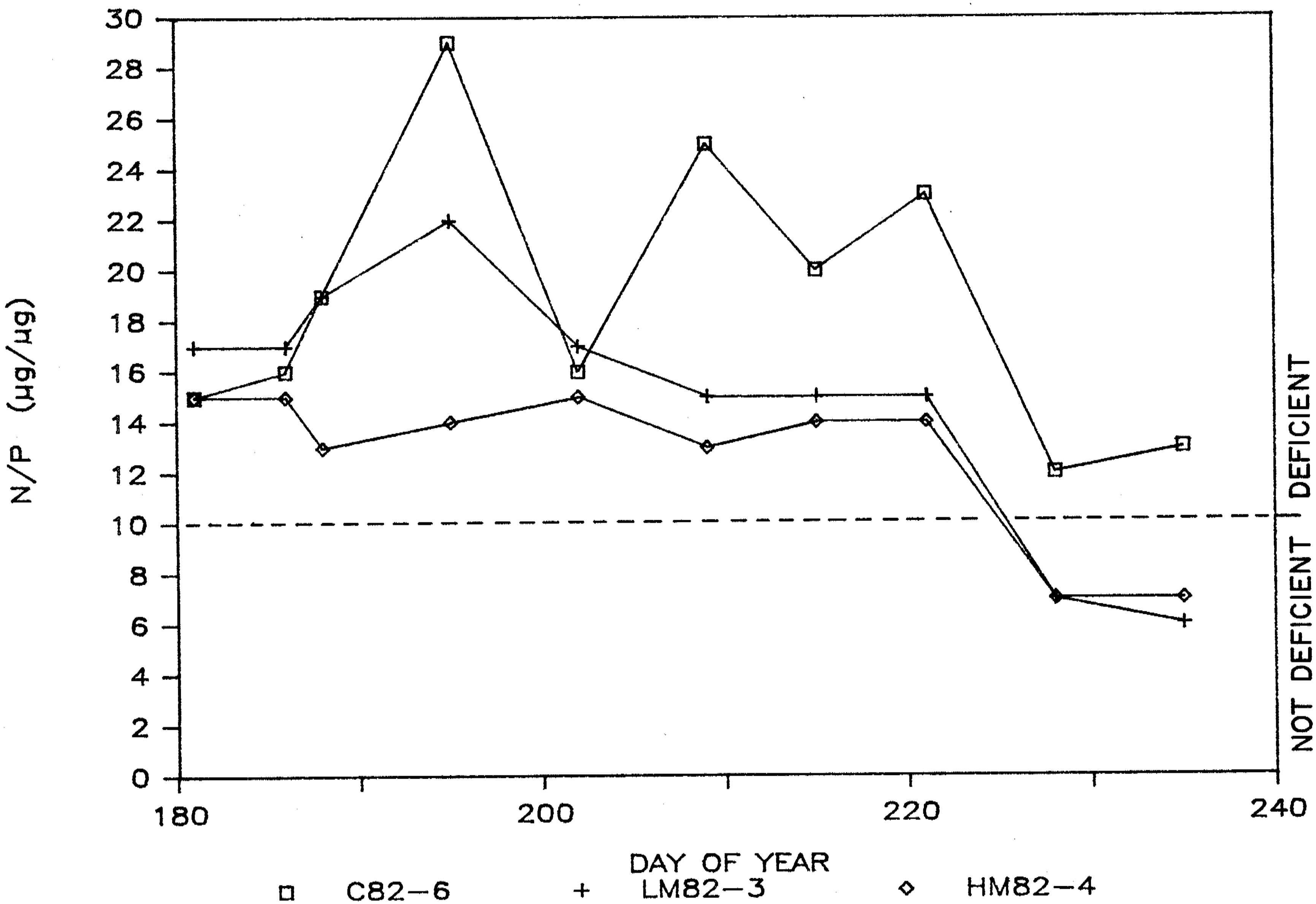

N/P (μg/μg)
26
24
22
20
18
16
14
12
10
8
6
4
2
0
180
200
220
240
DAY OF YEAR
DEFICIENT
NOT DEFICIENT
C81-1
LM81-2

FIGURE 50. Seasonal pattern of the particulate N/P ratio on the 1982 moss-peat and control limnocorrals. The broken horizontal line indicates the occurrence of P deficiency in algae as given by Healey and Hendzel (1980). Day 180 is June 29 and day 240 is August 28.



N/P (μg/μg)
DAY OF YEAR
DEFICIENT
NOT DEFICIENT
C82-6
LM82-3
HM82-4

DISCUSSION

The initial response to moss-peat addition

In the first four weeks after the moss-peat additions, increases in the concentrations of DHM, TDN, TDP, chlorophyll, suspended C and the rate of integral primary productivity were observed. This response is similar to the nutrient and trophic upsurge described for newly flooded reservoirs (Rodhe 1964, Baxter and Glaude 1980, Ostrofsky and Duthie 1980).

The increase in nutrients and humic matter was the result of leaching from the moss-peat material. Gjessing and Samdal (1968) measured an increase in humic color when a reservoir was formed in an area of peaty vegetation in Norway. Campbell et al. (1975), in an enclosure experiment involving flooded topsoils, measured increases in N, P, Fe and Mn. Ostrofsky (1978) calculated that about one-half of the P concentration in Smallwood Reservoir in Labrador could be accounted for by estimating the amount of leaching from newly flooded vegetation. He suggested most of the P was in the analytically reactive form. Over half the TDP in the moss-peat limnocorral (LM81-2) was SRP.

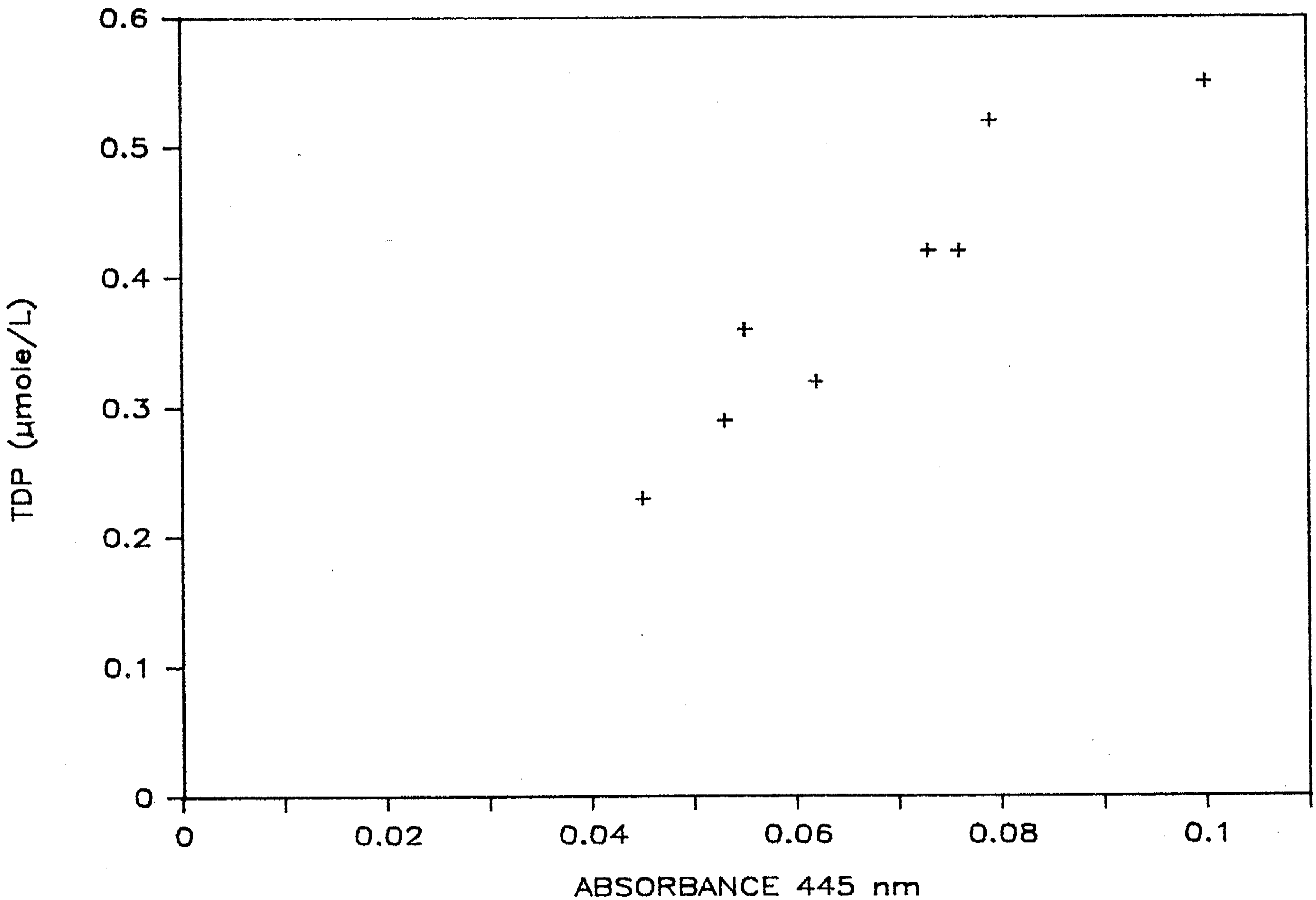
In a P-limited system the release of available P should result in an increase in biomass and productivity. Nutrient status indicators showed that P was limiting in limnocorrals that did not receive moss-peat material. It appears that initially at least available nutrients leached from flooded organic materials were transformed into biomass. Chlorophyll, suspended C and integral production were all higher than controls in the moss-peat limnocorrals immediately after the moss-peat additions. Campbell (1975) in enclosure experiments measured higher algal biomass in response to leached nutrients from flooded topsoils.

The long term response to moss-peat addition

After about four weeks a decrease in the levels of primary productivity, suspended C and chlorophyll was observed in the moss-peat limnocorrals (LM81-2 and LM82-3). TDN and TDP continued to be higher than in the controls. Nutrient status indicators showed that N was never limiting and that P was rarely limiting.

It is not surprising that N was not limiting because N was never limiting in the control limnocorrals either. However it was very interesting that P was not limiting in the moss-peat limnocorrals because in the controls P was clearly the limiting nutrient. TDP and humic color in the moss-peat limnocorrals were higher than in the controls, and in fact there was a direct correlation between humic color and TDP (Fig. 51). Koenings and Hooper (1976) and Francko and Heath (1983) have reported that PO_4^{-3} is bound to DHM via $Fe(OH)_3$. This may be what happened in the moss-peat limnocorrals. One might expect that, if DHM bound P, then P might have become limiting. However there is ample evidence that P was not limiting in the moss-peat limnocorrals and therefore a significant fraction of TDP must have been available to the algae. Alkaline phosphatase activity, P debt, P/C and N/P ratios all indicated much less P deficiency in the moss-peat limnocorrals than in the controls. In spite of this, chlorophyll, suspended C and integral productivity fell well below the levels of the controls. In HM82-4, the limnocorral receiving the largest moss-peat addition, the "trophic upsurge" appeared to last longer but by the end of the experiment this

FIGURE 51. The relationship between absorbance at 445 nm and total dissolved phosphorus (TDP) in moss-peat and control limnocorrals from 1981 and 1982. The data are mean values for each year.



TDP (µmole/L)
0.6
0.5
0.4
0.3
0.2
0.1
0
0.02
0.04
0.06
0.08
0.1
ABSORBANCE 445 nm

limnocorral also experienced decreasing chlorophyll and suspended C with no sign of P deficiency. Some factor other than the nutrients N or P must have been limiting productivity and biomass in the moss-peat limnocorrals.

Light may have been the limiting factor. The moss-peat limnocorrals were dark in color due to DHM leached from the moss-peat material. DHM decreases light penetration by absorbing light selectively at short wavelengths (especially 350-500 nm, Wetzel 1975). Thus the water in the the moss-peat limnocorrals transmitted less light and a different quality of light as well. As the major peak in the absorption spectra of both chlorophyll and carotenoids is within the range of maximum absorbance by DHM, high concentrations of DHM might significantly reduce light available for photosynthesis.

Mean light extinction coefficients (k) in two of the moss-peat limnocorrals (LM81-2 and HM82-4) were higher than in the controls; but, in LM82-3, k was lower than in the control. I_{24}, the mean water column light intensity, which is a function of depth as well as k was slightly lower, on average, in all three moss-peat limnocorrals than in the controls.

The slightly lower I_{24} values in the moss-peat limnocorrals cannot account for the low rates of integral production observed in the latter half of the experimental period. I_{24} in LM81-2 and LM82-3 was lower than in the controls all summer, not just in the latter half (Fig. 52 and 53). Production on the other hand remained high for the first month after the addition, and then it dropped sharply (Figs. 43 and 44).

FIGURE 52. Seasonal pattern of the mean water column light intensity (I_{24}) in the 1981 moss-peat and control limnocorrals. C = control and LM = low moss. Day 170 is June 19 and day 230 is August 18.

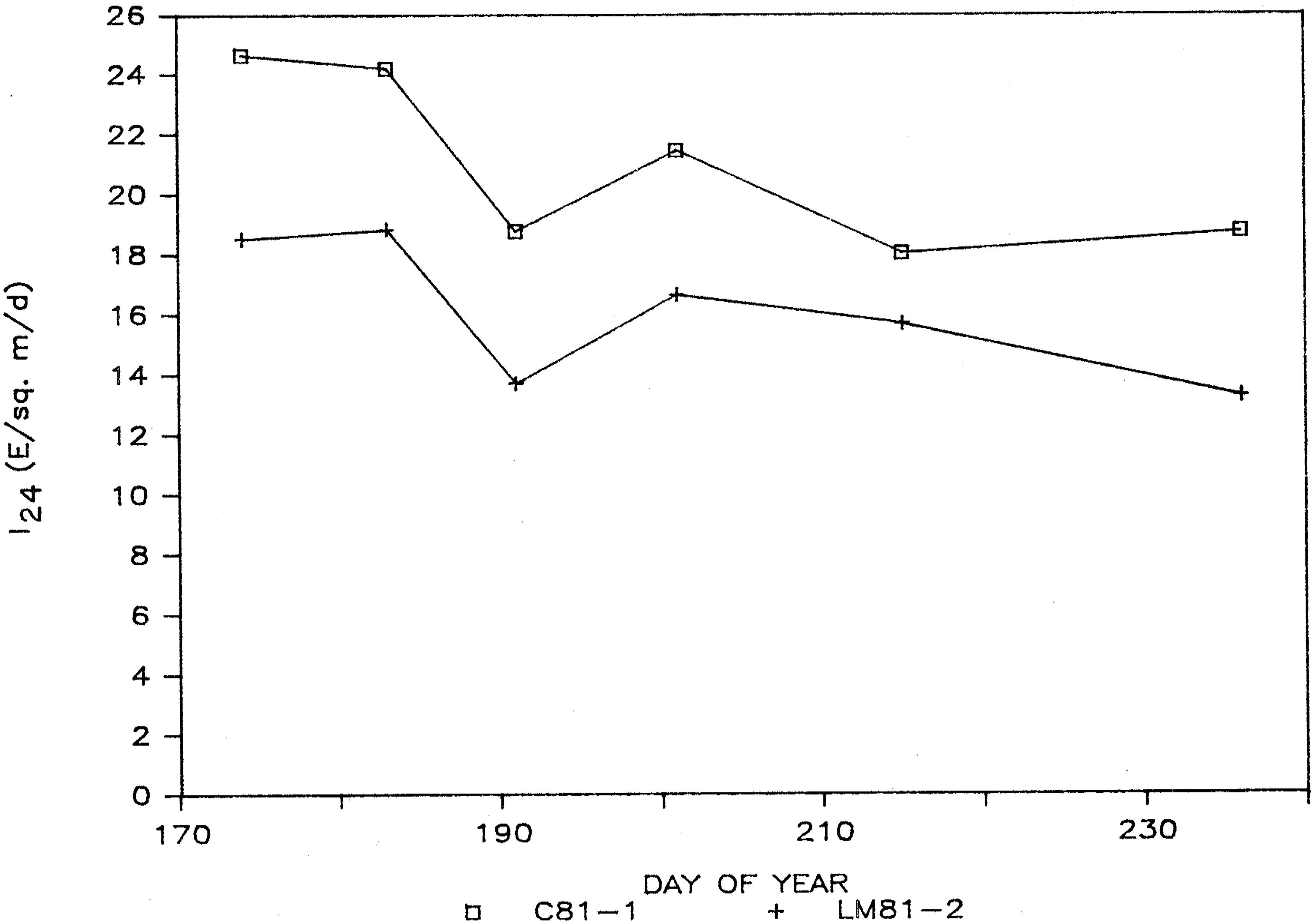
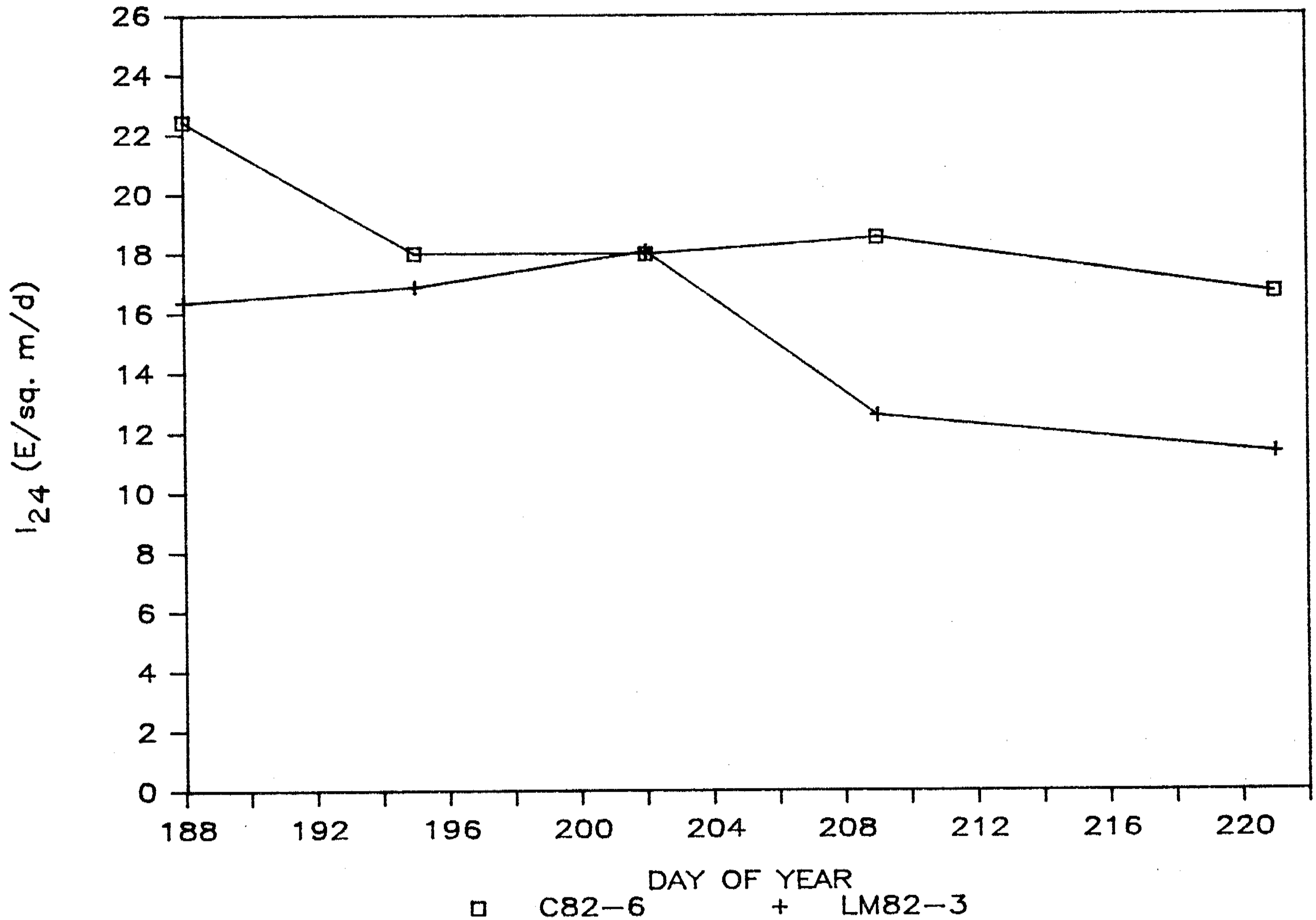

26
24
22
20
18
16
14
12
10
8
6
4
2
0
I_{24} (E/sq. m/d)
170
190
210
230
DAY OF YEAR
□ C81−1 + LM81−2

FIGURE 53. Seasonal pattern of the mean water column light intensity (I_{24}) in the 1982 moss-peat and control limnocorrals. C = control and LM = low moss. Day 188 is July 7 and day 220 is August 8.


I_{24} (E/sq. m/d)
DAY OF YEAR
C82-6
LM82-3

In the moss-peat limnocorrals P_m^B was slightly lower than in the controls in 1981 and 1982 and $alpha^B$ was considerably lower in 1981 and slightly lower in 1982 (Table 18). Low $alpha^B$ indicates that the algae in the moss-peat limnocorrals were less efficient at using subsaturating light intensities than algae in the controls. The fact that production in the moss-peat limnocorrals is related to $alpha^B$ means that the moss-peat material decreased primary productivity by affecting algal physiology rather than by reducing the availability of light. This suggests a nutrient rather than a physical limitation. It has already been demonstrated that the major nutrients N and P were not limiting ; however, other essential micronutrients could have been in short supply.

Fe may have been the limiting nutrient in the moss-peat limnocorrals. Fe is an essential element valuable to microorganisms because of the large energy difference between its reduced (Fe^{2+}) and oxidized (Fe^{3+}) states. Fe is a component of many important enzyme systems (ferredoxin, cytochromes, electron transport chains) and is involved in major cellular functions (e.g. photosynthesis, respiration, and N_2 fixation). Fe is usually in the oxidized state under aerobic conditions and in this form is readily chelated by humic matter (Giesy 1976). As mentioned above there was a good correlation between humic color and TDP in the limnocorrals (Fig. 51), and PO_4^{3-} has been shown to be bound to DHM by Fe^{3+} and $Fe(OH)_3$ (Koenings and Hooper 1976; Francko and Heath 1983). The P nutrient status indicators showed that P was not limiting for algae in the moss-peat limnocorrals, but Fe itself may have been.

Jackson and Hecky (1980), studying lakes and reservoirs in the boreal forest of northern Manitoba, including SIL, found an inverse correlation between primary production and humic - colloidal hydrated ferric oxide complexes. They hypothesized that humic matter binds Fe making it unavailable to algae. Sakamoto (1971) also found evidence for Fe limitation in the presence of humic matter. He found the addition of humic matter alone to lakewater reduced primary production but the addition of humic matter plus Fe and trace metals stimulated primary production. Limitation by Fe is difficult to prove. Although Fe chelating compounds have been identified for one species of algae (Murphy and Lean 1976), techniques to detect Fe limitation are just being developed (Trick 1983). To clarify whether Fe might be the limiting factor in the moss-peat limnocorrals, three enrichment experiments were conducted using water from the moss-peat limnocorrals. These experiments are discussed in a separate section.

In spite of overall lower rates of primary productivity in the moss-peat limnocorrals, the zooplankton numbers were much higher than in the controls. The zooplankton were probably feeding on the bacteria which were growing on the moss-peat material at the bottom of the limnocorral. During the two months the moss-peat material was submerged in 1981, the carbon content decreased by about 22%. If 22% of the total carbon added to the moss-peat limnocorral (23.9 Kg C) was metabolized by bacteria 5,250 grams organic C would be respired. This amount is about 3 times the cumulative integral primary productivity for the moss-peat limnocorral, more than enough carbon to explain the large zooplankton populations.

Thus in these moss-peat limnocorral experiments, the moss-peat material had a negative affect on primary productivity but the secondary levels of productivity were stimulated. In the sediment limnocorrals the addition of SIL shoreline sediments inhibited primary productivity by decreasing light, and zooplankton numbers decreased in direct proportion to primary productivity. The sediments added to these limnocorrals were mainly inorganic and apparently offered little suitable substrate for bacterial activity.

Moss-peat algal interactions in the one and six year old limnocorrals

In the moss-peat limnocorral studied for two years (OM82-8) the inhibitory effect of the moss-peat material disappeared after one year. Water was allowed to circulate with outside lake water for two days at the beginning of the second summer so this may have diluted the "inhibitory factor". However, once the limnocorral sides were sealed to the bottom sediments again, the moss at the bottom did not release sufficient humic material to color the water significantly or inhibit productivity. The inhibitory effect was probably nullified by a combination of photodegradation of DHM, mineralization of the moss-peat material by bacteria and flushing. Photodegradation of DHM has been demonstrated by Stewart and Wetzel (1981) and Francko and Heath (1979). The oxygen saturation data for the limnocorrals show that the moss-peat limnocorrals had consistently higher levels of O_2 consumption probably due to bacterial activity.

It is difficult to say whether after six years the flooded moss-peat vegetation still affected algal growth in FM82-1. Biomass was high relative to the control, and the limnocorral FM82-1 was more P deficient than the control. This suggests the moss-peat vegetation no longer inhibited the algal population. Production was measured only twice, and it was lower than the control, however this may have been due to the shallow depth of the limnocorral.

ENRICHMENT EXPERIMENTS

INTRODUCTION

The enrichment experiments were designed to test three hypotheses regarding the moss peat limnocorrals. The first hypothesis was that Fe or some other metal was limiting because it was bound tightly by DHM. This hypothesis was tested in all three enrichment experiments. The other two hypotheses arose as a result of the first enrichment experiment. It was expected that, if Fe or some other metal was limiting, a positive response to enrichment would be observed. The enrichment did stimulate the algae, but there was also a positive response in the untreated flask. Since the major change in the unenriched flask was exposure to continuous artificial light in the laboratory, it was hypothesized that light quantity or quality may have been a limiting factor in the moss peat limnocorral. This hypothesis was tested in an in situ experiment. The third hypothesis, also formed to explain the positive response in the untreated flask, was that in order for inhibition to occur the moss-peat material had to remain in contact with the water. This hypothesis was tested in the second enrichment experiment and in the in situ enrichment experiment.

RESULTS

Enrichment experiment I

The first enrichment experiment began on August 7,1981 (day 220). At this time inhibition in the moss-peat limnocorral was well established. LM81-2 had less chlorophyll, primary productivity and alkaline phosphatase activity than the control. Water from each limnocorral was treated with three types of enrichment: 1) trace metals, 2) Fe and EDTA, and 3) EDTA alone. After five days of incubation under continuous illumination in the laboratory, chlorophyll a, primary productivity and alkaline phosphatase activity increased in all four flasks containing water from moss peat LM81-2, including the "no enrichment" flask (Table 21). The largest response occurred in the two flasks enriched with Fe plus EDTA and EDTA alone. These two enrichments also stimulated chlorophyll a and primary productivity in the water from control C81-1 although not to the same degree.

Enrichment experiment II

The second enrichment experiment was started August 1, 1982 (day 213) after inhibition in moss-peat limnocorral LM82-3 was established. Water from both the control (C82-6) and the moss-peat (LM82-3) limnocorrals was enriched with: 1) Fe and EDTA or 2) moss-peat material dredged from LM82-3. As in the first enrichment experiment the water from the moss-peat limnocorral responded more to enrichment than the water from the control. The results of the experiment are given in Figs. 54 to 59. The largest response was to Fe and EDTA. After five days chlorophyll increased seven-fold, primary production nine-fold and alkaline phosphatase activity changed from indicating P deficiency to indicating severe P deficiency. The Fe and EDTA enriched water from the control C82-6 was not stimulated at all; chlorophyll, primary productivity, and alkaline phosphatase activity were all considerably lower at the end of five days.

TABLE 21. Results of the first enrichment experiment. Control water was from control limnocorral C81-1 and moss-peat water was from moss-peat limnocorral LM81-2.

Analysis	Water	Day	ENRICHMENT Trace metals	Fe, EDTA	EDTA	None
Chlorophyll ($ug\ L^{-1}$)	control	2	1.1	1.0	1.3	1.4
		5	1.1	1.7	1.5	1.4
	moss-peat	2	1.3	2.6	1.9	2.0
		5	2.7	5.1	4.1	3.2
Primary Productivity ($mg\ C\ m^{3}\ h^{-1}$)	control	2	3.3	3.8	3.2	3.8
		5	3.6	5.2	4.2	3.4
	moss-peat	2	6.0	5.7	5.3	7.4
		5	9.3	11.1	10.6	9.0
Allkaline Phosphatase ($umole\ P\ h^{-1}\ ug\ ATP^{-1}$)	control	2	0.13	0.31	0.16	0.11
		5	0.23	0.17	0.24	0.21
	moss-peat	2	0.02	0.02	0.00	0.00
		5	0.14	0.11	0.12	0.15

FIGURE 54. Chlorophyll a concentrations in water from control limnocorral C82-6 enriched with a solution of Fe and EDTA or flooded moss-peat material from moss-peat limnocorral LM82-3. "None" means no enrichment. Day 0 was August 1, 1982.

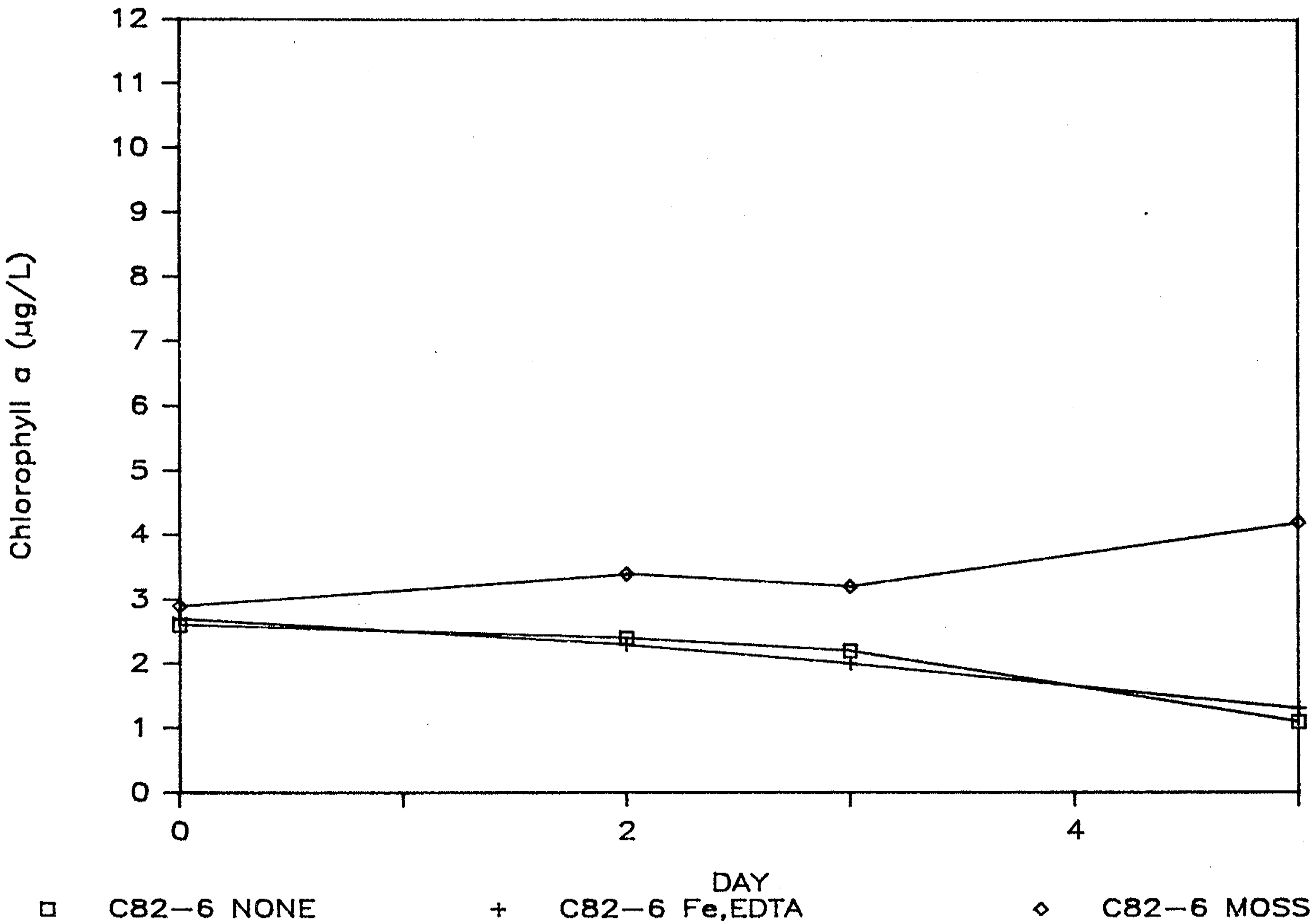

Chlorophyll a (µg/L)
0
1
2
3
4
5
6
7
8
9
10
11
12
0
2
4
DAY
C82–6 NONE
C82–6 Fe,EDTA
C82–6 MOSS

FIGURE 55. Chlorophyll a concentrations in water from moss-peat limnocorral LM82-3 enriched with a solution of Fe and EDTA or flooded moss-peat material from moss-peat limnocorral LM82-3. "None" means no enrichment. Day 0 was August 1, 1982.

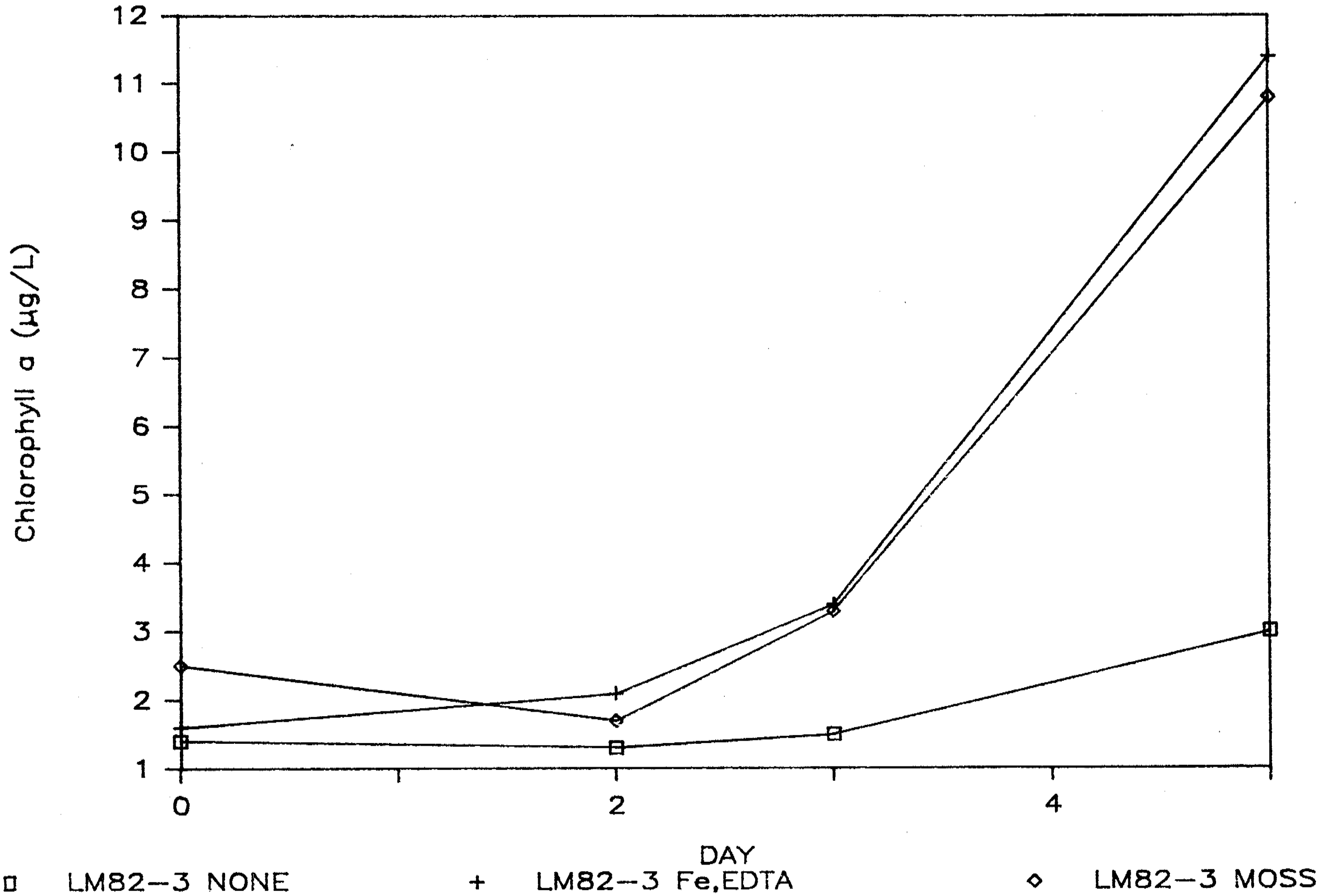
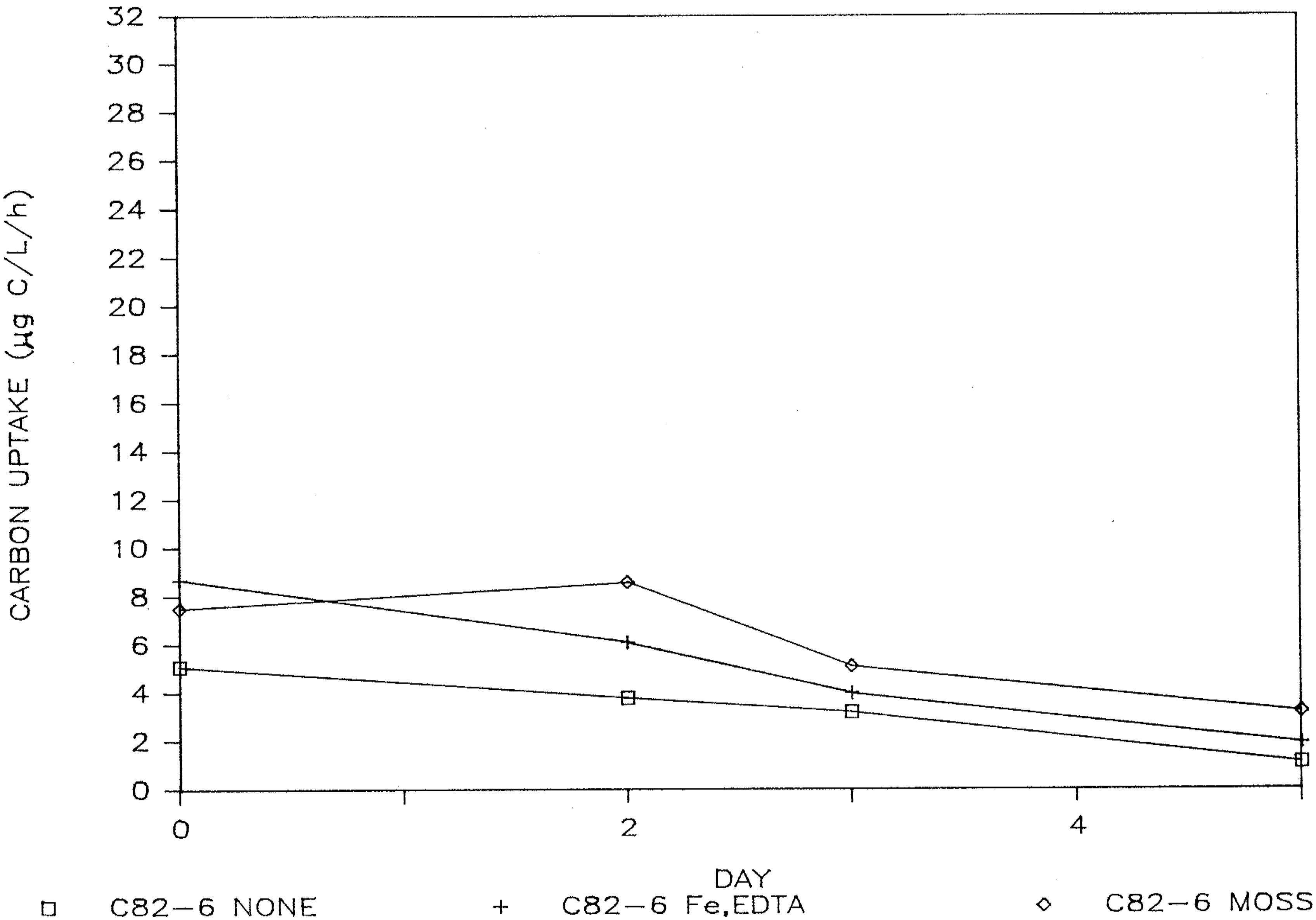
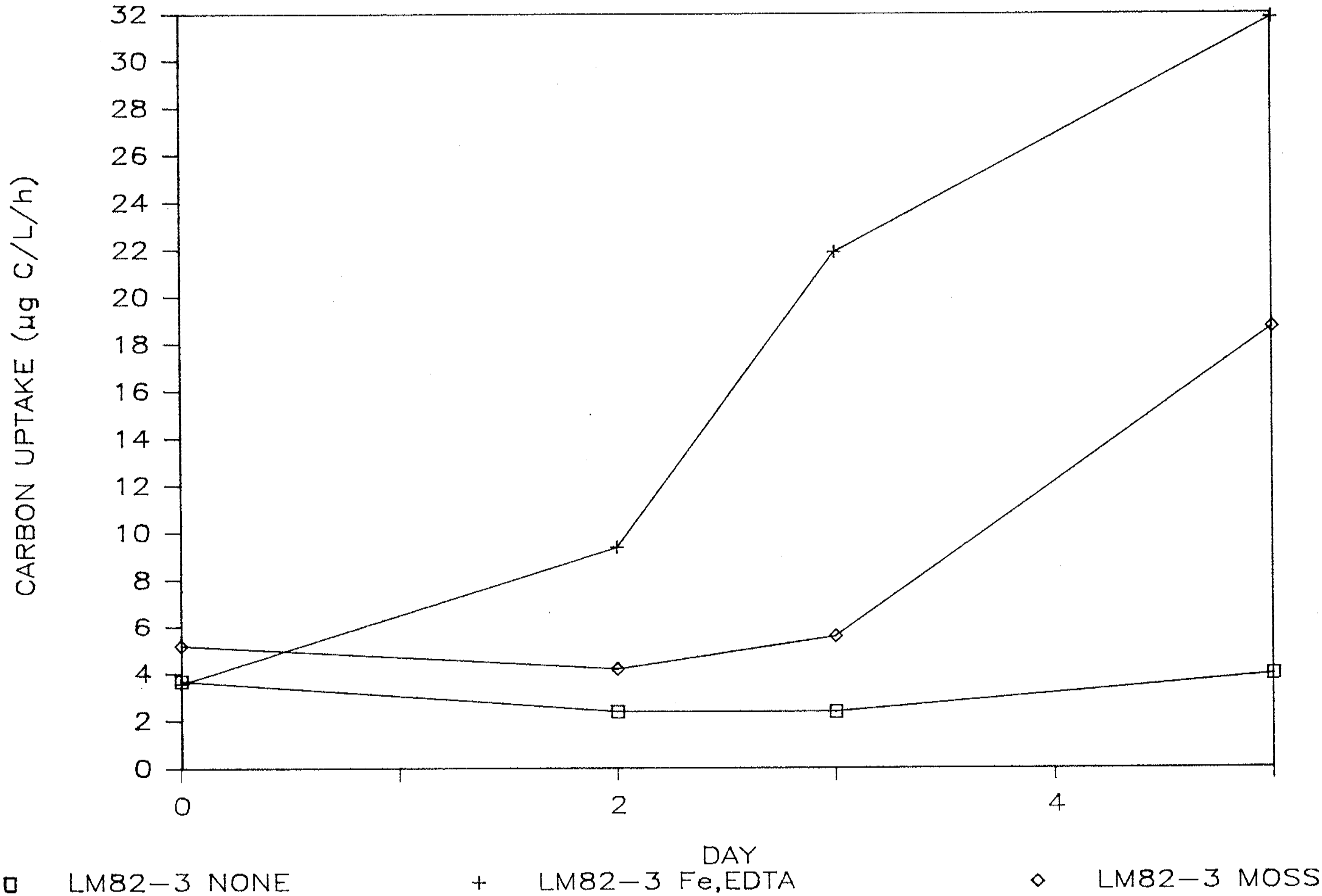

12
11
10
9
8
7
6
5
4
3
2
1
Chlorophyll a (μg/L)
0
2
4
DAY
LM82—3 NONE
LM82—3 Fe,EDTA
LM82—3 MOSS

FIGURE 56. Photosynthetic carbon uptake in water from control limnocorral C82-6 enriched with a solution of Fe and EDTA or flooded moss-peat material from moss-peat limnocorral LM82-3. "None" means no enrichment. Day 0 was August 1, 1982.



CARBON UPTAKE (µg C/L/h)
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
0
2
4
DAY
C82-6 NONE
C82-6 Fe,EDTA
C82-6 MOSS

FIGURE 57. Photosynthetic carbon uptake in water from moss-peat limnocorral LM82-3 enriched with a solution of Fe and EDTA or flooded moss-peat material from moss-peat limnocorral LM82-3. "None" means no enrichment. Day 0 was August 1, 1982.



CARBON UPTAKE (µg C/L/h)
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
0
2
4
DAY
LM82-3 NONE
LM82-3 Fe,EDTA
LM82-3 MOSS

FIGURE 58. Alkaline phosphatase activity (Pase) in water from control limnocorral C82-6 enriched with a solution of Fe and EDTA or flooded moss-peat material from moss-peat limnocorral LM82-3. The broken horizontal line indicates the occurrence of severe P deficiency in algae as given by Healey and Hendzel (1979). The range for moderate P deficiency is denoted by the symbol "M". "None" means no enrichment. Day 0 was August 1, 1982.

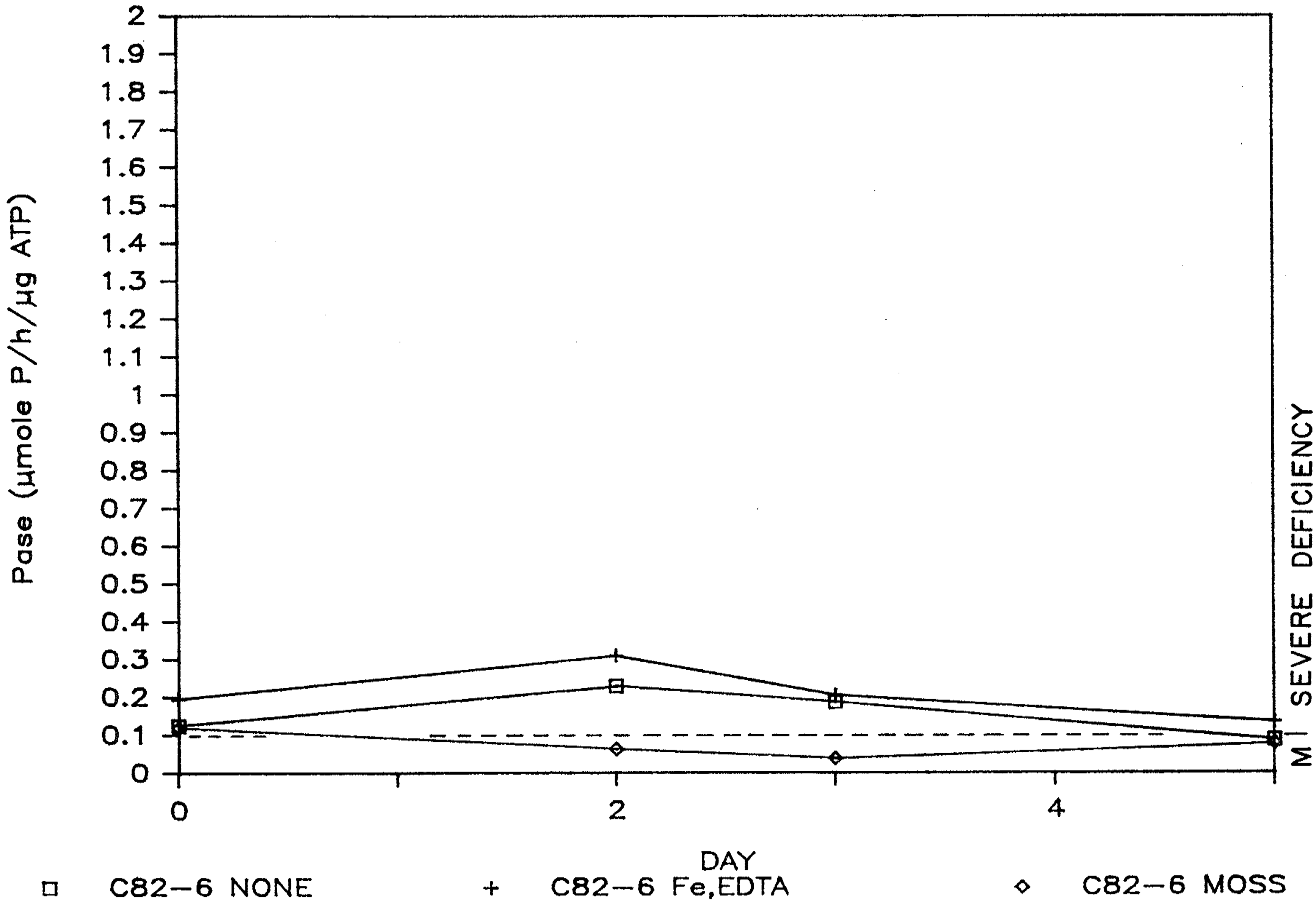
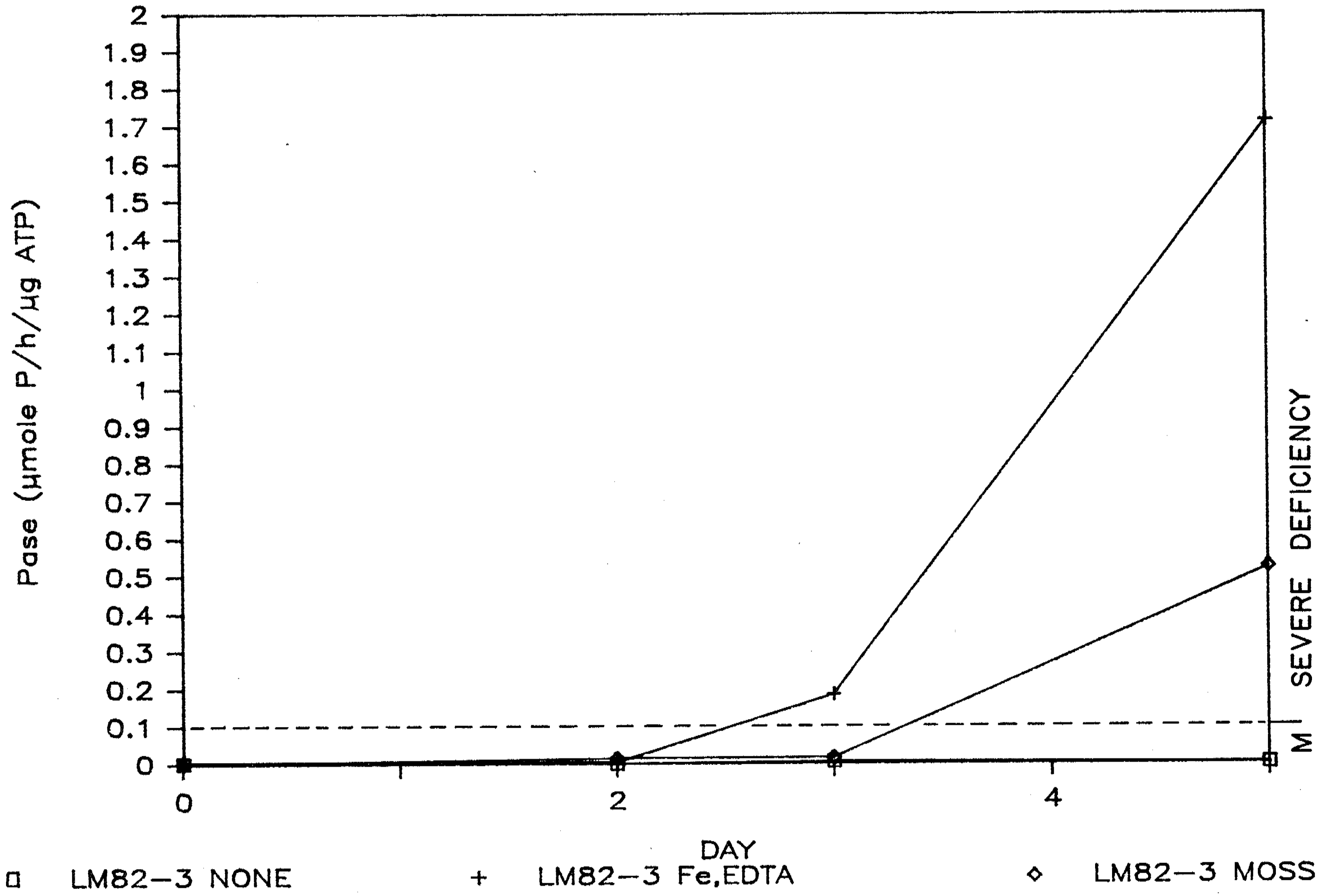

Pase (µmole P/h/µg ATP)
2
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
2
4
DAY
SEVERE DEFICIENCY
M
C82−6 NONE
C82−6 Fe,EDTA
C82−6 MOSS

FIGURE 59. Alkaline phosphatase activity (Pase) in water from moss-peat limnocorral LM82-3 enriched with a solution of Fe and EDTA or flooded moss-peat material from moss-peat limnocorral LM82-3. The broken horizontal line indicates the occurrence of severe P deficiency in algae as given by Healey and Hendzel (1979). The range for moderate P deficiency is denoted by the symbol "M". "None" means no enrichment. Day 0 was August 1, 1982.



Pase (μmole P/h/μg ATP)
2
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
2
4
DAY
SEVERE DEFICIENCY
M
LM82-3 NONE
LM82-3 Fe,EDTA
LM82-3 MOSS

Unlike the first enrichment experiment, enclosing water from moss-peat limnocorral LM82-3 in a flask with no enrichment did not stimulate primary productivity or alkaline phosphatase activity although chlorophyll doubled. The water from the control C82-6 responded negatively to enclosure in a flask with no enrichment.

Enclosing the water from the moss-peat limnocorral LM82-3 with moss-peat material dredged from LM82-3 resulted in a four-fold increase in chlorophyll and primary production and caused the development of severe P deficiency. Moss-peat material incubated with water from control C82-6 stimulated chlorophyll a slightly but not primary productivity or alkaline phosphatase activity.

In situ enrichment experiment

The *in situ* experiment was conducted simultaneously with the second enrichment experiment and was similar in design except that only water from the moss-peat limnocorral was used and the water was incubated in larger containers suspended within the moss-peat limnocorral. The containers were incubated at two depths to determine whether light was limiting. One container was shaded with a screen and suspended at the surface. This container received the same amount of light as a container suspended at 0.8 m without a screen. These two containers were compared to see whether the change in light quality due to absorbance by DHM would affect productivity.

Results for the *in situ* enrichment experiment are in Figures 60 to 68. Fe and EDTA enrichment of the container suspended at the surface stimulated chlorophyll and primary productivity four-fold and resulted in severe P deficiency. A smaller response was observed at 0.8 m.

FIGURE 60. Chlorophyll a concentrations in water from the moss-peat limnocorral LM82-3 in 20 L containers suspended _in situ_ at the surface (0 m). The containers were enriched with either a solution of Fe and EDTA or flooded moss-peat material from moss-peat limnocorral LM82-3. "None" means no treatment. Day 0 was August 1, 1982.

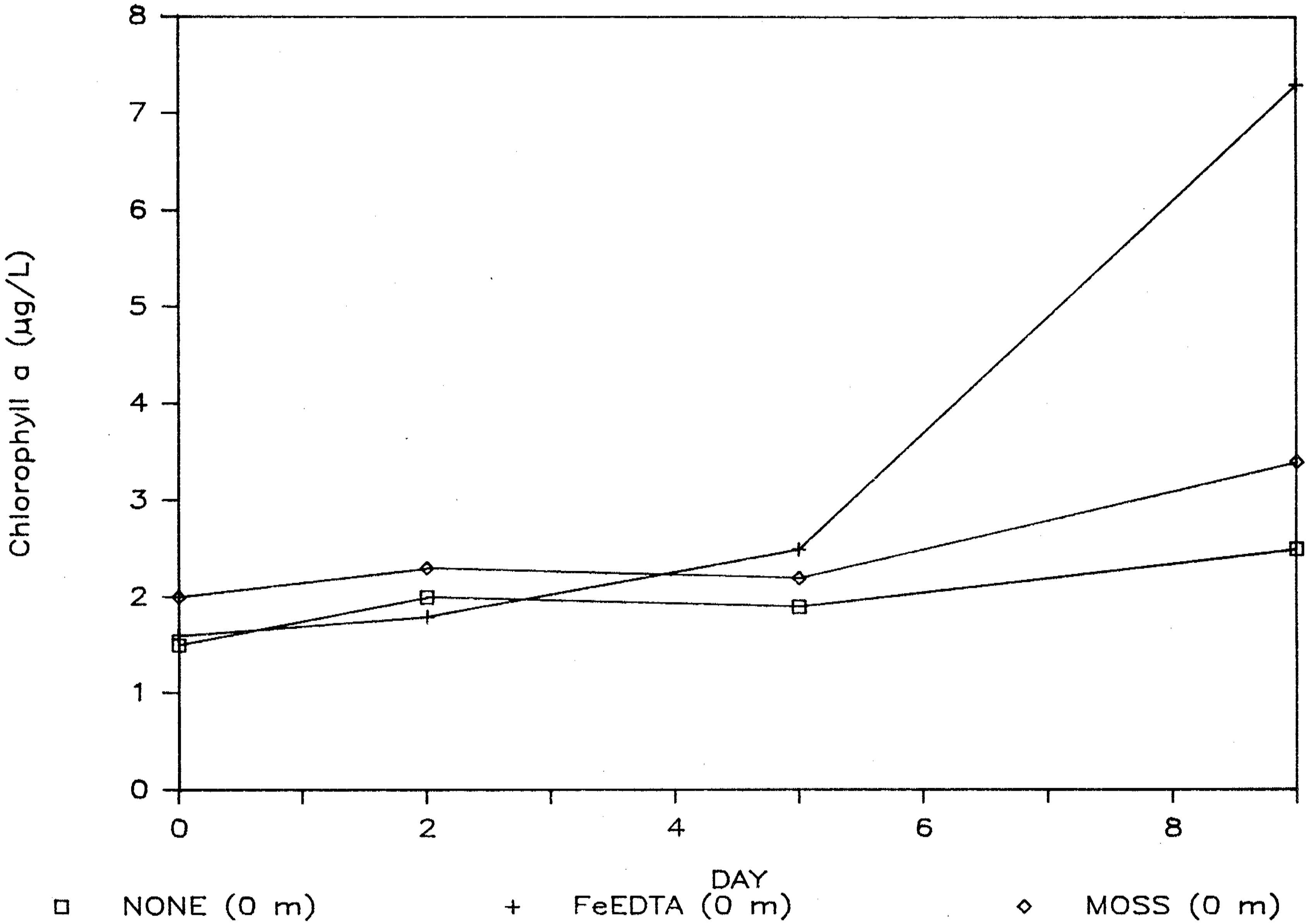
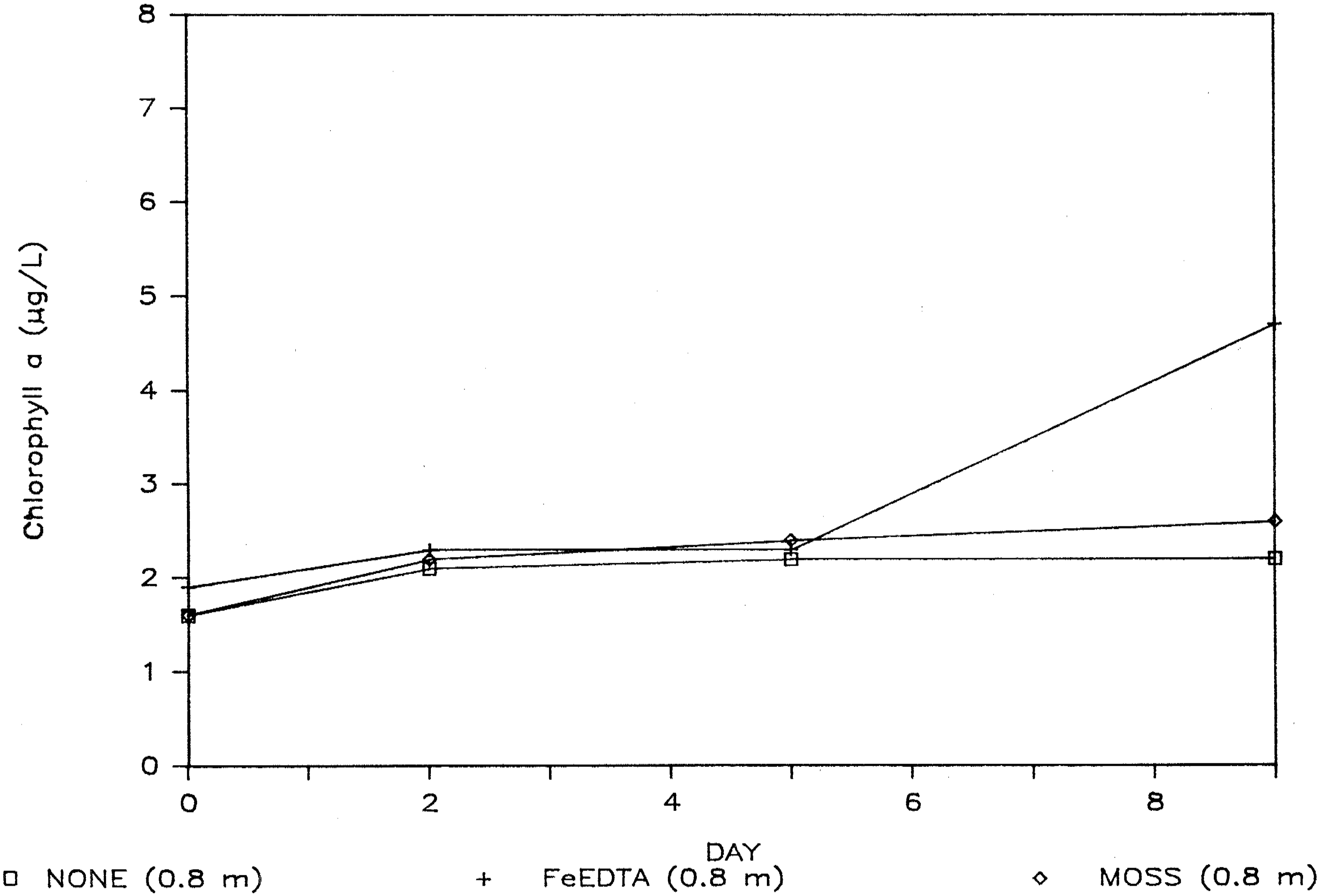
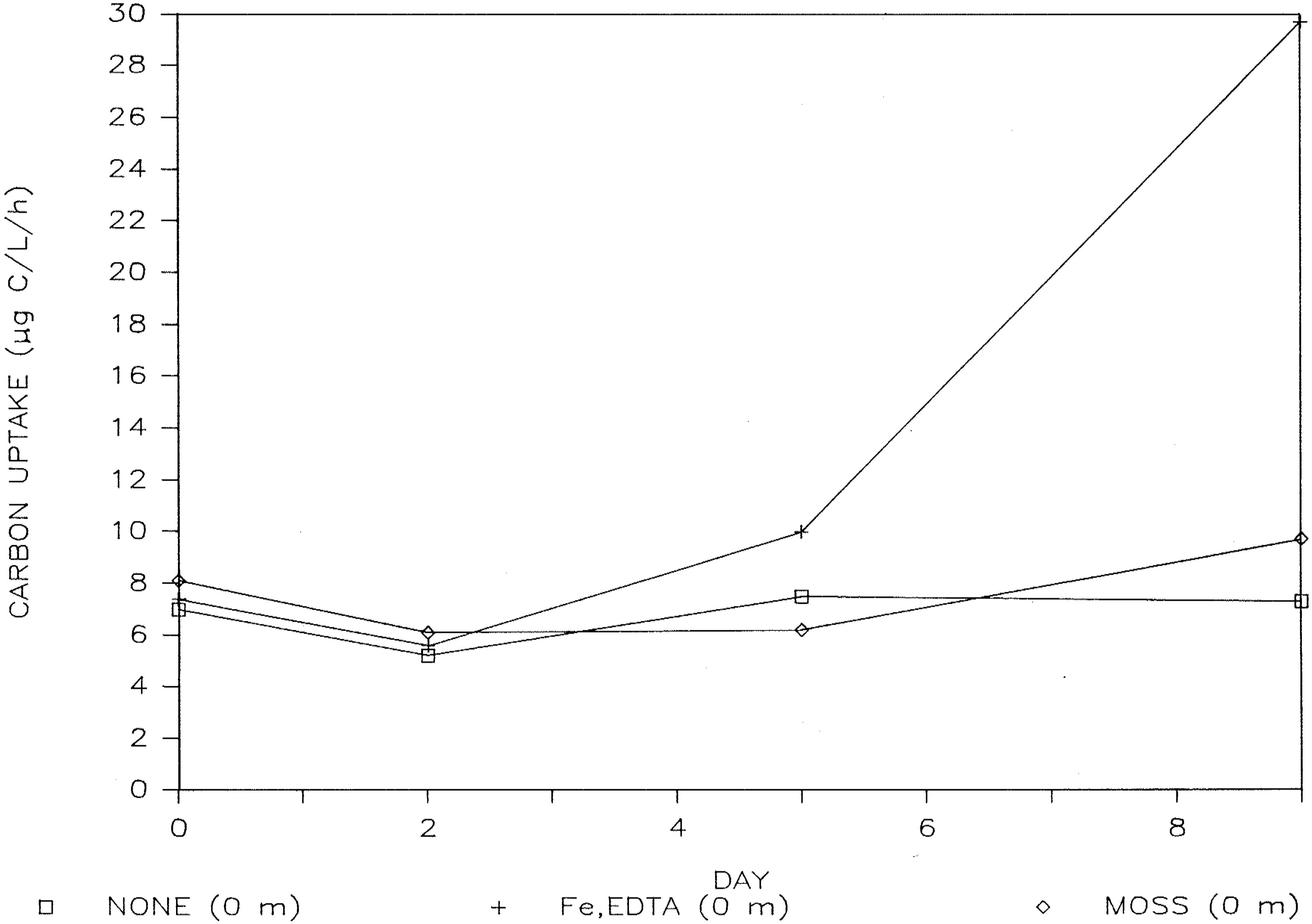

Chlorophyll a (μg/L)
0
1
2
3
4
5
6
7
8
0
2
4
6
8
DAY
NONE (0 m)
FeEDTA (0 m)
MOSS (0 m)

FIGURE 61. Chlorophyll a concentrations in water from the moss-peat limnocorral LM82-3 in 20 L containers suspended *in situ* below the surface (0.8 m). The containers were enriched with either a solution of Fe and EDTA or flooded moss-peat material from moss-peat limnocorral LM82-3. "None" means no treatment. Day 0 was August 1, 1982.



8
7
6
5
4
3
2
1
0
Chlorophyll a (µg/L)
0
2
4
6
8
DAY
□ NONE (0.8 m)
+ FeEDTA (0.8 m)
◇ MOSS (0.8 m)

FIGURE 62. Photosynthetic carbon uptake in water from the moss-peat limnocorral LM82-3 in 20 L containers suspended *in situ* at the surface (0 m). The containers were enriched with either a solution of Fe and EDTA or flooded moss-peat material from moss-peat limnocorral LM82-3. "None" means no treatment. Day 0 was August 1, 1982.



CARBON UPTAKE (µg C/L/h)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
DAY
NONE (0 m)
Fe,EDTA (0 m)
MOSS (0 m)

FIGURE 63. Photosynthetic carbon uptake in water from the moss-peat limnocorral LM82-3 in 20 L containers suspended *in situ* below the surface (0.8 m). The containers were enriched with either a solution of Fe and EDTA or flooded moss-peat material from moss-peat limnocorral LM82-3. "None" means no treatment. Day 0 was August 1, 1982.

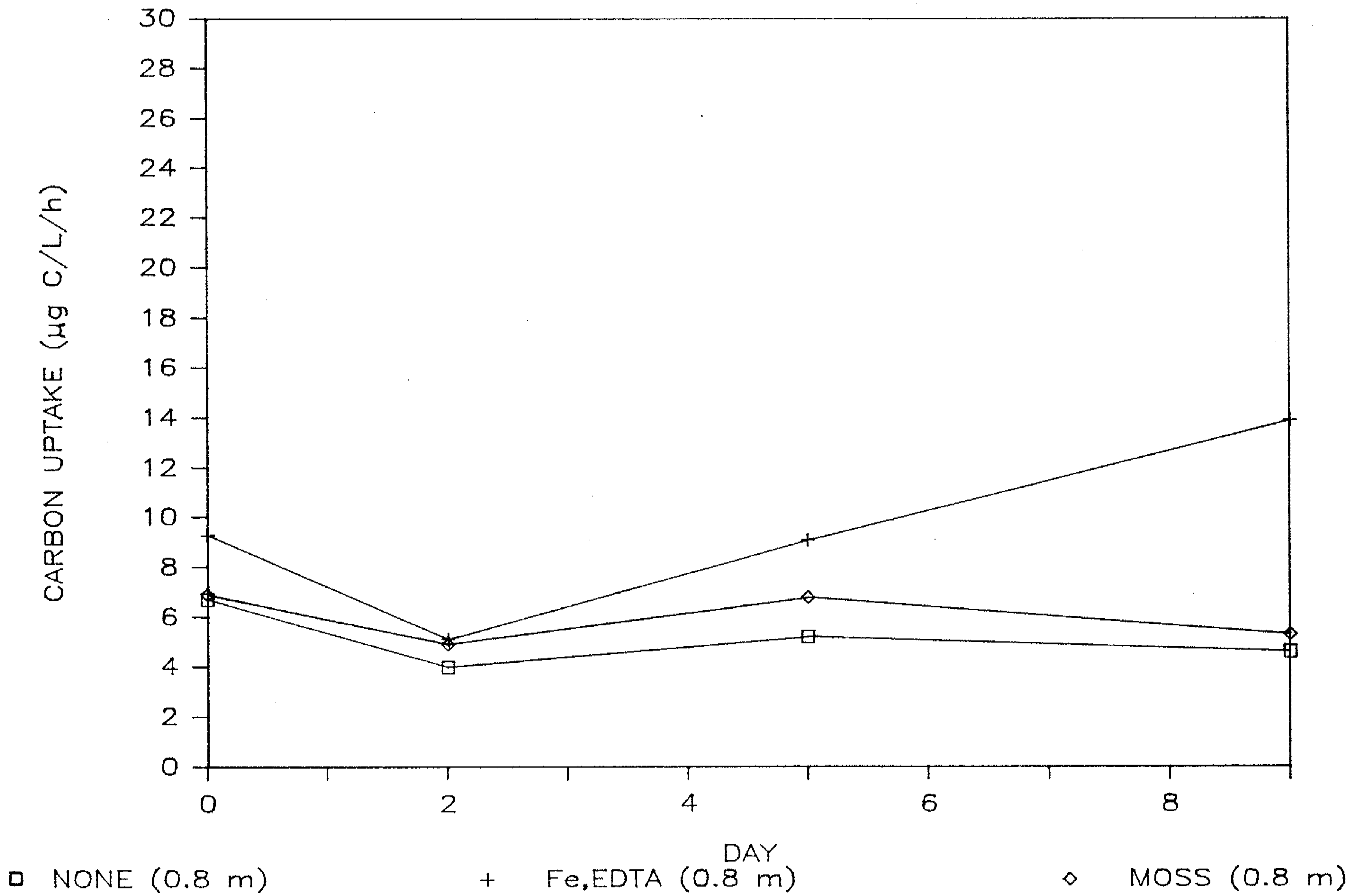
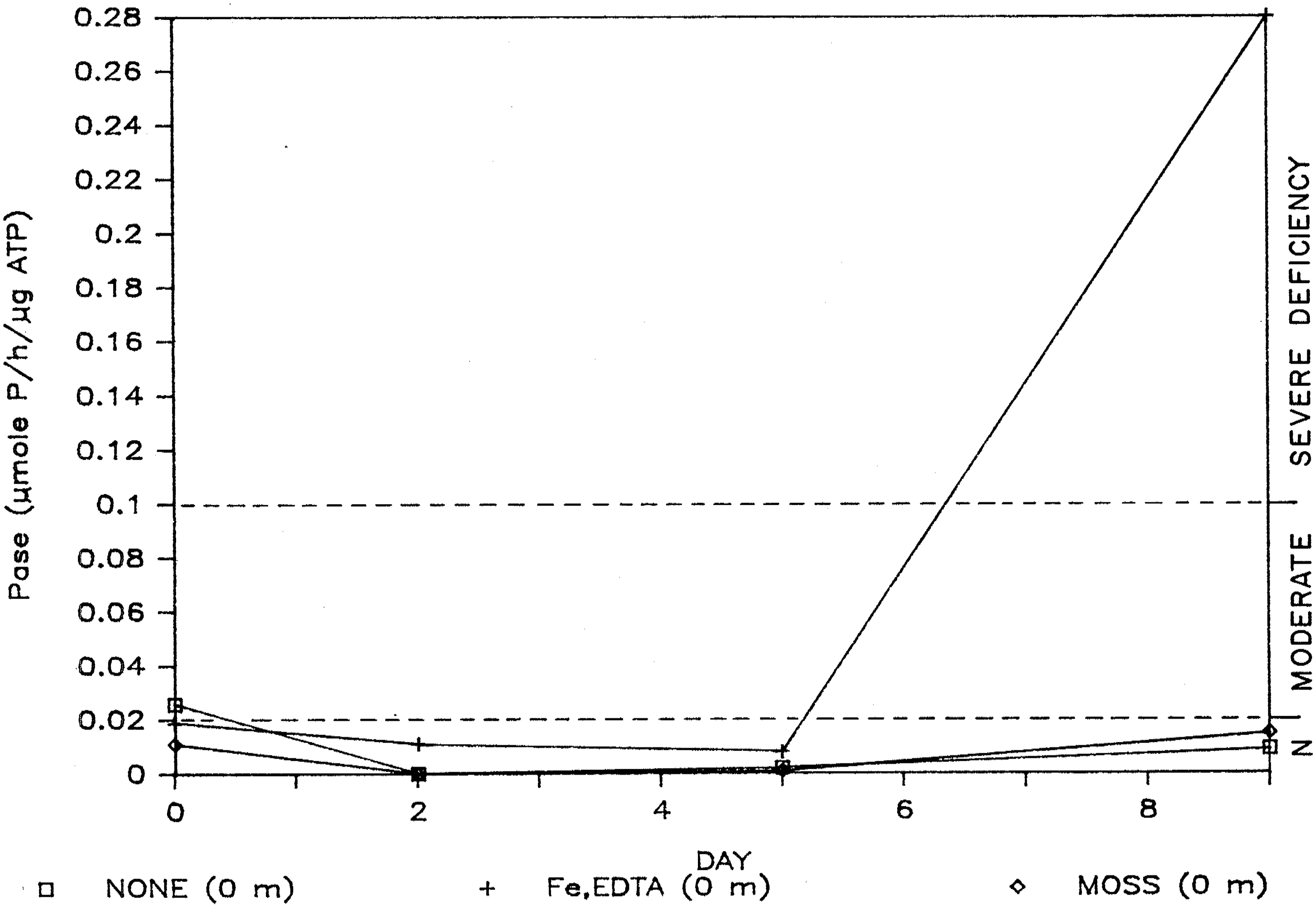

CARBON UPTAKE (µg C/L/h)
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
0
2
4
6
8
DAY
NONE (0.8 m)
Fe,EDTA (0.8 m)
MOSS (0.8 m)

FIGURE 64. Alkaline phosphatase activity (Pase) in water from the moss-peat limnocorral LM82-3 in 20 L containers suspended *in situ* at the surface (0 m). The broken horizontal lines indicate the occurrence of severe, moderate, and no P deficiency in algae as given by Healey and Hendzel (1980). The containers were enriched with either a solution of Fe and EDTA or flooded moss-peat material from moss-peat limnocorral LM82-3. "None" means no treatment. Day 0 was August 1, 1982.



0.28
0.26
0.24
0.22
0.2
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Pase (µmole P/h/µg ATP)
0
2
4
6
8
DAY
SEVERE DEFICIENCY
MODERATE
N
□ NONE (0 m)
+ Fe,EDTA (0 m)
◇ MOSS (0 m)

FIGURE 65. Alkaline phosphatase activity (Pase) in water from the moss-peat limnocorral LM82-3 in 20 L containers suspenede *in situ* below the surface (0.8 m). The broken horizontal lines indicate the occurrence of severe, moderate, ane no P deficiency in algae as given by Healey and Hendzel (1980). The containers were enriched with either a solution of Fe and EDTA or flooded moss-peat material from moss-peat limnocorral LM82-3. "None" means no treatment. Day 0 was August 1, 1982.

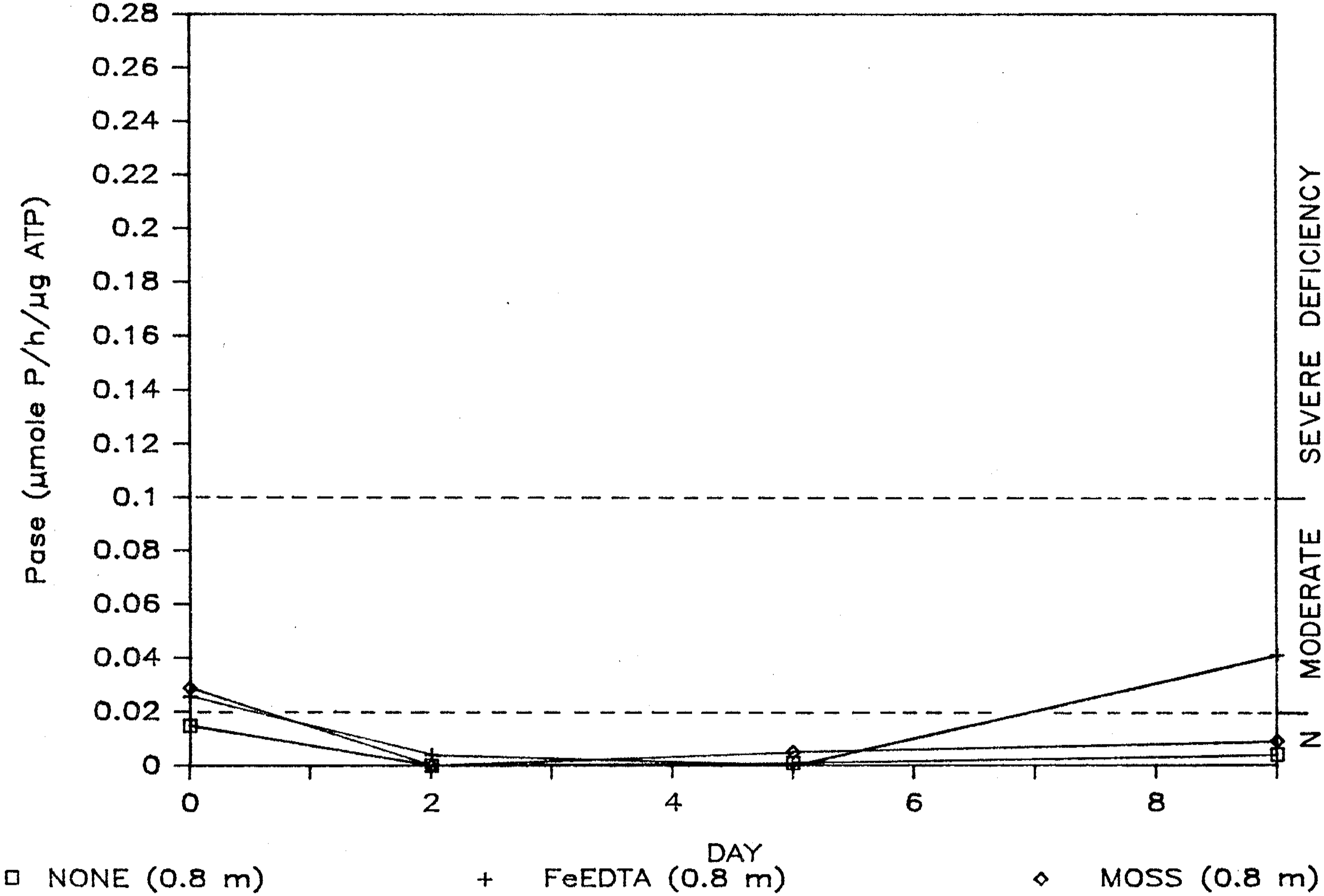
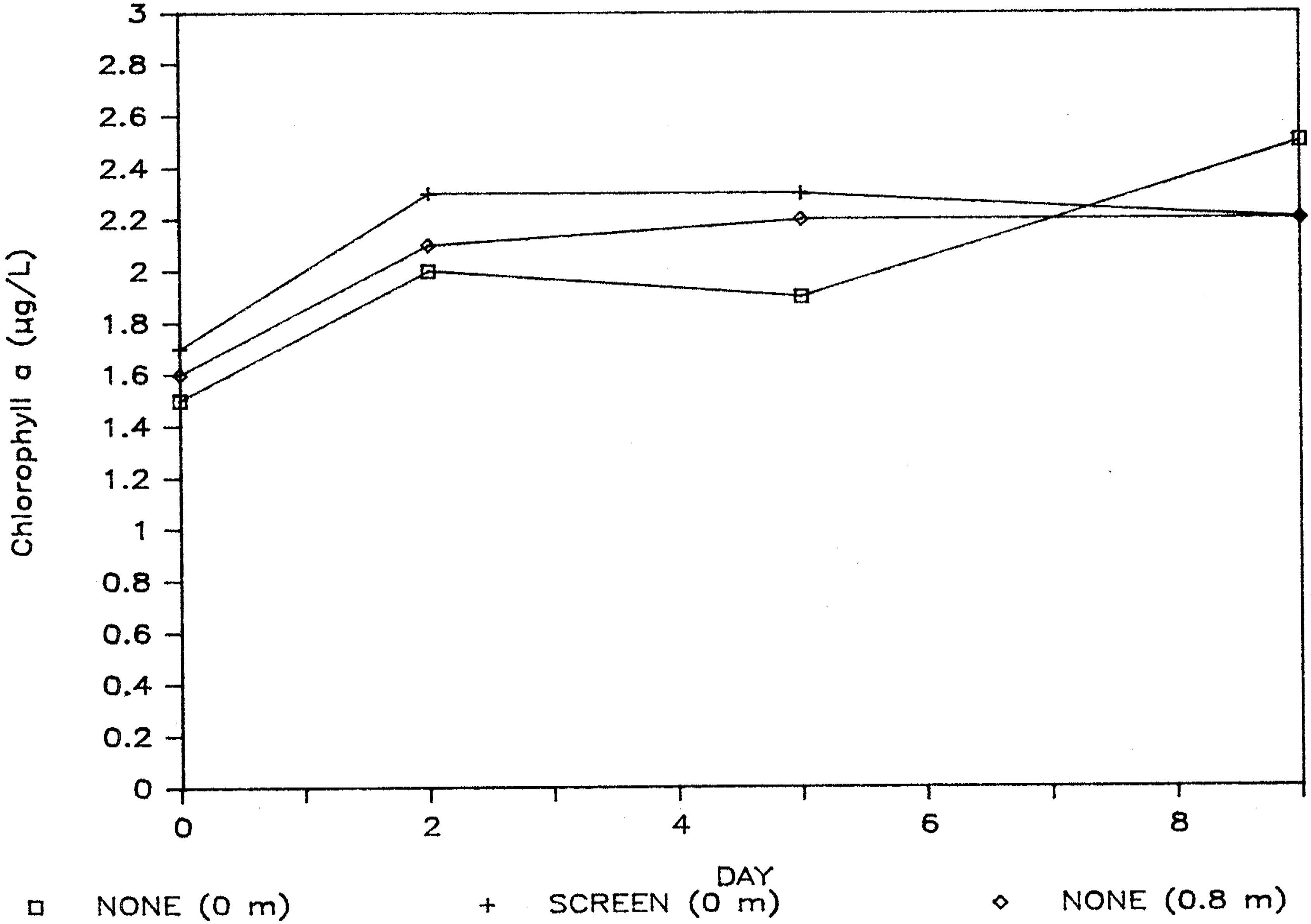

0.28
0.26
0.24
0.22
0.2
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Pase (µmole P/h/µg ATP)
0
2
4
6
8
DAY
SEVERE DEFICIENCY
MODERATE
N
NONE (0.8 m)
FeEDTA (0.8 m)
MOSS (0.8 m)

FIGURE 66. Chlorophyll a concentrations in water from the moss-peat limnocorral LM82-3 in 20 L containers suspended *in situ* at the surface (0 m) and below the surface (0.8 m). One of the containers at the surface was covered with a screen which reduced the light intensity inside the container to the same as the light intensity in the container at 0.8 m. "None" means no screen. Day 0 was August 1, 1982.



Chlorophyll a (µg/L)
3
2.8
2.6
2.4
2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
2
4
6
8
DAY
□ NONE (0 m)
+ SCREEN (0 m)
◇ NONE (0.8 m)

FIGURE 67. Photosynthetic carbon uptake in water from the moss-peat limnocorral LM82-3 in 20 L containers suspended *in situ* at the surface (0 m) and below the surface (0.8 m). One of the containers at the surface was covered with a screen which reduced the light intensity inside the container to the same as the light intensity in the container at 0.8 m. "None" means no screen. Day 0 was August 1, 1982.

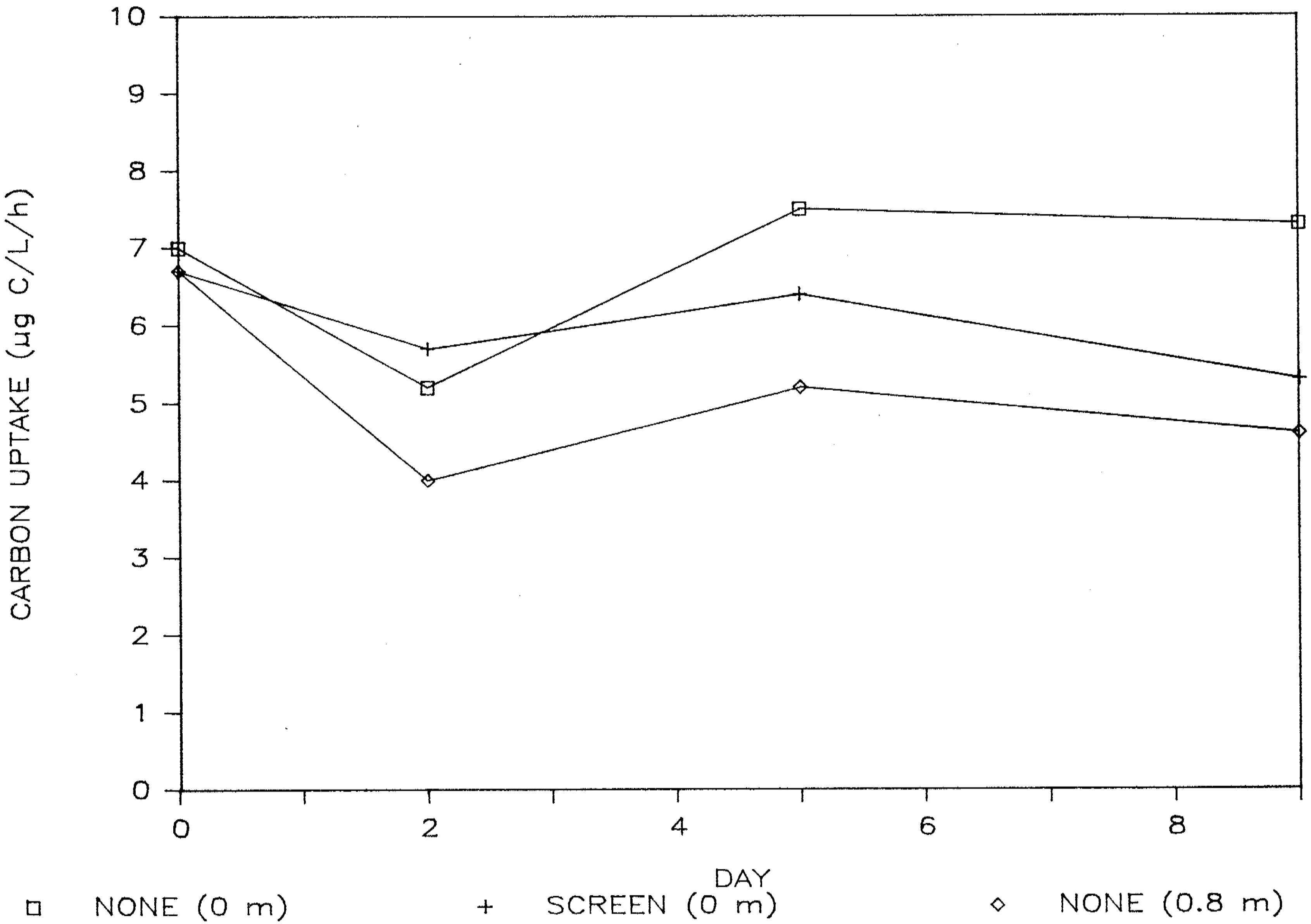
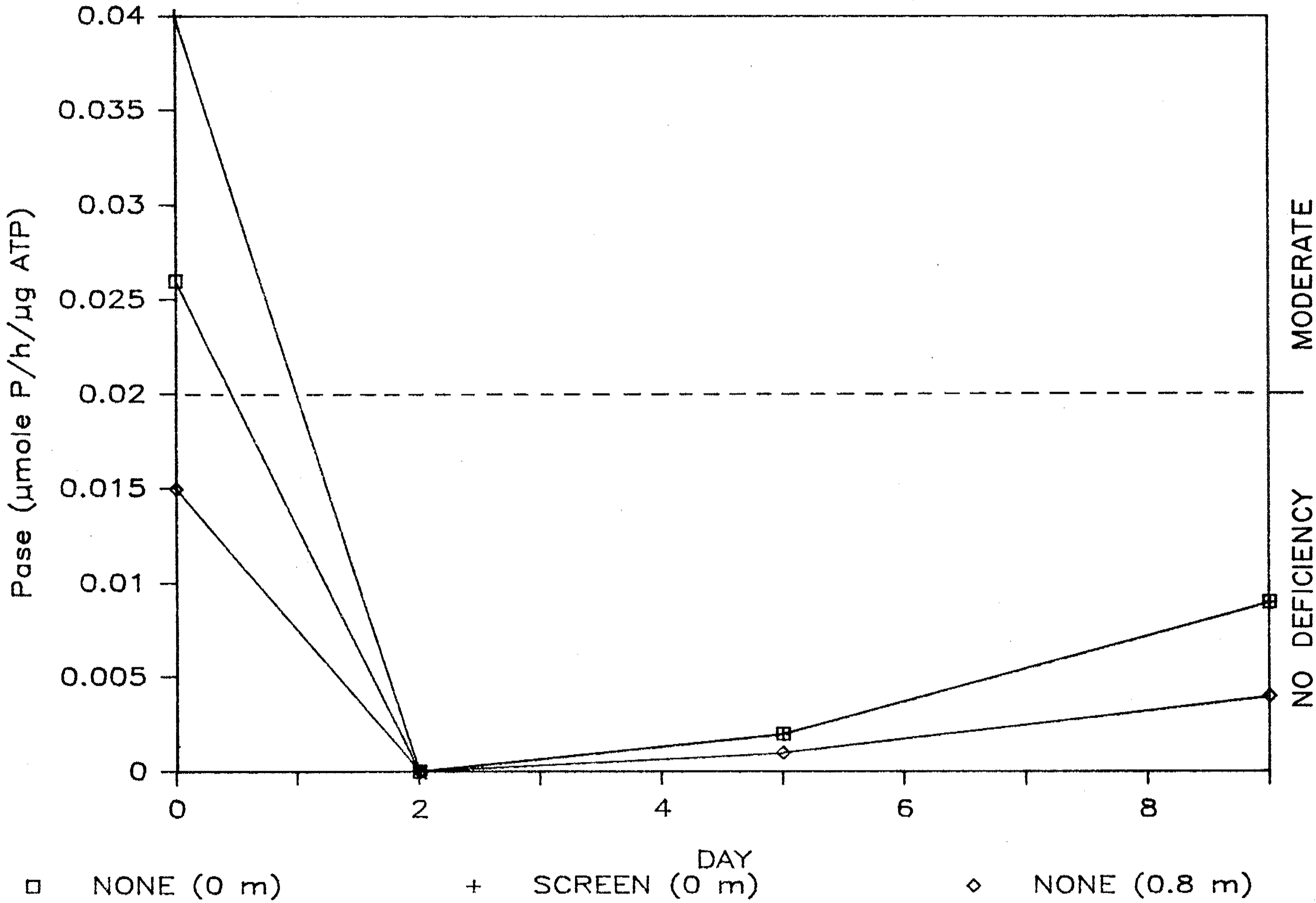

10
9
8
7
6
5
4
3
2
1
0
CARBON UPTAKE (µg C/L/h)
0
2
4
6
8
DAY
□ NONE (0 m)
+ SCREEN (0 m)
◇ NONE (0.8 m)

FIGURE 68. Alkaline phosphatase activity (Pase) in water from the moss-peat limnocorral LM82-3 in 20 L containers suspended *in situ* at the surface (0 m) and below the surface (0.8 m). One of the containers at the surface was covered with a screen which reduced the light intensity inside the container to the same as the light intensity in the container at 0.8 m. The broken horizontal line indicates the occurrence of moderate P deficiency in algae as given by Healey and Hendzel (1979). "None" means no screen. Day 0 was August 1, 1982.



0.04
0.035
0.03
0.025
0.02
0.015
0.01
0.005
0
Pase (µmole P/h/µg ATP)
0
2
4
6
8
DAY
MODERATE
NO DEFICIENCY
□ NONE (0 m)
+ SCREEN (0 m)
◇ NONE (0.8 m)

In the unenriched container at the surface, the chlorophyll increased 70% over nine days, primary productivity remained constant and alkaline phosphatase activity decreased. At 0.8 m, chlorophyll increased 40%, and primary productivity and alkaline phosphatase activity decreased.

Moss-peat material, dredged from LM82-3, caused a small but consistent increase in chlorophyll, primary productivity and alkaline phosphatase activity in the surface container. At 0.8 m chlorophyll also increased but productivity and alkaline phosphatase activity decreased.

After nine days the chlorophyll in the screen-covered container was the same as in the container suspended at 0.8 m. Primary productivity and alkaline phosphatase activity were slightly higher.

DISCUSSION

Hypothesis I: The moss-peat limnocorrals are limited by Fe or some other metal bound by DHM

In all three enrichment experiments Fe and EDTA relieved the inhibition brought on by the moss peat vegetation. The results of the enrichment experiments support but do not prove the hypothesis that the moss-peat limnocorrals were limited by Fe or some other metal associated with DHM.

EDTA and other compounds with chelating properties such as TRIS and BICINE are used routinely in culturing algae. Chelators are added to media to prevent the precipitation of essential nutrients (Droop 1960, Lewin and Chen 1971). Without chelators, precipitates often form when the pH of the media is elevated during autoclaving. These precipitates can be insoluble and essentially remove available Fe and PO_4 from solution. In theory EDTA allows Fe to remain available because Fe is chelated rather than precipitated.

Anderson and Morel (1978) using labelled ^{59}Fe showed that EDTA chelated Fe so tightly that it was unavailable to Fe limited algae. However in the light EDTA broke down rapidly, ^{59}Fe became available, and the Fe-limited algae were stimulated. This may have been the mechanism by which EDTA stimulated the algae in the enrichment experiments. The largest response to Fe and EDTA was observed in the laboratory experiments where the flasks were illuminated constantly. In the _in situ_ experiment ambient light was lower than in the laboratory and the response to enrichment was not as great. The container at 0.8 m had the lowest response to Fe and EDTA enrichment.

Another way in which artificial chelators such as EDTA appear to stimulate algal growth is by chelating toxic metals. Sunda and Guillard (1976) and Anderson and Morel (1978) demonstrated that algae could grow at concentrations of Cu that are normally toxic as long as EDTA was present. In the moss-peat limnocorrals it is possible that toxic concentrations of metals were released when the moss-peat material was submerged and that EDTA stimulated growth by chelating these toxic metals.

Hypothesis II: Light quality and/or quantity due to absorbance by DHM was limiting in the moss-peat limnocorrals

It was expected that if DHM significantly reduced light penetration in the moss-peat limnocorrals, an increase in chlorophyll and productivity would be observed in the untreated carboy suspended at the suface of the moss peat limnocorral. At the end of the nine day in situ experiment there was slightly more chlorophyll a, primary production and alkaline phosphatase activity in the untreated carboy at the surface compared to the 0.8 m carboy. There was a much greater increase in the parameters measured in the two carboys enriched with Fe and EDTA suspended at both depths. This suggests that light intensity was not a limiting factor. It was only when the limiting factor was relieved by Fe + EDTA that a significant response to light was observed. Similarly, if light quality due to selective absorption by DHM was a limiting factor in the moss-peat limnocorrals, it was expected that chlorophyll a and productivity would be greater in the screen-covered container suspended at the surface, than in the carboy suspended at 0.8 m. There was no difference in chlorophyll a concentration but primary production was slighty higher at the surface.

The results of the in situ experiment suggest that light quantity and quality are potentially limiting in waters rich in DHM. However in this particular situation some other factor was limiting growth.

Hypothesis III: In order for inhibition to occur the moss-peat material must remain in contact with the water.

When moss-peat material dredged from the moss-peat limnocorral was incubated with the water in flasks in the laboratory or in large containers at the surface of the limnocorral, chlorophyll and productivity were stimulated. This is the opposite effect to what was expected if the moss peat vegetation was causing inhibition in the limnocorral. The fact that no stimulation occurred in the carboy suspended at 0.8 m and that the response in the flask incubated in the laboratory was much greater than the response insitu at the surface suggested that the reason for the stimulation by the moss peat vegetation might be related to light. Humic matter is broken down by sunlight (Stewart and Wetzel 1981; Francko and Heath 1983). Therefore Fe may have been released from humic matter in a manner similar to that described for EDTA and Fe by Anderson and Morel (1978). The fact that moss-peat material stimulated rather than inhibited growth in these experiments indicates moss-peat material did not release toxic concentrations of metals.

COMPARISON OF LIMNOCORRAL EXPERIMENTS AND SIL RESPONSES TO IMPOUNDMENT

The limnocorrals were designed to clarify the response of Southern Indian Lake to flooding by isolating the response to the two main types of flooded material. The overall response to impoundment in the lake was a decrease in mean water column light intensity (I_{24}), a decrease or disappearance of P deficiency and, on average, no change in integral primary productivity (Hecky and Guildford 1984).

The sediment limnocorrals demonstrated that inorganic sediments were not a major source of nutrients. I_{24} decreased due to increased light extinction from scattering by suspended sediments and P deficiency decreased because light limitation replaced P limitation.

The moss-peat limnocorrals demonstrated that the moss-peat material was a ready source of available P and N and inititially this nutrient release caused increased primary productivity. The upsurge in productivity ended when Fe or some other essential metal was chelated by leached humic matter to the extent that it limited growth.

In the two regions of the lake (regions 1 and 2 in Fig. 2) where the largest proportion of eroded material was inorganic sediment and increased light extinction combined with increased mean depth to yield very low light intensities, P deficiency and integral primary productivity decreased (Hecky and Guildford 1984) which is what was observed in the sediment-additon limnocorrals.

One major region of the lake (region 5 in Fig. 2) and a small bay where flooding of moss-peat material predominated experienced trophic upsurges as indicated by dramatic increases in chlorophyll and integral productivity (Hecky and Guildford 1984). In region 5 the algae were neither P nor light limited which was similar to the situation in the moss-peat limnocorrals where it was hypothesized that Fe was limiting. In the small bay P was the limiting nutrient. This small bay differed from region 5 in that the exchange time of the water was much shorter in the bay and the inhibiting effect of leached humic matter may have been diluted.

In most of the lake, although inorganic sediments reduced light drastically, the photosynthetic efficiency of the algae as measured by $alpha^B$ and P_m^B increased and mean integral primary productivity remained the same or increased (Hecky and Guildford 1984). In comparison adaptation to decreased light conditions was not observed in the sediment limnocorrals. The ability of the lake to adapt compared to the limnocorrals was probably the result of a combination of two factors: nutrient availability and algal succession.

Firstly, all regions of the lake received at least some nutrient-rich organic moss-peat material, but the sediment limnocorrals received only inorganic mineral material. In addition the limnocorrals were cut off from nutrient input from the watershed. During both summers of the limnocorral experiments, the lake just outside the limnocorrals was less P deficient than the controls; and, although chlorophyll and suspended carbon concentrations were lower in the lake, integral productivity was essentially the same as the controls in the one year it was measured.

The whole lake provided access to a variety of algal species some of which may have been more suited to low light intensities. In the limnocorrals the number and variety of potential successional species was limited to what was present when the curtain was dropped. In the lake importation and colonization by a large variety of different species were always possible.

REFERENCES

Anderson, M.A. and F.M.M. Morel. 1978. Growth limitation of a coastal diatom by low zinc ion activity. Nature 276. 70-71.

Anderson, M.A. and F.M.M. Morel. 1982. The influence of aqueous iron chemistry on the uptake of ion by the coastal diatom Thalasiosira weissflogii. Limnol. Oceanogr. 27:789-813.

Arruda, J.A., G.R. Marzolf, and R.T. Faulk. 1983. The role of suspended sediments in the nutrition of zooplankton in turbid reservoirs. Ecology. 64:1225-1235.

Bannister, T.T. 1974. Production equations in terms of chlorophyll concentrations, quantum yield and upper limit to production. Limnol. Oceanogr. 19:1-12.

Baxter, R.M., and P. Glaude. 1980. Environmental effects of dams and impoundments in Canada: experience an prospects. Can. Bull. Fish. Aquat. Sci. 205:34p.

Bodaly, R.A., R.E. Hecky and R.J. P. Fudge. 1984. Increases in fish mercury levels in lakes flooded by the Churchill River diversion, northern Manitoba. Can. J. Fish. Aquat. Sci. 41:682-691.

Campbell, P.G., B. Bobee, A. Caille, M.J. Demalsy, P. Demalsy, J.L. Sassevville and S. A. Uisser. 1975. Pre-impoundment site preparation: a study of the effects of topsoil stripping on reservoir water quality. Verh. Internat. Verein. Limnol. 19, 1768-1777.

Chamberlain, L.L. 1972. Primary productivity in a new and older California reservoir. Calif. Fish Game 58(4): 254-267.

DeHaan, H., J.B.W. Wanders and J.R. Moed. 1982. Multiple addition bioassy of Tjeukemeer water. Hydrobiol. 88, 233-244.

Devol, A.H., A. Dos Santos, B.R. Forsberg and T.M. Zaret. 1984. Nutrient addition experiments in Lago Jacaretinga, Central Amazon. Brazil: 2. The effect of humic and fulvic acids. Hydrobiol 109, 97-103.

Dorich, R.A., D.W. Nelson, and L.E. Somers. 1980. Algal availability of sediment phosphorus in drainage water of the Black Creek watershed. J. Environ. Qual. 9, 557-563.

Droop, M.R. 1960. Some chemical considerations in the design of synthetic culture media for marine algae. Botanica Marina Vol. II Fasc 3/4 pg. 231-246.

Duthie, H.C., and M.L. Ostrofsky. 1975. Environmental impact of the Churchill Falls (Labrador) hydroelectric project: a preliminary assessment. J. Fish. Res. Board Can. 32:117-125.

Ellis, M.M. 1936. Some fisheries problems in impounded waters. Trans. Am. Fish. Soc. 66:63-75.

Eppley, R.W. and E.H. Renger. 1974. Nitrogen assimilation of an oceanic diatom in nitrogen limited continuous culture. J. Phycol. 10. 15-23.

Falkowski, P.G. 1980. Light-shade adaptation in marine phytoplankton, pp. 99-120. In. Falkowski, P.G. (ed.) Primary productivity in the sea. Plenum, New York.

Fawley, M.W. 1984. Effects of light intensity and temperature interactions on growth characteristics of Phaeodactylum tricornutum (Bacillariophyceae) J. Phycol. 20:67-72.

Fee, E.J. 1973. Modelling primary production in water bodies: a numerical approach that allows for vertical inhomogeneities. J. Fish. Res. Board. Can. 30:1469-1473.

Fee, E.J. 1976. The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: Implications for primary production estimates. Limnol.. Oceanogr. 21(6): 767-783.

Fee, E.J. 1977. A computer program for estimating annual primary production in vertically stratified waterbodies with an incubator technique. Fish. Mar. Serv. Tech. Rep. 741: v + 38 p.

Fee, E.J. 1979. A relation between lake morphometry and primary productivity and its use in interpreting whole-lake eutrophication experiments. Limnol. Oceanogr. 24:401-416.

Francko, D.A. and R.T. Heath. 1979. Functionally distinct classes of complex phosphorus compounds in lake water. Limnol. Oceanogr. 24, 463-473.

Francko, D.A. and R.T. Heath. 1983. Abiotic uptake and photo dependent release of phosphate from high molecular weight humic iron complexes in bog lakes. In: Aquatic and Terrestrial Humic Materials. R.F. Christman and E.T. Gjessing ed. Ann Arbor Science 538 pp.

Giesy, J.P. Jr. 1976. Stimulation of growth in Scenedesmus Obliquus (Chlorophyceaceae) by humic acids under iron limited conditions. J. Phycol. 12: 172-179.

Gjessing, E.T., and J.E. Samdal. 1968. Humic substances in water and the effects of impoundmnt. J. Amer. Water Works Assoc. 60:451-454.

Gjessing, E.T. 1976. Physical and chemical characteristics of aquatic humus. Ann Arbor Sciece Publishers Inc. Ann Arbor, Mich. 120 p.

Grobbelaar, J.U. 1983. Availability to algae of N and P absorbed on suspended solids in turbid waters of the Amazon River. Arch. Hydrobiol. 96, 302-316.

Guildford, S.J. 1978. Adenosine triphosphate concentrations and nutrient status measurements in Southen Indian Lake 1975-1977. Fish. Mar. Serv. Data Rep. 108: iv + 24 p.

Guillard, R.R. L. andC.J. Lorenzen. 1972. Yellow-green algae with chlorophyllide C. J. Phycol. 8:10-4.

Hallegraeff, G.M. 1977. A comparison of different methods used for the quantitative evaluation of biomass of freshwater phytoplankton. Hydrobiol. 55: 145-165.

Healey, F.P. 1973. Inorganic nutrient uptake and deficiency in algae. Crit. Rev. Microbiol. 3:69-113.

Healey, F.P. and L.L. Hendzel. 1979. Indicators of phosphorus and nitrogen deficiency in five algae in culture. Can. J. Fish. Aquat. Sci. 36: 1364-1369.

Healey, F.P. and L.L. Hendzel. 1980. Physiological indicators of nutrient deficiency in lake phytoplankton. Can. J. Fish. Aquat. Sci. 37: 442-453.

Healey, F.P. 1983. Effect of temperature and light intensity on the growth rate of Synura sphagnicola. J. of Plankton Research 5: 767-774.

Healey, F.P. 1985. Interacting effects of light and nutrient limitation on the growth rate of Synechococcus linearis (Cyanophyceae). J. Phycol (in press).

Hecky, R.E. 1984. Thermal and optical characteristics of Southern Indian Lake before, during, and after impoundment and Churchill River diversion. Can. J. Fish. Aquat. Sci. 41:579-590.

Hecky, R.E., J. Alder, C. Anema, K. Burridge, and S.J. Guildford. 1979. Physical data on Southern Indian Lake, 1974 through 1978, before and after impoundment and Churchill River diersion. (In two parts.) Can. Fish. Mar. Serv. Data Rep. 158: iv + 523 p.

Hecky, R.E. andS.J. Guildford. 1984. Primary productivity of Southern Indian Lake before, during, and after impoundment and Churchill River diversion. Can. J. Fish. Aquat. Sci. Vol. 41:591-604.

Helfrich, L.A., and N.R. Kivern. 1973. Availability of phosphorus -32, absorbed on clay particles to a green alga. Michigan Academian 6, 71-81.

Hobbie, J.E., R.J.Daley, and S.Jasper. 1977. Use of nucleopore filters for counting bacteria by fluoresence microscopy. Appl. Environ. Microbiol. 33:1225-1228.

Hutchinson, G.E. 1957. A treatise on limnology. V.I. Wiley, New York. 1015 p.

Jackson, T.A. and R.E. Hecky. 1980. Depression of primary productivity by humic matter in lake and rservoir waters of the boreal forest zone. Can. J. Fish. Aquat. Sci. 37:2300-2317.

Jassby, A.D. and C.R. Goldman. 1974. Loss rates from a phytoplankton community. Limnol. Oceanogr. 19: 618-627.

Jorgensen, E.G. 1969. The adaptation of plankton algae IV. Light adaptation in different algal species. Physiol. Plant. 22: 1307-1315.

Kelly, D.M. 1978. Effects of Wreck Cover hydroelectric project construction upon water quality. M. Eng. thesis, Nova Scotia Technical College, Halifax. 325 p.

Kelly, D.M., J.K. Underwood and D. Thirumurthi. 1978. Impact of construction of a hydroelectric project on the water quality of five lakes in Nova Scotia. Can. J. Civ. Eng. 7:173-184.

Koenings, J.P. and F.F. Hooper. 1976. The influence of colloidal organic matter on iron and iron phosphorus clycling in an acid bog lake. Limnol. and Oceanogr. 21, 684-696.

Laws, E.A. and T.T. Bannister. 1980. Nutrient and light limited growth of Thalassissira fluvialilis in continuous culture, with implications for phytoplankton growth in the ocean. Limnol. Oceanogr. 25:457-474.

Lewin J. and C.H. Chen. 1971. Available iron: a limiting factor for marine phytoplankton. Limnol. Oceanogr. 16, 670- .

Lind, O.T. 1979. Handbook of common methods in limnology. The C.V. Mosby Company, St. Louis, MO. 199 pp.

Marzolf, G.R., and J.A. Osborne. 1972. Primary production in a Great Plains reservoir. Verh. Int. Ver. Limnol. 18: 126-133.

Messon, B.W. and B.M. Sweeney. 1982. Adaptation of Ceratium furca and Gonyaulax polyedra (Dinophyceae) to different temperatures and irradiances: growth rates and cell volumes. J. Phycol. 18:241-245.

Murphy, T.P. and D.R.S. Lean. 1976. Blue-green algae: Their excretion of iron selective chelators enables them to dominate other algae. Science 192, 900-902.

Newbury, R.W., and G.K. McCullough. 1984. Shoreline erosion and restabilization in the Southern Indian Lake reservoir. Can. J. Fish. Aquat. Sci. 41:558-566.

Newbury, R.W., G.K. McCullough and R.E. Hecky. 1984. The Southern Indian Lake impoundment and Churchill River diversion. Can. J. Fish. Aquat. Sci. 41:548-557.

Ostrofsky, M.L. 1978. Trophic changes in reservoirs: an hypothesis using phosphorus budget models. Int. Rev. Gesamten Hydrobiol. 63:481-499.

Ostrofsky, M.L. and H.C. Duthie. 1980. Trophic upsurge and the relationship between phytoplankton biomass and productivity in Smallwood Reservoir, Canada. Can. J. Bot. 58:1174-1180.

Perry, M.J. 1972. Alkaline phosphatase activity in subtropical central North Pacific waters using a sensitive fluorometric method. Marine Biology 15:113-119.

Prezelin, B.B. 1981. Light reactions in photosynthesis, p. 1-43. In: Physiological bases of phytoplankton ecology. Can. Bull. Fish. Aquat. Sci. 210.

Prakash, A. and M.A. Rashed. 1968. Influence of humic substances on the growth of marine phytoplankton: dinoflagellates. Limnol. Oceanogr. 13, 598-606.

Pyrina, I.L. 1979. Primary production of the phytoplankton of the Volga, p. 180-194. In Ph.D. Nordukhai-Boltovskoi (ed.) The river Volga and is life. Junk, The Hague.

Ramburg, L. 1979. Relations between phytoplankton and light climate. Int. Revue ges. Hydrobiol. 64:749-782.

Rhee, G-Y. 1973. A continuous culture study of phosphate uptake, growth rate and polyphosphate in Scenedesmus sp. J. Phycol. 9, 495-506.

Rhee, G-Y., and I.J. Gotham. 1981a. The effect of environmental factors on phytoplankton growth: temperature and the interactions of temperature with nutrient limitation. Limnol. Oceanogr. 26:635-648.

Rhee, G-Y and I.J. Gotham. 1981b. The effect of environmental factors on phytoplankton growth: light and the interactions of light with nitrate limitation. Limnol. Oceanogr. 26: 649-59.

Rhode, W. 1964. Effects of impoundment on water chemistry and plankton in Lake Ransaren. Verh. Internat. Verein. Limnol. 15, 437-443.

Romanenko, V.I. 1979. Microbiology of the Volga, p. 106-136. In Ph.D. Mordukhai-Boltovskoi (ed.) The river Volga and its life. Junk, The Hague.

Rudd, J.W.M., and R.D. Hamilton. 1973. Measurement of adenosine triphosphate (ATP) in two Precambrian Shield lakes of northwestern Ontario. J. Fish. Res. Board Can. 30:1537-1546.

Rzoska, J. 1966. The biology of reservoirs in the U.S.S.R. p. 149-154. In R.H. Lowe-McConnell (ed.) Man made lakes. Academic Press, London, 218 p.

Sakamoto, M. 1971. Chemical factors involved in the control of phytoplankton production in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Canada 28:203-213.

Sakshaug, E. 1980. Problems in the methodology of studying phytoplankton. In The Physiological Ecology of Phytoplankton. Ed. I. Morris. Univ. California Press.

Schindler, D.W. 1976. Biogeochemical evolution of phosphorus limitation in nutrient-enriched lakes of the Precambrian Shield in J.O. Nriagu (ed) Environmental Biogeochemistry. Vol. 2 pg 647-664. Ann Arbor Science Publ. Inc., Ann Arbor, Mich.

Schnitzer, M. and S.U. Khan. 1972. Humic substances in the environment. Marcel Dekker, Inc. New York. 327 p.

Shearer, J.A. 1976. Construction and operation of a portable incubator for phytoplankton primary production studies. Fish. Mar. Serv. Tech. Rep. 638: vi +22p.

Shearer, J.A., and E.J. Fee. 1974. Phytoplankton primary production in the Experimental Lakes Area using an incubator technique - 1973. Fish Mar. Serv. Tech. Rep. 474: iii + 110.

Smith, E.A., C.I. Mayfield, and P.T.S. Wong. 1978. Naturally occuring apatite as a source of orthophosphate for growth of bacteria and algae. Microbiol. Ecol. 4, 105-117.

Stainton, M.P., M.S. Capel, and F.A.J. Armstrong. 1977. Chemical analysis of freshwater. 2nd ed. Can. Fish. Mar. Serv. Misc. Spec. Publ. 25:166p.

Stewart, A.J. and R.G. Wetzel. 1981. Dissolved humic materials: photodegradation, sediment effects, and reactivity with phosphate and calcium carbonate precipitation. Arch. Hydrobiol. 92, 265-286.

Sundra, W. and R.R.L Guillard. 1976. The relationship between cupric ion activity and the toxicity of copper to phytoplankton. J. Mar. Res. 34:511-529.

Tilman, D. and S.S. Kilham. 1976. Phosphate and silicate growth and uptake kinetics of the diatoms Asterionella formosa and Cyclotella meneghiniana in batch culture and semi-continuous culture. J. Phycol. 12, 375-383.

Titman, D. 1976. Ecological competition between algae: experimental confirmation of resource - based competition theory. Science 192: 463-465.

Titman, D. and P. Kilham. 1976. Sinking in freshwater phytoplankton: Some ecological implicatons of cell nutrient status and physical mixing processes. Limnol. Oceanogr. 21: 409-417.

Toledo, A.P.P., J.G. Tundisi and V.A. D'Aquino. 1980. Humic acid influence on the growth and copper tolerance of chlorella sp. Hydrobiol. 71, 261-263.

Trick, C.G., R.J. Andersen, N.M. Price, A. Gillam and P.J. Harrison. 1983. Examination of hydroxamate-siderophore production by neritic eukaryotic marine phytoplankton. Marine Biology 75:9-17.

Wetzel, R.G. 1975. Limnology. W.B. Aunders Co. Philidelphia, PA. 743 p.

Williams, J.D.H., H. Shear and R.L. Thomas. 1980. Availability to Scenedesmus quadricaurda of different forms of phosphorus in sedimentry materials from the Great Lakes. Limnol. Oceanogr. 25, 1-11.

Zevenboom, W., G.J. deGroot and L.R. Mur. 1980. Effects of light on nitrate limited Oscilitoria agardhii in chemostat cultures. Arch. Microbiol. 125, 59-65.

APPENDIX 1

The effect of suspended sediment on ATP extraction

Three experiments were conducted to determine whether increasing amounts of suspeneded sediment interfered with the measurement of ATP. In each experiment the sediment was the same as that routinely added to the sediment limnocorrals. ATP extractions were done as described in the methods section. Absorbance at 543 nm was used as a relative measure of suspended sediment (Hecky and McCullough 1984).

Experiment I.

ATP was measured in two water samples from the 1982 high sediment limnocorral (HS82-7) ; one taken immediately before the weekly sediment addition and one immediately after. The addition takes about 30 minutes so it was not expected that there would be any change in the actual ATP concentration during that time. The sample taken after the sediment addition contained 13 % less ATP than the pre-addition sample (table 22); however the variance among replicates was greater than the difference between the two samples.

Experiment II.

Increasing amounts of sediment were added to a water sample from SIL. The initial absorbance at 543 nm was 0.380 (table 23). The addition of sufficient sediment to double the absorbance had no significant affect on ATP. At higher sediment concentrations the amount of ATP

TABLE 22. ATP concentration (ug L^{-1}) in the 1982 high sediment limnocorral (HS82-7) immediately before and after one of the weekly sediment additions. Absorbance at 543 nm is given as a relative measure of suspended sediment in the samples (Hecky and McCullough 1984).

	Absorbance (543 nm)	ATP (ug L^{-1})	Mean ATP (ug L^{-1})
Before addition	0.405	0.470 0.751 0.489	0.570
After addition	0.567	0.597 0.390 0.502	0.496

TABLE 23. ATP concentrations (ug L^{-1}) in a water sample containing increasing amounts of sediment. Absorbance at 543 nm is given as a relative measure of suspended sediment (Hecky and McCullough 1984).

Absorbance (543 nm)	ATP (ug L^{-1})	Mean ATP (ug L^{-1})
0.38	0.567	0.564
	0.539	
	0.586	
0.660	0.539	0.529
	0.508	
	0.539	
0.925	0.301	0.311
	0.321	
1.750	0.019	0.068
	0.084	
	0.102	

extracted from the water samples was greatly reduced (table 23). However the two highest sediment concentrations were much higher than any of the sediment concentrations achieved in the SIL high sediment limnocorrals. The highest Absorbance at 543 nm recorded in a high sediment limnocorral was 0.600 in HS82-7.

Experiment III.

Increasing amounts of sediment were added to a laboratory culture of Scenedesmus sp.. The initial absorbance at 543 nm of the culture was 0.053 (Table 24) and the average ATP concentration was 1.250 ug/L. The addition of sediment clearly interfered with the extraction of ATP. The ATP concentration decreased dramatically as more sediment was added and the variablity between replicates increased (Table 24).

Based on the results of these three experiments it was concluded that ATP measurements made in the sediment limnocorrals may be unreliable. No attempt was made to quantify the effect of suspended sediments on the extraction of ATP from water samples using the data from these experiments.

TABLE 24. ATP concentrations (ug L^{-1}) in a laboratory culture of *Scenedesmus sp.* containing increasing amounts of sediment. Absorbance 543 nm is given as a relative measure of suspended sediment (Hecky and McCullough 1984).

Absorbance (543 nm)	ATP (ug L^{-1})	Mean ATP (ug L^{-1})
0.053	0.849	1.250
	1.185	
	1.300	
	1.220	
	1.780	
	1.180	
0.130	0.658	0.761
	0.781	
	0.843	
0.215	0.303	0.559
	0.093	
	1.280	
0.307	0.268	0.451
	0.332	
	0.752	
0.409	0.232	0.169
	0.050	
	0.225	
0.531	0.003	0.216
	0.135	
	0.511	

APPENDIX 2

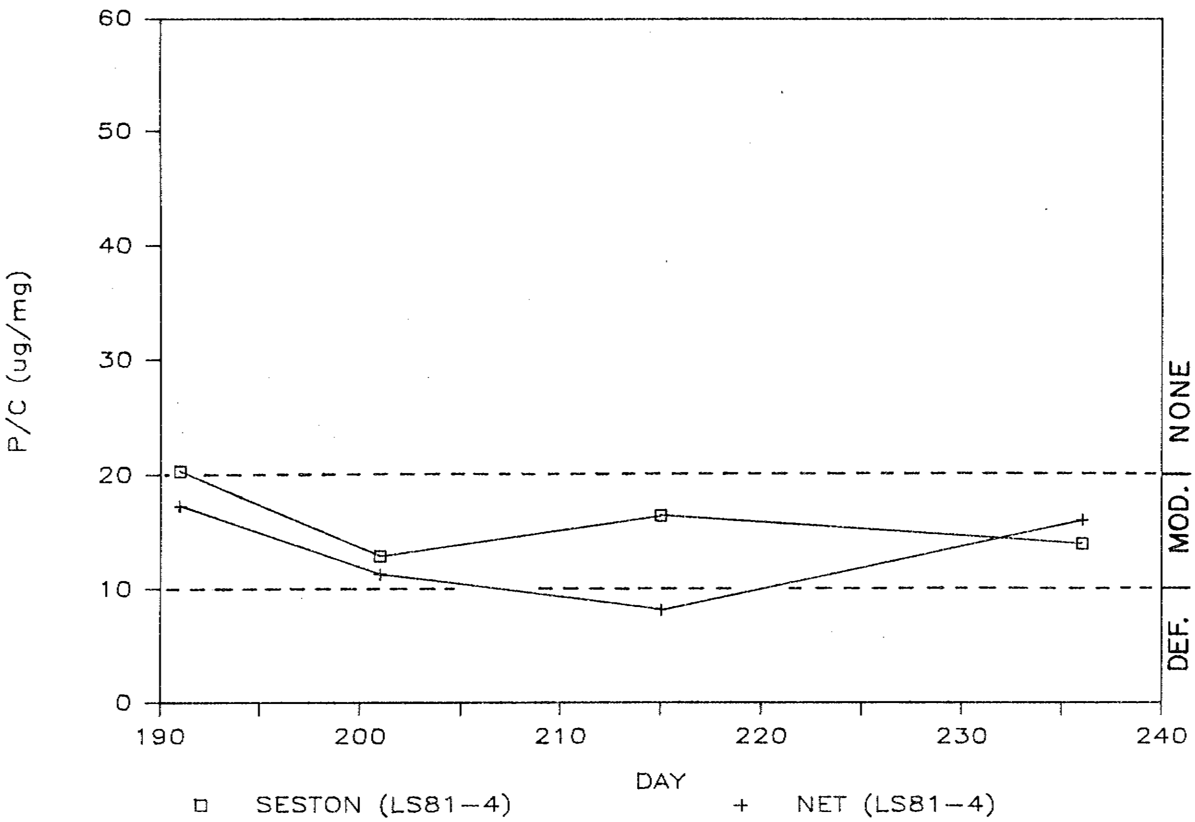
The effect of suspended sediment on composition ratios involving P

There was concern that composition ratios, involving P, used as indicators of nutrient status would be unreliable in the sediment limnocorrals because of the P associated with the added sediments. The sediment was rich in mineral P (appendix 3). In order to determine whether P/C and N/P ratios in the sediment limnocorrals were affected by sediment P, net samples were taken and compared with the routinely collected water samples. It was expected that the net samples would more accurately reflect the P/C and N/P ratios of the algae whereas the seston samples would reflect the composition of the entire water sample.

The P/C ratios in the seston samples from the high sediment limnocorral HS81-6 (fig. 69) were significantly higher than the P/C ratios in the net samples (fig 69). There was no consistent difference in the P/C ratios in the net and seston samples from the low sediment limnocorral LS81-4 or the two control limnocorrals C81-5 and C81-7 (fig. 69 and 70). There was a similar pattern when the N/P ratios were compared (fig 71 and 72) i.e. the N/P ratio in the seston sample from the high sediment limnocorral HS81-6 was affected by P associated with suspended sediment .

Based on these comparisons it was concluded that seston P/C and N/P ratios in the sediment limnocorrals probably underestimated the degree of P deficiency of the algae.

FIGURE 69. P/C ratios in net and seston samples from the sediment limnocorrals LS81-4 and HS81-6. The broken horizontal lines indicate the occurrence of severe, moderate, and no P deficiency in algae as given by Healey and Hendzel (1980).


60
50
40
30
20
10
0
P/C (ug/mg)
NONE
MOD.
DEF.
190
200
210
220
230
240
DAY
SESTON (LS81−4)
NET (LS81−4)

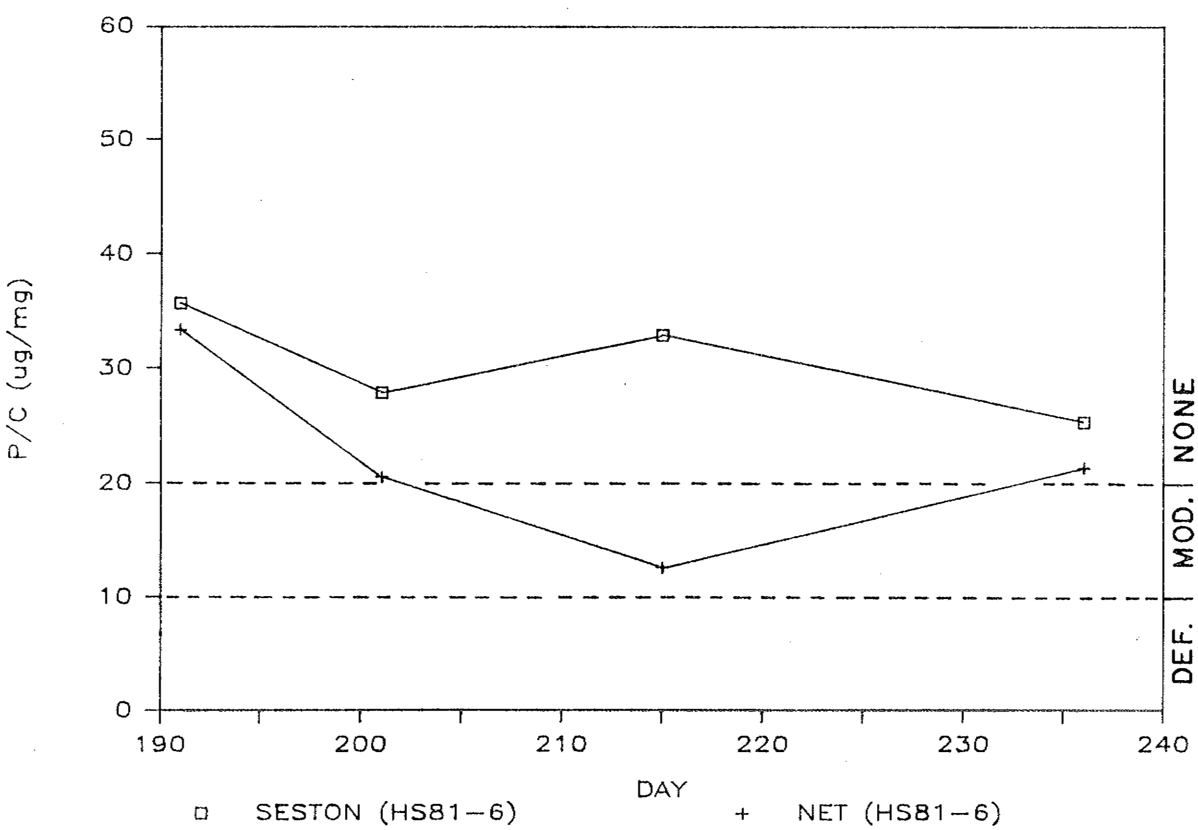
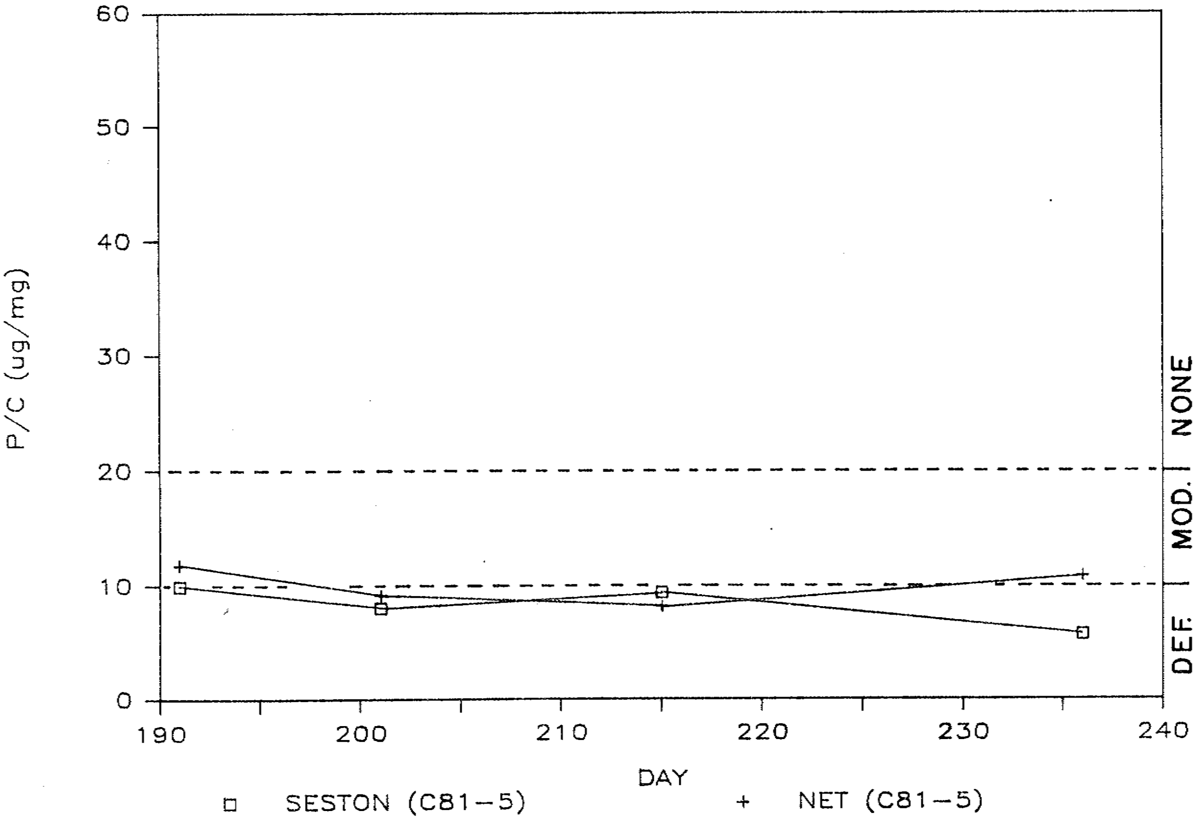
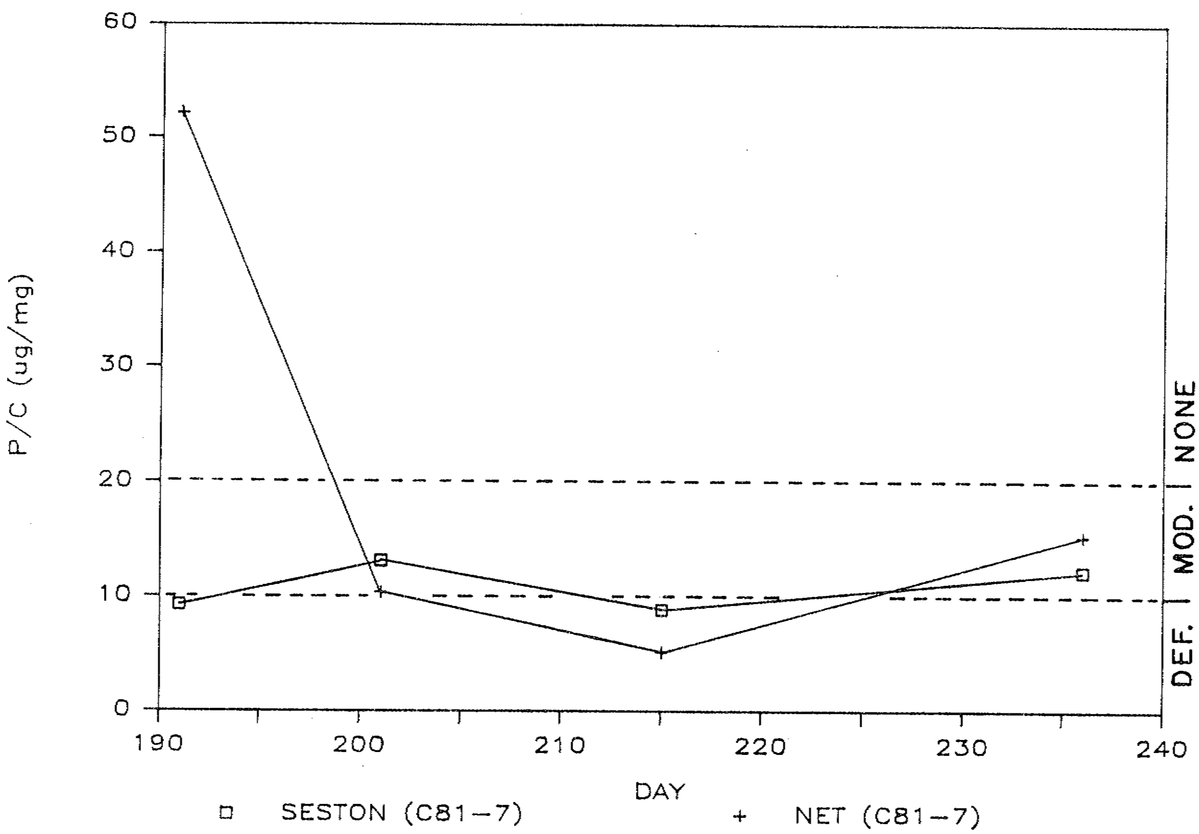

60
50
40
30
20
10
0
P/C (ug/mg)
NONE
MOD.
DEF.
190
200
210
220
230
240
DAY
SESTON (HS81−6)
NET (HS81−6)

FIGURE 70. P/C ratios in net and seston samples from the control limnocorrals C81-5 and C81-7. The broken horizontal lines indicate the occurrence of severe, moderate, and no P deficiency in algae as given by Healey and Hendzel (1980).

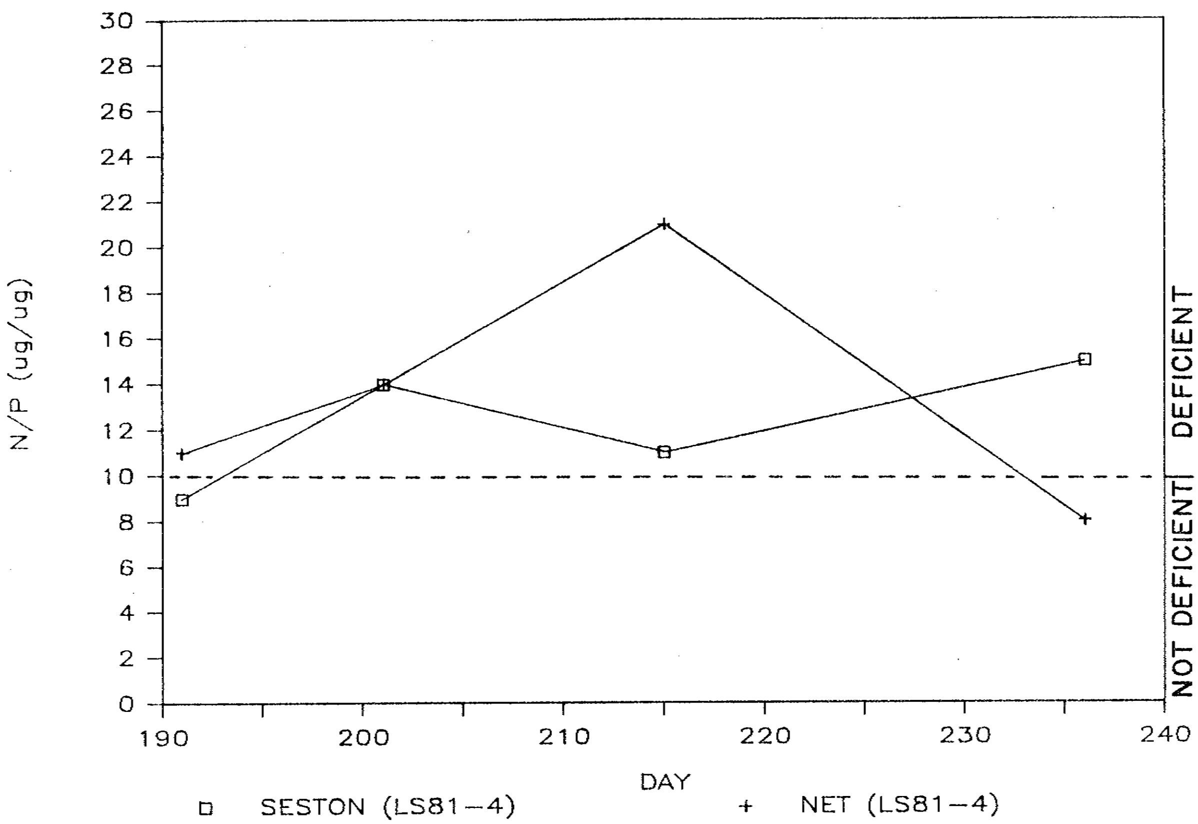


60
50
40
30
20
10
0
P/C (ug/mg)
NONE
MOD.
DEF.
190
200
210
220
230
240
DAY
SESTON (C81−5)
NET (C81−5)

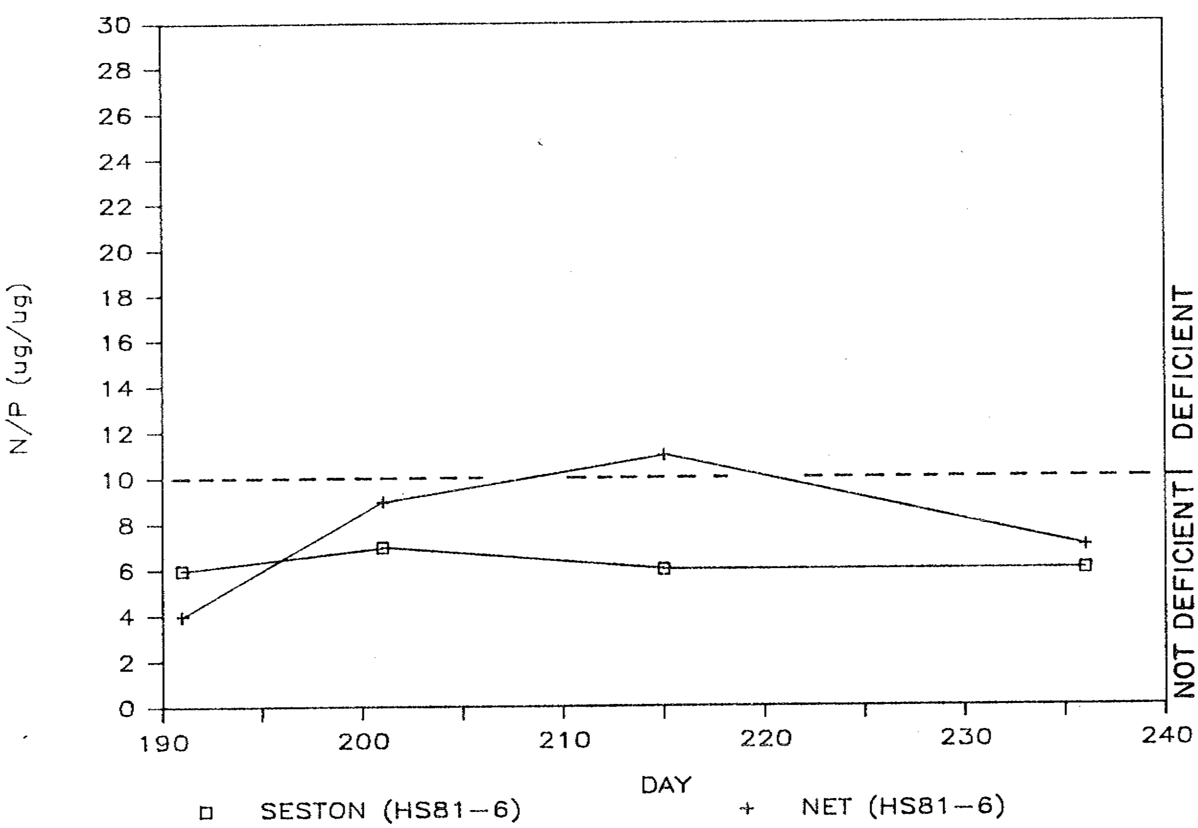


60
50
40
30
20
10
0
P/C (ug/mg)
NONE
MOD.
DEF.
190
200
210
220
230
240
DAY
SESTON (C81−7)
NET (C81−7)

FIGURE 71. N/P ratios in net and seston samples from the sediment limnocorrals LS81-4 and HS81-6. The broken horizontal line indicates the occurrence of P deficiency in algae as given by Healey and Hendzel (1980).

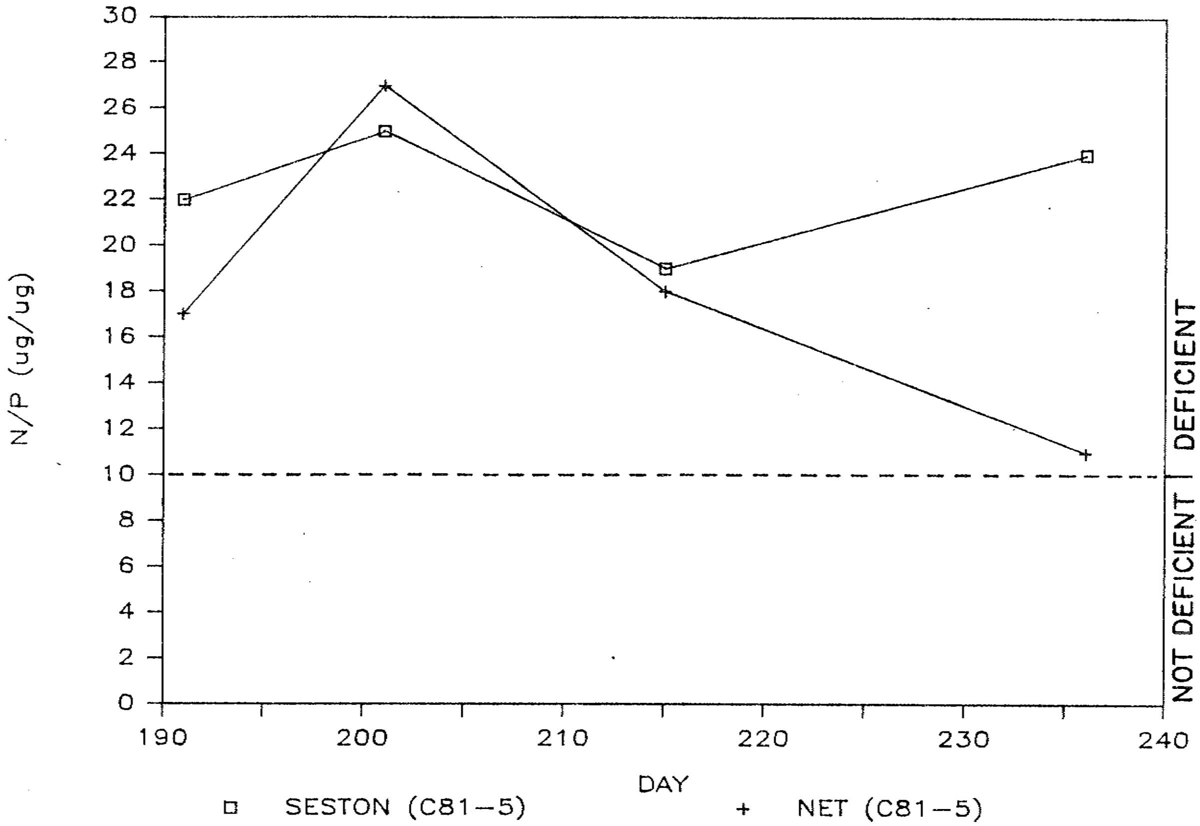


N/P (ug/ug)
DEFICIENT
NOT DEFICIENT
DAY
SESTON (LS81-4)
NET (LS81-4)

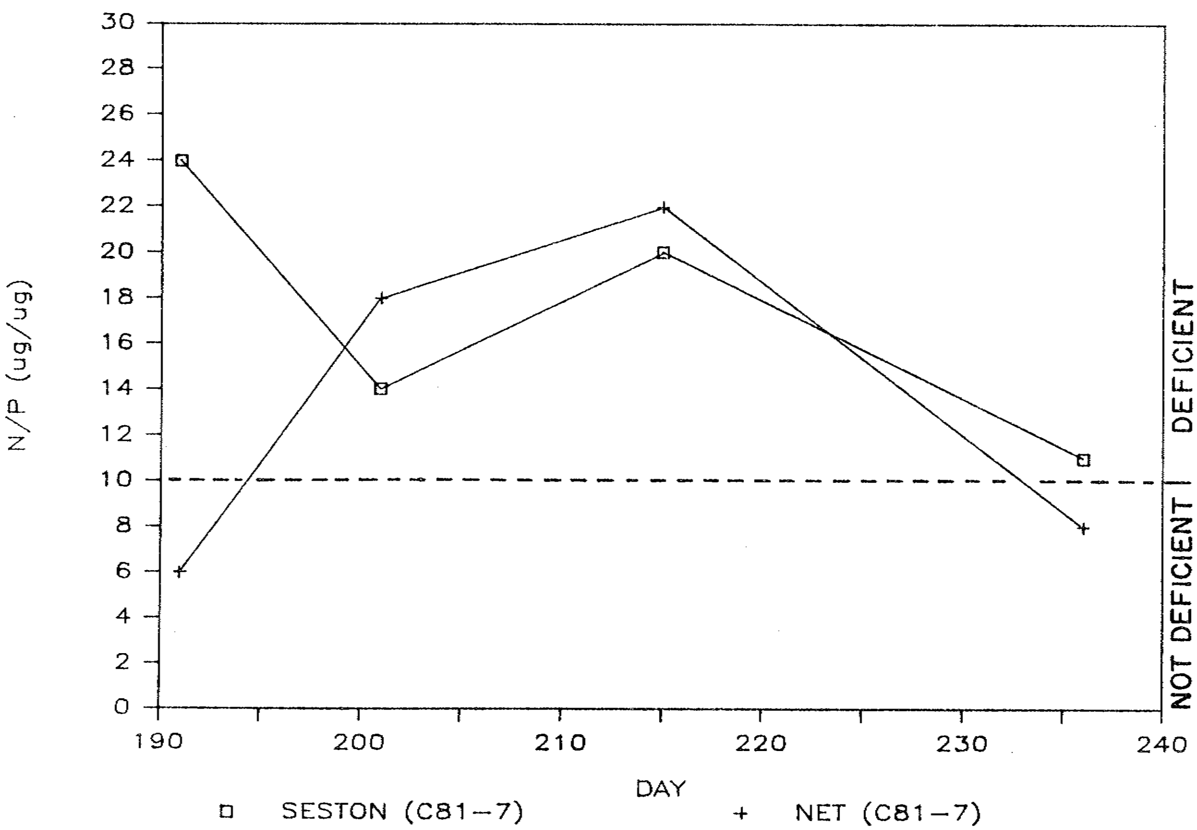


N/P (ug/ug)
DEFICIENT
NOT DEFICIENT
DAY
SESTON (HS81-6)
NET (HS81-6)

FIGURE 72. N/P ratios in net and seston samples from the control limnocorrals C81-5 and C81-7. The broken horizontal line indicates the occurrence of P deficiency in algae as given by Healey and Hendzel (1980).



N/P (ug/ug)
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
190
200
210
220
230
240
DAY
DEFICIENT
NOT DEFICIENT
SESTON (C81–5)
NET (C81–5)



N/P (ug/ug)
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
190
200
210
220
230
240
DAY
DEFICIENT
NOT DEFICIENT
SESTON (C81–7)
NET (C81–7)

APPENDIX 3

CNP and CO_3 analysis of sediment added to the limnocorrals.

TABLE 25. C, N, P, and CO_3 anaylysis of sediment added to the limnocorrals. Each group of data consists of several subsamples taken each time bank material was removed from site F for the limnocorral additions. The average ratio for the four sets of data is 230.50.616.

Date		C	N	P	CO_3-C
			($mg\ g^{-1}$ dry wt.)		
June 1981		19	0.4	0.6	14
		46	0.4	0.6	12
		21	0.3	0.6	16
		21	0.1	0.6	18
		49	0.2	0.6	27
	mean	31	0.3	0.6	17
July 1981		23	0.2	0.6	17
		23	0.3	0.6	10
		11	0.1	0.6	22
		19	0.3	0.6	8
		17	0.2	0.7	12
	mean	19	0.2	0.6	14
August 1981		20	0.3	0.7	10
		21	0.2	0.6	27
		23	0.4	0.6	12
	mean	21	0.3	0.6	16
June 1982		17	1.4	0.6	13
		20	1.0	0.6	17
		23	1.0	0.7	20
		23	1.1	0.6	16
		16	1.0	0.6	12
		18	1.2	0.6	15
		17	1.5	0.6	14
	mean	19	1.2	0.6	15

APPENDIX 4

Seasonal data for Secchi depths and light extinction coefficients.

TABLE 26. Secchi depths (m) in the limnocorrals and lake during 1981. C = control, LM = low moss, PN = phosphorus and nitrogen, L = lake, LS = low sediment, and HS = high sediment. All limnocorrals except C81-1 and C81-2 had plastic bottoms. Day is day of the year and "n.d." means no data.

Date	Day	C81-1	LM81-2	PN81-3	C81-5	C81-7	L81-9
20-Jun-81	171	1.75	1.90	1.90	2.00	2.10	1.30
21-Jun-81	172	1.90	1.70	1.90	2.00	2.05	n.d.
23-Jun-81	174	1.70	1.85	2.15	2.25	2.60	1.50
26-Jun-81	177	1.60	1.50	2.10	1.90	2.00	1.45
01-Jul-81	182	2.30	2.25	2.30	2.50	2.80	1.80
02-Jul-81	183	1.60	1.70	1.60	2.10	2.75	1.30
03-Jul-81	184	2.10	2.10	1.80	2.50	n.d.	1.10
07-Jul-81	188	1.90	2.10	1.60	2.10	2.00	1.30
10-Jul-81	191	1.50	1.40	1.20	1.95	1.90	0.88
13-Jul-81	194	1.90	1.80	1.50	2.10	2.00	1.40
19-Jul-81	200	1.90	2.50	1.20	2.20	2.00	1.70
27-Jul-81	208	1.35	2.20	1.00	n.d.	2.05	1.70
02-Aug-81	214	1.90	>3.00	1.10	2.05	2.35	1.70
03-Aug-81	215	1.50	>3.00	0.90	1.90	2.50	1.70
13-Aug-81	225	1.80	2.95	1.20	3.05	2.80	1.10
14-Aug-81	226	1.90	>2.90	1.40	>3.20	>3.00	n.d.
16-Aug-81	228	1.70	2.80	1.30	>3.30	>3.00	1.70
21-Aug-81	233	2.10	2.50	1.30	>3.20	>3.00	1.80
23-Aug-81	235	2.60	>2.80	1.20	>3.40	>3.00	1.55
	Mean	1.84	2.31	1.51	2.43	2.44	1.47

Date	Day	LS81-4	HS81-6
20-Jun-81	171	1.90	2.30
21-Jun-81	172	0.45	0.20
23-Jun-81	174	0.62	0.30
24-Jun-81	175	0.67	0.35
26-Jun-81	177	1.10	0.40
01-Jul-81	182	1.80	0.80
02-Jul-81	183	0.80	0.30
03-Jul-81	184	1.00	0.35
07-Jul-81	188	1.40	0.60
08-Jul-81	189	0.50	0.30
10-Jul-81	191	0.55	0.39
13-Jul-81	194	1.30	0.70
15-Jul-81	196	1.50	1.00
15-Jul-81	196	0.50	0.30
19-Jul-81	200	0.90	0.60
22-Jul-81	203	1.10	0.80
22-Jul-81	203	0.40	0.30
27-Jul-81	208	0.65	0.60
30-Jul-81	211	0.80	0.60
30-Jul-81	211	0.45	0.30
02-Aug-81	214	0.55	0.50
04-Aug-81	216	0.70	0.55
06-Aug-81	218	0.80	0.60
06-Aug-81	218	0.50	0.35
13-Aug-81	225	1.00	0.60
13-Aug-81	225	0.50	0.40
14-Aug-81	226	0.60	0.40
16-Aug-81	228	0.65	0.50
20-Aug-81	232	0.80	0.65
20-Aug-81	232	0.50	0.35
21-Aug-81	233	0.60	0.40
23-Aug-81	235	0.60	0.45
	Mean	0.82	0.54

TABLE 27. Secchi depths (m) in the limnocorrals and lake during 1982. FM = flooded moss, SC = screen covered, LM = low moss, HM = high moss, OC = 1 year old control, C = control , OM = 1 year old moss, L = lake, HS = high sediment. All limnocorrals had natural bottoms. Day is day of the year and "n.d." means no data.

Date	Day	FM82-1	SC81-2	LM82-3	HM82-4	OC82-5	C82-6	OM82-8	L82-9	Date	Day	HS82-7
29-Jun-82	180	1.00	n.d.	1.00	1.05	1.15	1.20	1.30	1.00	29-Jun-82	180	1.15
04-Jul-82	185	1.60	n.d.	1.60	n.d.	1.60	n.d.	1.80	1.20	02-Jul-82	183	1.10
07-Jul-82	188	1.40	1.55	1.90	1.70	1.70	1.60	1.65	n.d.	02-Jul-82	183	0.35
08-Jul-82	189	1.50	n.d.	2.00	1.90	1.70	1.80	2.10	0.95	04-Jul-82	185	0.45
10-Jul-82	191	1.50	n.d.	2.00	2.10	2.00	2.00	2.20	1.25	05-Jul-82	186	0.55
12-Jul-82	193	1.80	n.d.	2.85	2.50	2.20	2.10	3.20	n.d.	05-Jul-82	186	0.33
14-Jul-82	195	1.65	1.90	2.30	1.70	2.10	2.20	2.20	1.30	07-Jul-82	188	0.40
15-Jul-82	196	2.20	2.20	2.30	1.90	2.20	2.20	3.00	1.50	08-Jul-82	189	0.50
19-Jul-82	197	>2.00	n.d.	n.d.	n.d.	n.d.	n.d.	2.90	n.d.	08-Jul-82	189	0.30
19-Jul-82	200	n.d.	n.d.	2.40	2.30	2.20	2.30	n.d.	n.d.	10-Jul-82	191	0.40
21-Jul-82	202	1.75	2.20	2.70	2.70	2.40	2.15	2.30	0.90	12-Jul-82	193	0.40
26-Jul-82	207	>2.45	n.d.	>3.50	>3.50	2.90	2.90	>3.50	1.30	12-Jul-82	193	0.33
28-Jul-82	209	>2.35	n.d.	2.70	2.80	2.70	2.50	3.50	1.30	14-Jul-82	195	0.55
29-Jul-82	210	n.d.	2.70	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	15-Jul-82	196	0.60
31-Jul-82	212	n.d.	n.d.	3.00	n.d.	n.d.	n.d.	n.d.	n.d.	15-Jul-82	196	0.45
01-Aug-82	213	n.d.	2.60	2.95	n.d.	n.d.	n.d.	n.d.	n.d.	19-Jul-82	200	1.00
02-Aug-82	214	2.40	n.d.	2.80	2.80	2.50	2.00	2.55	1.60	19-Jul-82	200	0.35
03-Aug-82	215	n.d.	n.d.	3.00	n.d.	2.60	n.d.	3.25	1.20	21-Jul-82	202	0.40
04-Aug-82	216	1.90	n.d.	2.60	1.80	n.d.	n.d.	n.d.	n.d.	22-Jul-82	203	0.47
06-Aug-82	218	1.80	n.d.	n.d.	1.70	2.30	1.90	2.60	1.80	22-Jul-82	203	0.40
09-Aug-82	221	1.80	2.90	2.80	n.d.	n.d.	2.90	2.70	1.40	28-Jul-82	209	0.55
09-Aug-82	222	n.d.	n.d.	n.d.	1.65	2.75	n.d.	n.d.	n.d.	29-Jul-82	210	0.55
13-Aug-82	225	1.70	n.d.	2.70	1.65	2.70	2.10	2.35	1.40	29-Jul-82	210	0.39
16-Aug-82	228	1.80	n.d.	2.10	1.70	2.50	2.20	2.00	n.d.	02-Aug-82	214	0.60
20-Aug-82	232	1.80	n.d.	1.80	1.45	2.65	2.05	2.10	1.40	02-Aug-82	214	0.35
23-Aug-82	235	1.60	n.d.	1.70	1.30	2.50	1.90	2.00	1.40	06-Aug-82	218	0.55
26-Aug-82	238	1.65	n.d.	2.00	1.90	2.10	1.80	1.95	1.20	06-Aug-82	218	0.40
30-Aug-82	242	1.75	n.d.	2.00	1.85	2.15	2.05	2.30	1.30	09-Aug-82	221	0.60
										09-Aug-82	222	0.35
	Mean	1.82	2.29	2.36	2.00	2.25	2.09	2.43	1.30	13-Aug-82	225	0.65
										13-Aug-82	225	0.38
										16-Aug-82	228	0.80
										16-Aug-82	228	0.30
										20-Aug-82	232	0.65
										20-Aug-82	232	0.39
										23-Aug-82	235	0.50
										26-Aug-82	238	0.35
										30-Aug-82	242	0.45
											Mean	0.51

TABLE 28. Light extinction coefficients (ln m^{-1}) in the limnocorrals and lake during 1981. C = control, LM = low moss, PN = phosphorus and nitrogen, LS = low sediment, HS = high sediment, and L = lake. All limnocorrals except C81-1 and C81-2 had plastic bottoms. Day is day of the year and "n.d." means no data.

Date	Day	C81-1	LM81-2	PN81-3	C81-5	C81-7	L81-8
23-Jun-81	174	0.95	1.06	0.99	0.91	0.81	1.05
01-Jul-81	182	0.96	1.03	0.99	0.85	0.88	0.98
07-Jul-81	188	1.00	1.17	1.13	0.87	0.90	n.d.
10-Jul-81	191	1.26	1.41	n.d.	n.d.	n.d.	1.31
13-Jul-81	194	0.95	1.21	1.06	0.78	0.78	1.10
19-Jul-81	200	1.02	1.09	1.21	0.88	0.90	1.07
27-Jul-81	208	1.05	0.95	1.22	0.85	0.74	0.95
02-Aug-81	214	1.11	1.04	1.14	0.83	0.87	1.03
13-Aug-81	225	1.19	0.94	1.17	0.66	0.81	1.07
14-Aug-81	226	0.97	0.90	0.93	0.59	0.67	n.d
16-Aug-81	228	1.07	1.34	1.19	0.94	0.95	0.99
23-Aug-81	235	0.82	1.00	1.01	0.69	0.76	1.05
	Mean	1.03	1.10	1.10	0.80	0.83	1.06

Date	Day	LS81-4	HS81-6
23-Jun-81	174	1.50	2.46
01-Jul-81	182	1.16	1.50
03-Jul-81	184	1.44	2.38
07-Jul-81	188	1.12	2.14
10-Jul-81	191	1.69	2.51
13-Jul-81	194	1.11	1.93
15-Jul-81	196	1.12	1.71
15-Jul-81	196	2.12	2.81
19-Jul-81	200	1.47	2.06
22-Jul-81	203	1.36	1.76
22-Jul-81	203	1.88	2.08
27-Jul-81	208	1.72	1.84
30-Jul-81	211	1.59	1.91
30-Jul-81	211	2.11	2.47
02-Aug-81	214	2.03	2.03
06-Aug-81	218	1.77	1.95
06-Aug-81	218	1.99	2.37
13-Aug-81	225	1.60	2.08
13-Aug-81	225	2.16	2.13
14-Aug-81	226	1.97	2.54
16-Aug-81	228	1.87	2.40
20-Aug-81	232	1.65	2.01
20-Aug-81	232	2.18	2.81
23-Aug-81	235	1.85	2.21
	Mean	1.69	2.17

TABLE 29. Light extinction coefficients (ln m^{-1}) in the limnocorrals and lake during 1982. FM = flooded moss, LM = low moss, HM = high moss, OC = 1 year old control, C = control, OM = 1 yearld moss, L = lake, HS = high sediment, and SC = screen covered. All limnocorrals had natural bottoms. Day is day of the year and "n.d." means no data.

Date	Day	FM82-1	LM82-3	HM82-4	OC82-5	C82-6	OM82-8	L82-9
04-Jul-82	185	1.31	1.25	n.d.	1.19	1.05	1.10	n.d.
07-Jul-82	188	1.28	1.15	1.36	1.03	1.00	1.02	1.35
14-Jul-82	195	1.21	1.08	1.02	0.95	1.25	0.91	1.23
21-Jul-82	202	1.06	0.96	1.20	0.82	1.20	0.84	1.23
28-Jul-82	209	1.02	1.35	1.38	0.78	1.10	0.81	1.08
31-Jul-82	212	n.d.	0.93	n.d.	n.d.	n.d.	n.d.	n.d.
01-Aug-82	213	n.d.	1.15	n.d.	n.d.	n.d.	n.d.	n.d.
03-Aug-82	215	n.d.	1.12	n.d.	n.d.	n.d.	n.d.	n.d.
04-Aug-82	216	1.22	1.00	1.36	0.83	n.d.	0.87	1.14
06-Aug-82	218	n.d.	0.93	n.d.	n.d.	n.d.	n.d.	n.d.
09-Aug-82	221	1.10	1.35	1.42	1.34	1.10	1.39	1.08
	Mean	1.17	1.12	1.29	0.99	1.12	0.99	1.19

Date	Day	HS82-7	Date	Day	SC82-2
02-Jul-82	183	2.21	04-Jul-82	185	1.31
04-Jul-82	185	2.02	07-Jul-82	188	1.20
05-Jul-82	186	1.89	08-Jul-82	189	1.08
05-Jul-82	186	2.91	12-Jul-82	193	1.02
07-Jul-82	188	2.07	14-Jul-82	195	1.05
08-Jul-82	189	2.13	15-Jul-82	196	1.00
08-Jul-82	189	2.81	19-Jul-82	200	0.94
12-Jul-82	193	1.83	21-Jul-82	202	1.18
12-Jul-82	193	2.90	22-Jul-82	203	1.19
14-Jul-82	195	2.09	28-Jul-82	209	1.24
15-Jul-82	196	1.91	29-Jul-82	210	0.86
15-Jul-82	196	2.27	31-Jul-82	212	0.90
15-Jul-82	196	2.19	02-Aug-82	214	1.08
19-Jul-82	200	1.49	03-Aug-82	215	0.91
19-Jul-82	200	2.97	06-Aug-82	218	1.33
21-Jul-82	202	2.17	09-Aug-82	221	0.83
22-Jul-82	203	2.07			
22-Jul-82	203	2.48		Mean	1.07
28-Jul-82	209	2.11			
29-Jul-82	210	2.06			
29-Jul-82	210	2.50			
31-Jul-82	212	2.16			
02-Aug-82	214	2.81			
03-Aug-82	214	2.34			
06-Aug-82	218	1.94			
06-Aug-82	219	2.29			
09-Aug-82	221	1.87			
09-Aug-82	221	2.33			
	Mean	2.24			

APPENDIX 5

Seasonal primary productivity data.

TABLE 30. Seasonal data for all relevant primary productivity parameters in all limnocorrals and the lake during 1981 and 1982. I.P. is the daily rate of primary productivity (mg C m^{-2} d^{-1}), I_{24} is the mean water column light intensity during 24 hours (E m^{-2} d^{-1}) , $Alpha^B$ is the initial slope of the primary productivity irradiance curve in the incubator expressed per unit of chlorophyll (mg C E^{-1} m^2 mg Chl a^{-1}), P_m^B is the maximum rate of primary productivity observed in the incubator expressed per unit of chlorophyll (mg C mg Chl a^{-1} h^{-1}) and I_k is irradiance at the onset of light saturation (E m^{-2} d^{-1}). Day is day of the year, Chl is chlorophyll a (mg m^{-3}) and k is the light extinction codfficient (ln m^{-1}). C = control, LM = low moss, HM = high moss, FM = flooded moss, OM = 1 year old moss, OC = 1 year old control, LS = low sediment, HS = high sediment, SC = screen covered, PN = phosphorus and nitrogen, and L = lake.

TABLE 30.

Limnocorral	Date	Day	I.P.	$Alpha^B$	P_m^B	I_k	I_{24}	Chl	k
CB81-1	22-Jun-81	174	289	8.16	4.26	14.7	24.6	1.6	0.95
	02-Jul-81	183	584	6.29	4.32	17.7	24.2	3.6	0.96
	10-Jul-81	191	686	8.84	5.10	15.3	18.8	4.9	1.26
	20-Jul-81	201	607	6.29	4.38	17.4	21.5	4.4	1.02
	03-Aug-81	215	429	5.44	3.24	15.0	18.0	4.5	1.11
	24-Aug-81	236	357	9.35	8.34	22.5	18.8	2.4	0.82
		mean	500	7.07	4.80	17.1	21.1	3.9	1.02
LM81-2	22-Jun-81	174	291	5.44	3.06	14.4	18.5	3.0	1.06
	02-Jul-81	183	679	6.46	3.90	16.1	18.8	5.2	1.03
	10-Jul-81	191	759	7.31	5.58	18.7	13.7	5.4	1.41
	20-Jul-81	201	227	2.55	2.46	22.9	16.7	3.0	1.09
	03-Aug-81	215	339	5.10	7.02	22.0	15.7	1.7	1.04
	24-Aug-81	236	208	4.60	3.54	20.4	13.3	2.7	1.00
		mean	399	5.05	4.62	20.2	16.2	2.7	1.11
PN81-3	23-Jun-81	174	346	4.76	3.78	19.9	21.9	2.4	0.99
	02-Jul-81	183	890	5.27	3.72	17.9	21.7	6.7	0.99
	10-Jul-81	191	1688	6.12	3.42	13.5	19.4	13.7	1.10
	20-Jul-81	201	1003	4.42	2.22	12.4	16.9	14.0	1.21
	03-Aug-81	215	768	5.10	2.34	12.4	16.1	10.9	1.14
	13-Aug-81	225	641	4.76	2.46	12.4	15.1	10.9	1.17
	14-Aug-81	226	906	5.78	2.88	12.8	17.3	10.7	0.93
	16-Aug-81	228	617	4.93	1.86	10.2	13.6	12.0	1.19
	20-Aug-81	232	692	4.59	2.94	16.3	13.9	9.6	1.10
	24-Aug-81	236	795	5.61	4.50	18.4	14.6	9.4	1.01
		mean	924	5.07	2.88	14.1	17.0	10.8	1.08
LS81-4	23-Jun-81	174	194	6.29	3.48	14.1	11.7	2.1	1.50
	02-Jul-81	183	329	4.42	3.84	21.2	13.3	4.1	1.30
	10-Jul-81	191	660	7.48	3.60	13.0	10.1	7.6	1.69
	20-Jul-81	201	528	5.44	3.30	14.8	11.4	6.2	1.42
	03-Aug-81	215	341	7.82	3.96	14.3	7.2	4.7	2.03
	13-Aug-81	225	234	7.48	4.74	15.6	7.5	3.6	1.88
	14-Aug-81	226	221	6.46	4.62	17.0	6.7	3.0	1.97
	16-Aug-81	228	254	7.65	4.20	12.5	6.9	3.0	1.87
	20-Aug-81	232	104	7.31	4.74	16.7	7.4	1.8	1.65
	24-Aug-81	236	135	10.37	8.10	18.0	6.5	1.8	1.85
		mean	369	6.74	4.02	15.6	8.7	4.5	1.72

TABLE 30. (continued)

Limnocorral	Date	Day	I.P.	$Alpha^B$	P_m^B	I_k	I_{24}	Chl	k
C81-5	23-Jun-81	174	148	4.25	2.22	14.0	21.2	1.4	0.91
	02-Jul-81	183	446	5.95	3.30	14.5	22.3	3.6	0.85
	10-Jul-81	191	1023	7.31	3.84	13.8	22.3	6.8	0.83
	20-Jul-81	201	571	4.93	2.94	15.3	20.1	5.3	0.88
	03-Aug-81	215	488	6.12	4.26	18.0	19.1	3.4	0.83
	13-Aug-81	225	324	18.19	11.34	15.6	21.9	0.9	0.66
	14-Aug-81	226	134	7.48	6.00	18.7	22.3	0.7	0.59
	16-Aug-81	228	163	10.54	12.42	29.7	15.1	0.6	0.94
	20-Aug-81	232	109	7.82	4.62	16.3	16.2	0.9	0.82
	24-Aug-81	236	101	4.42	4.50	22.0	18.1	1.0	0.69
		mean	480	7.29	4.74	16.4	20.0	3.5	0.80
HS81-6	23-Jun-81	174	116	11.39	4.92	11.7	7.2	1.4	2.46
	02-Jul-81	183	341	9.18	5.88	16.1	9.0	3.5	1.94
	10-Jul-81	191	404	7.14	5.64	19.0	6.8	5.1	2.51
	20-Jul-81	201	284	6.12	3.54	14.7	8.5	3.7	1.91
	03-Aug-81	215	235	10.20	5.52	14.5	7.2	2.4	2.03
	13-Aug-81	225	76	7.14	4.44	16.0	6.6	2.2	2.11
	14-Aug-81	226	183	9.69	6.06	16.1	5.2	2.6	2.54
	16-Aug-81	228	143	9.35	5.16	14.3	5.4	2.2	2.40
	20-Aug-81	232	78	7.82	6.12	19.6	6.1	1.6	2.01
	24-Aug-81	236	108	10.37	8.16	19.3	5.4	1.5	2.21
		mean	239	8.42	5.22	16.0	6.7	3.0	2.21
C81-7	23-Jun-81	174	256	6.46	4.74	19.2	23.4	1.3	0.81
	02-Jul-81	183	606	4.76	4.62	22.6	21.6	3.5	0.88
	10-Jul-81	191	1003	6.29	3.72	14.7	22.0	7.1	0.84
	20-Jul-81	201	622	5.61	3.30	15.1	19.8	4.9	0.90
	03-Aug-81	215	513	13.43	6.66	13.5	18.4	2.2	0.87
	24-Aug-81	236	163	6.46	6.00	22.3	16.7	0.7	0.76
		mean	541	8.04	5.04	17.0	20.4	3.3	0.84
L81-8	23-Jun-81	174	224	7.31	4.26	14.8	19.7	1.5	1.05
	02-Jul-81	183	390	9.86	3.84	10.9	20.7	3.0	0.98
	10-Jul-81	191	681	7.48	4.68	15.4	15.6	4.7	1.31
	20-Jul-81	201	534	11.10	4.92	12.5	17.9	3.1	1.07
	03-Aug-81	215	403	7.48	8.88	28.7	16.7	1.9	1.03
	24-Aug-81	236	339	8.84	7.50	23.0	13.4	2.2	1.05
		mean	449	8.74	6.30	19.3	17.4	2.7	1.08

TABLE 30. (continued)

Limnocorral	Date	Day	I.P.	$Alpha^B$	P_m^B	I_k	I_{24}	Chl	k
CB2-6	07-Jul-82	188	113	3.06	3	23.6	22.5	1.7	1.00
	14-Jul-82	195	188	5.10	4.74	16.1	18.0	1.6	1.25
	21-Jul-82	202	255	3.57	4.62	20.0	18.0	1.9	1.20
	28-Jul-82	209	361	5.27	6.66	19.4	18.5	1.8	1.10
	09-Aug-82	221	442	3.06	4.02	19.7	16.7	3.9	1.10
		mean	290	4.24	4.98	19.3	18.7	2.2	1.13
SC82-2	07-Jul-82	188	220	4.25	4.26	16.0	20.4	2.2	1.20
	14-Jul-82	195	223	4.42	4.92	16.8	22.3	2.0	1.05
	21-Jul-82	202	187	4.25	4.92	17.9	19.4	2.7	1.18
	28-Jul-82	209	82	1.02	1.38	18.1	17.8	2.9	1.24
	09-Aug-82	221	260	2.72	3.06	16.7	22.1	3.2	0.83
		mean	181	3.08	3.48	17.3	20.4	2.7	1.10
HS82-7	07-Jul-82	188	174	4.59	5.1	17.4	11.4	2.0	2.07
	14-Jul-82	195	238	3.91	5.52	22.2	11.0	2.6	2.09
	21-Jul-82	202	176	3.06	4.02	20.3	10.2	3.2	2.17
	28-Jul-82	209	226	3.06	4.56	22.6	10.1	2.9	2.11
	09-Aug-82	221	203	3.06	3.36	17.6	10.3	3.5	1.85
		mean	208	3.40	4.5	20.6	10.6	2.9	2.08
LM82-3	07-Jul-82	188	320	4.08	4.5	17.1	16.4	2.1	1.15
	14-Jul-82	195	195	3.91	4.08	17.0	16.9	1.4	1.08
	21-Jul-82	202	293	4.76	6.72	21.7	18.1	1.4	0.96
	28-Jul-82	209	141	3.57	4.08	34.6	12.6	1.8	1.35
	09-Aug-82	221	186	2.89	3.48	19.2	11.3	2.0	1.35
		mean	212	3.83	4.56	23.3	15.1	1.7	1.18
OC82-5	07-Jul-82	188	236	4.42	3.9	14.5	19.6	1.7	1.03
	14-Jul-82	195	256	2.38	2.82	19.0	20.5	2.7	0.95
	21-Jul-82	202	246	2.89	2.94	15.0	22.3	2.2	0.82
	28-Jul-82	209	172	2.21	3.24	21.9	22.1	1.5	0.78
	09-Aug-82	221	203	2.72	3.54	20.3	12.4	2.0	1.34
		mean	217	2.71	3.24	18.9	19.4	2.0	0.98
OM82-8	07-Jul-82	188	306	4.42	5.04	18.0	20.3	1.7	1.02
	14-Jul-82	195	227	4.76	5.4	18.4	21.8	1.4	0.91
	21-Jul-82	202	193	2.04	3.12	22.8	22.4	1.8	0.84
	28-Jul-82	209	327	3.57	5.16	22.0	22.0	1.8	0.81
	09-Aug-82	221	449	2.72	3.36	19.0	12.3	4.6	1.39
		mean	296	3.45	4.44	20.4	19.8	2.5	0.99

TABLE 30. (continued)

Limnocorral	Date	Day	I.P.	$Alpha^B$	P_m^B	I_k	I_{24}	Chl	k
FM82-1	21-Jul-82	202	165	2.04	2.88	22.3	25.9	2.4	1.06
	09-Aug-82	221	187	3.06	3.48	19.0	21.6	2.4	1.10
		mean	176	2.55	3.18	20.7	23.8	2.4	1.08
HM82-4	21-Jul-82	202	292	3.74	4.02	17.1	19.2	2.6	1.20
	09-Aug-82	221	580	2.21	3.24	20.9	14.2	8.9	1.42
		mean	436	2.98	3.66	19.0	16.7	5.8	1.31
LM82-3	21-Jul-82	202	293	4.76	6.72	21.7	18.1	1.4	0.96
	09-Aug-82	221	186	2.89	3.48	19.2	11.3	2.0	1.35
		mean	240	3.83	5.1	20.4	14.7	1.7	1.16
L82-9	21-Jul-82	202	234	2.89	3.78	20.2	15.6	2.4	1.23
	09-Aug-82	221	217	2.89	3.24	17.6	15.1	2.3	1.08
		mean	226	2.89	3.54	18.9	15.4	2.4	1.16
C82-6	21-Jul-82	202	255	3.57	4.62	20.0	18.0	1.9	1.20
	09-Aug-82	221	442	3.06	4.02	19.7	16.7	3.9	1.10
		mean	349	3.32	4.32	19.9	17.3	2.9	1.15

APPENDIX 6

Seasonal nutrient status data.

TABLE 31. Seasonal values for various physiological indicators of N and P deficiency in all limnocorrals and the lake during 1981 and 1982. N and P headings indicate parameters indicative of N and P deficiency respectively: general indicators cannot on the basis of present evidence be ascribed with any certainty to either N or P deficiency (Healey and Hendzel 1980). Composition ratios are ug particulate P, N, ATP, or chlorophyll a (chl) mg particulate C^{-1}; ug particulate N ug particulate P^{-1}. Nutrient debts are umoles ammonium or phosphate removed in 24 h darkness ug ATP^{-1} or ug chl^{-1}. Negative debt means net release of nutrient. Alkaline phosphatase activity (Pase) is umole o-methyl fluoresein phosphate hydrolyzed h^{-1} ug ATP^{-1} or ug chl^{-1}. Values that indicate nutrient status for each parameter are given below.

Ndebt/chl: > 0.150 = N deficiency
Ndebt/ATP: > 1.000 = N deficiency
N/C: 80-140 = moderate, < 80 = severe N deficiency

Pase/chl: 0.003-0.005 = moderate, > 0.005 = severe P deficiency
Pase/ATP: 0.020-0.100 = moderate, > 0.100 = severe P deficiency
Pdebt/chl: > 0.075 = P deficiency
Pdebt/ATP: > 0.500 = P deficiency
P/C 10-20 = moderate, < 10 severe P deficiency
N/P > 10 = P deficiency

Chl/C < 10 = deficiency
ATP/C < 2.00 = deficiency

TABLE 31.

			N			P						GENERAL	
Limnocorral	Date	Day	Ndebt (chl)	Ndebt (ATP)	N/C	Pase (chl)	Pase (ATP)	Pdebt (chl)	Pdebt (ATP)	P/C	N/P	Chl/C	ATP/C
CB1-1	02-Jul-81	183	n.d.	n.d.	190	n.d.	n.d.	n.d.	n.d.	18	11	6.4	n.d.
	10-Jul-81	191	-0.020	-0.152	210	0.157	1.167	0.180	1.334	13	16	5.7	0.77
	20-Jul-81	201	0.075	0.388	220	0.191	0.987	0.240	1.234	11	21	5.9	1.13
	03-Aug-81	215	0.167	1.940	180	0.164	1.915	0.420	4.916	10	17	5.7	0.50
	20-Aug-81	232	n.d.	n.d.	270	n.d.	n.d.	n.d.	n.d.	25	11	4.2	n.d.
	24-Aug-81	236	0.079	0.517	160	0.058	0.381	0.160	1.052	9	18	5.3	0.82
		mean	0.101	0.962	210	0.146	1.226	0.285	2.635	14	16	5.5	0.77
LM81-2	02-Jul-81	183	n.d.	n.d.	180	n.d.	n.d.	n.d.	n.d.	21	8	7.4	n.d.
	10-Jul-81	191	-0.061	-0.475	220	0.041	0.317	0.050	0.403	19	12	8.3	1.07
	20-Jul-81	201	-0.253	-0.604	180	0.030	0.072	0.030	0.072	24	7	5.5	2.33
	03-Aug-81	215	-0.112	-0.214	170	0.006	0.011	0.030	0.056	25	7	5.4	2.82
	20-Aug-81	232	n.d.	n.d.	130	n.d.	n.d.	n.d.	n.d.	43	3	4.2	n.d.
	24-Aug-81	236	0.074	0.161	150	0.004	0.008	0.070	0.149	17	9	3.7	1.72
		mean	-0.100	-0.259	170	0.016	0.061	0.042	0.120	27	7	5.8	2.23
PN81-3	02-Jul-81	183	n.d.	n.d.	240	n.d.	n.d.	n.d.	n.d.	17	14	9.6	n.d.
	10-Jul-81	191	0.024	0.375	220	0.100	1.560	0.224	3.484	8	27	8.1	0.52
	20-Jul-81	201	0.070	1.264	230	0.079	1.420	0.323	5.820	8	29	7.4	0.41
	03-Aug-81	215	0.028	0.390	180	0.108	1.480	0.451	6.188	8	22	5.7	0.42
	20-Aug-81	232	n.d.	n.d.	170	n.d.	n.d.	n.d.	n.d.	8	20	4.2	n.d.
	24-Aug-81	236	0.318	3.042	150	0.079	0.750	0.415	3.970	8	19	4.7	0.49
		mean	0.106	1.240	200	0.093	1.303	0.383	5.272	9	23	6.5	0.45
LS81-4	02-Jul-81	183	n.d.	n.d.	180	n.d.	n.d.	n.d.	n.d.	22	8	9.0	n.d.
	10-Jul-81	191	-0.021	-0.401	180	0.086	1.630	0.109	2.080	20	9	10.3	0.54
	20-Jul-81	201	0.106	1.735	180	0.126	2.050	0.269	4.389	13	14	7.3	0.45
	03-Aug-81	215	0.028	0.817	180	0.162	4.780	0.446	13.201	17	11	5.2	0.18
	20-Aug-81	232	n.d.	n.d.	180	n.d.	n.d.	n.d.	n.d.	14	12	2.6	n.d.
	24-Aug-81	236	0.100	0.875	210	0.078	0.680	0.183	1.585	14	15	2.8	0.33
		mean	0.060	0.940	180	0.124	2.745	0.300	6.905	16	11	6.2	0.33
CB1-5	02-Jul-81	183	n.d.	n.d.	220	n.d.	n.d.	n.d.	n.d.	15	15	7.6	n.d.
	10-Jul-81	191	-0.006	-0.072	220	0.141	1.730	0.191	2.339	10	22	7.5	0.62
	20-Jul-81	201	0.083	0.786	200	0.151	1.430	0.460	4.357	8	25	5.3	0.56
	03-Aug-81	215	0.018	0.135	180	0.200	1.530	0.632	4.831	9	19	4.0	0.52
	20-Aug-81	232	n.d.	n.d.	150	n.d.	n.d.	n.d.	n.d.	8	18	1.8	n.d.
	24-Aug-81	236	-0.460	-1.244	140	0.090	0.220	0.140	0.376	6	24	2.9	1.06
		mean	-0.079	-0.036	190	0.155	1.220	0.422	3.388	9	21	4.6	0.67

TABLE 31. (continued)

			N			P						GENERAL	
Limnocorral	Date	Day	Ndebt (chl)	Ndebt (ATP)	N/C	Pase (chl)	Pase (ATP)	Pdebt (chl)	Pdebt (ATP)	P/C	N/P	Chl/C	ATP/C
HSB1-6	02-Jul-81	183	n.d.	n.d.	180	n.d.	n.d.	n.d.	n.d.	43	4	7.9	n.d.
	10-Jul-81	191	0.067	0.953	210	0.070	1.010	0.045	0.645	36	6	10.1	0.71
	20-Jul-81	201	0.143	1.743	180	0.070	0.860	0.219	2.665	28	7	7.4	0.60
	03-Aug-81	215	-0.234	-4.847	180	0.100	2.160	0.238	4.934	33	6	5.3	0.26
	20-Aug-81	232	n.d.	n.d.	170	n.d.	n.d.	n.d.	n.d.	27	6	3.3	n.d.
	24-Aug-81	236	-0.146	-1.876	150	0.050	0.680	0.153	1.978	25	6	4.2	0.33
		mean	-0.079	-1.752	190	0.077	1.340	0.192	3.163	32	6	6.4	0.42
C81-7	02-Jul-81	183	n.d.	n.d.	220	n.d.	n.d.	n.d.	n.d.	14	15	7.1	n.d.
	10-Jul-81	191	-0.047	0.443	220	0.124	1.180	0.183	1.744	9	24	7.4	0.78
	20-Jul-81	201	-0.006	-0.037	200	0.155	0.094	0.449	2.731	13	14	5.4	0.89
	03-Aug-81	215	-0.086	-0.376	180	0.227	0.990	0.650	2.831	9	20	3.3	0.76
	20-Aug-81	232	n.d.	n.d.	150	n.d.	n.d.	n.d.	n.d.	11	13	1.6	n.d.
	24-Aug-81	236	-0.200	-0.433	140	0.129	0.280	0.357	0.767	12	11	1.7	0.78
		mean	-0.087	-0.208	190	0.173	0.607	0.476	2.202	11	17.2	4.4	0.80
L81-8	02-Jul-81	183	n.d.	n.d.	160	n.d.	n.d.	n.d.	n.d.	26	6	8.5	n.d.
	10-Jul-81	191	0.151	0.974	170	0.047	0.302	0.060	0.384	23	7	9.8	1.51
	20-Jul-81	201	0.032	0.092	150	0.087	0.247	0.300	0.385	19	8	6.6	2.33
	03-Aug-81	215	-0.163	-0.491	170	0.058	0.174	0.230	0.681	20	9	5.3	1.76
	20-Aug-81	232	n.d.	n.d.	170	n.d.	n.d.	n.d.	n.d.	16	11	3.7	n.d.
	24-Aug-81	236	0.027	1.064	160	0.023	0.053	0.120	0.280	14	12	5.2	2.22
		mean	-0.032	0.190	160	0.056	0.179	0.204	0.476	20	8.7	6.3	1.99
FM82-1	30-Jun-82	181			160	n.d.	n.d.			10	16	1.6	n.d.
	05-Jul-82	186			130	n.d.	n.d.			9	23	1.7	n.d.
	07-Jul-82	188			180	0.029	0.076			6	22	1.4	0.55
	14-Jul-82	195			180	0.026	0.073			8	22	1.5	0.52
	21-Jul-82	202			180	0.094	0.246			16	11	2.6	1.00
	28-Jul-82	209			190	0.043	0.099			10	18	1.7	0.75
	03-Aug-82	215			180	n.d.	n.d.			9	21	1.5	n.d.
	09-Aug-82	221			170	0.035	0.098			10	17	1.6	0.57
	16-Aug-82	228			70	n.d.	n.d.			5	13	1.1	n.d.
	23-Aug-82	235			120	n.d.	n.d.			12	10	2.3	n.d.
		mean			160	0.049	0.122			10	17	1.7	0.70

TABLE 31. (continued)

			N			P						GENERAL	
Limnocorral	Date	Day	Ndebt (chl)	Ndebt (ATP)	N/C	Pase (chl)	Pase (ATP)	Pdebt (chl)	Pdebt (ATP)	P/C	N/P	Chl/C	ATP/C
SC82-2	30-Jun-82	181			210	n.d.	n.d.			13	17	2.4	n.d.
	05-Jul-82	186				n.d.	n.d.			n.d.	n.d.	n.d.	n.d.
	07-Jul-82	188			180	0.011	0.028			9	21	2.3	0.93
	14-Jul-82	195			190	0.007	0.019			9	21	2.2	0.83
	21-Jul-82	202			160	0.023	0.081			9	17	3.1	0.9
	28-Jul-82	209			170	0.017	0.047			9	18	3.3	1.18
	03-Aug-82	215			210	n.d.	n.d.			12	18	3.3	n.d.
	09-Aug-82	221			230	0.03	0.078			12	19	3.8	1.48
	16-Aug-82	228			150	n.d.	n.d.			18	9	3.5	n.d.
	23-Aug-82	235			170	n.d.	n.d.			18	9	4.1	n.d.
	mean				180	0.019	0.052			12	17	3.1	1.07
LM82-3	30-Jun-82	181			220	n.d.	n.d.			12	17	2.1	n.d.
	05-Jul-82	186			220	n.d.	n.d.			13	17	2.6	n.d.
	07-Jul-82	188			220	0.01	0.022			12	19	2.8	1.25
	14-Jul-82	195			210	0	0.000			9	22	2.2	1.41
	21-Jul-82	202			180	0.001	0.001			11	17	2.5	1.33
	28-Jul-82	209			190	0.006	0.012			13	15	2.2	1.16
	03-Aug-82	215			210	n.d.	n.d.			15	15	2.5	n.d.
	09-Aug-82	221			200	0.005	0.008			14	15	2.7	1.58
	16-Aug-82	228			160	n.d.	n.d.			24	7	7.1	n.d.
	23-Aug-82	235			160	n.d.	n.d.			28	6	6.3	n.d.
	mean				200	0.004	0.007			15	15	3.3	1.33
HM82-4	30-Jun-82	181			210	n.d.	n.d.			14	15	2.2	n.d.
	05-Jul-82	186			180	n.d.	n.d.			12	15	2.0	n.d.
	07-Jul-82	188			170	0.005	0.010			16	13	2.7	1.33
	14-Jul-82	195			170	0	0.000			18	14	2.6	1.31
	21-Jul-82	202			140	0	0.000			9	15	1.8	0.78
	28-Jul-82	209			200	0.003	0.009			16	13	3.3	1.08
	03-Aug-82	215			210	n.d.	n.d.			15	14	3.6	n.d.
	09-Aug-82	221			210	0.001	0.002			15	14	4.3	1.27
	16-Aug-82	228			180	n.d.	n.d.			26	7	6.8	n.d.
	23-Aug-82	235			180	n.d.	n.d.			25	7	8.4	n.d.
	mean				180	0.001	0.004			17	13	3.8	1.13

TABLE 31. (continued)

Limnocorral	Date	Day	N: Ndebt (chl)	N: Ndebt (ATP)	N: N/C	P: Pase (chl)	P: Pase (ATP)	P: Pdebt (chl)	P: Pdebt (ATP)	P: P/C	P: N/P	GENERAL: Chl/C	GENERAL: ATP/C
OC82-5	30-Jun-82	181			170	n.d.	n.d.			13	14	2.0	n.d.
	05-Jul-82	186			230	n.d.	n.d.			14	17	2.8	n.d.
	07-Jul-82	188			190	0.015	0.027			11	18	2.3	1.28
	14-Jul-82	195			180	0.013	0.043			8	23	2.2	0.54
	21-Jul-82	202			200	0.014	0.049			10	20	2.8	0.76
	28-Jul-82	209			180	0.032	0.073			9	21	2.2	0.94
	03-Aug-82	215			210	n.d.	n.d.			13	16	2.4	n.d.
	09-Aug-82	221			200	0.012	0.021			13	16	2.3	1.28
	16-Aug-82	228			170	n.d.	n.d.			18	10	5.8	n.d.
	23-Aug-82	235			160	n.d.	n.d.			17	9	3.6	n.d.
		mean			190	0.016	0.047			12	17	2.9	0.92
C82-6	30-Jun-82	181			200	n.d.	n.d.			14	15	1.9	n.d.
	05-Jul-82	186			210	n.d.	n.d.			14	16	2.7	n.d.
	07-Jul-82	188			220	0.027	0.046			12	19	2.2	1.24
	14-Jul-82	195			190	0.017	0.042			7	29	1.8	0.71
	21-Jul-82	202			190	0.003	0.010			12	16	2.5	0.66
	28-Jul-82	209			190	0.044	0.162			8	25	2.0	0.54
	03-Aug-82	215			200	n.d.	n.d.			10	20	3.4	n.d.
	09-Aug-82	221			210	0.031	0.091			9	23	3.0	1.02
	16-Aug-82	228			170	n.d.	n.d.			14	12	5.8	n.d.
	23-Aug-82	235			170	n.d.	n.d.			13	13	3.4	n.d.
		mean			190	0.026	0.079			11	20	3.0	0.76
HS82-7	30-Jun-82	181			230	n.d.	n.d.			13	19	1.8	n.d.
	05-Jul-82	186			140	n.d.	n.d.			23	6	1.7	n.d.
	07-Jul-82	188			180	0.017	0.036			17	10	2	0.96
	14-Jul-82	195			190	0.007	0.024			19	10	2.7	0.67
	21-Jul-82	202			190	0.001	0.007			19	10	3.8	0.67
	28-Jul-82	209			230	0.002	0.012			23	10	3.4	0.7
	03-Aug-82	215			180	n.d.	n.d.			18	10	3.5	n.d.
	09-Aug-82	221			160	0.002	0.008			14	11	2.8	0.73
	16-Aug-82	228			140	n.d.	n.d.			31	5	5.9	n.d.
	23-Aug-82	235			150	n.d.	n.d.			31	5	5.9	n.d.
	mean				180	0.003	0.015			21	10	3.5	0.72

TABLE 31. (continued)

Limnocorral	Date	Day	N: Ndebt (chl)	N: Ndebt (ATP)	N: N/C	P: Pase (chl)	P: Pase (ATP)	P: Pdebt (chl)	P: Pdebt (ATP)	P: P/C	P: N/P	GENERAL: Chl/C	GENERAL: ATP/C
DM82-B	30-Jun-82	181			230	n.d.	n.d.			14	17	2.7	n.d.
	05-Jul-82	186			210	n.d.	n.d.			14	15	2.7	n.d.
	07-Jul-82	188			220	0.019	0.030			19	16	2.5	1.63
	14-Jul-82	195			200	0.025	0.057			11	19	2.1	0.94
	21-Jul-82	202			190	0.003	0.006			10	18	2.3	1.02
	28-Jul-82	209			190	0.043	0.115			10	19	2.1	0.77
	03-Aug-82	215			180	n.d.	n.d.			8	23	2.8	n.d.
	09-Aug-82	221			190	0.035	0.181			9	22	3.3	0.64
	16-Aug-82	228			150	n.d.	n.d.			17	9	7.0	n.d.
	23-Aug-82	235			120	n.d.	n.d.			14	9	4.6	n.d.
		mean			190	0.019	0.083			12	17	3.2	0.93
L82-9	30-Jun-82	181			230	n.d.	n.d.			12	20	1.7	n.d.
	05-Jul-82	186				n.d.	n.d.			n.d.	n.d.	n.d.	n.d.
	07-Jul-82	188			230	0.015	0.025			14	17	2.4	1.47
	14-Jul-82	195			230	0.003	0.011			12	20	2.9	0.79
	21-Jul-82	202			240	0.002	0.006			16	15	4.3	1.45
	28-Jul-82	209			240	0.02	0.037			n.d.	n.d.	2.9	1.57
	03-Aug-82	215			200	n.d.	n.d.			14	15	3.2	n.d.
	09-Aug-82	221			220	0.004	0.008			13	18	3.7	1.59
	16-Aug-82	228			160	n.d.	n.d.			20	7	4.8	n.d.
	23-Aug-82	235			160	n.d.	n.d.			24	7	4.8	n.d.
	mean				210	0.008	0.018			15	15	3.4	1.37

APPENDIX 7

Seasonal ATP concentrations.

TABLE 32. ATP concentrations (ug L^{-1}) in the limnocorrals and lake during 1981 and 1982. C = control, PN = phosphorus and nitrogen, LS = low sediment, HS = high sediment, LM = low moss, HM = high moss, FM = flooded moss, SC = screen covered, OC = 1 year old control, OM = 1 year old moss-peat, and L = lake. Limnocorrals C81-5, C81-7, LS81-4, HS81-6, PN81-3 had plastic bottoms. All other limnocorrals had natural bottoms. Day is day of the year.

		Limnocorral							
Date	Day	C81-1	C81-2	PN81-3	LS81-4	C81-5	HS81-6	C81-7	L81-8
10-Jul-81	191	0.66	0.69	0.88	0.40	0.56	0.36	0.75	0.73
20-Jul-81	201	0.85	1.26	0.80	0.38	0.56	0.30	0.81	1.09
03-Aug-81	215	0.39	0.89	0.80	0.16	0.45	0.12	0.51	0.63
24-Aug-81	236	0.37	1.25	0.98	0.21	0.37	0.12	0.32	0.94

Date	Day	FM82-1	SC82-2	LM82-3	HM82-4	OC82-5	C82-6	HS82-7	OM82-8	L82-9
08-Jul-82	189	0.88	0.88	0.95	1.09	0.94	0.97	0.96	1.10	0.97
15-Jul-82	196	0.70	0.75	0.89	1.23	0.67	0.64	0.63	0.62	0.54
22-Jul-82	203	0.92	0.78	0.76	1.13	0.61	0.50	0.57	0.79	0.80
28-Jul-82	209	0.74	1.03	0.70	1.57	0.66	0.49	0.59	0.68	0.86
09-Aug-82	221	0.85	1.25	1.17	2.62	1.10	1.34	0.91	0.90	1.00

APPENDIX 8

CNP and CO_3 analysis of moss-peat material added to the limnocorrals.

TABLE 33. C, N, P, and CO_3 analysis of moss-peat material added to the limnocorrals in 1981 and 1982. Each group of data consists of several subsamples taken as the moss-peat material was collected and added to the limnocorrals. The average ratio for the two years was 3854.20.47.

Date		C	N	P	CO_3-C
		(mg g^{-1} dry wt.)			
June 1981		447	3.9	0.2	8
		433	5.2	0.4	7
		403	5.6	0.9	6
		384	2.1	0.2	7
		417	3.6	0.6	7
		442	3.7	0.4	7
		404	2.9	0.3	7
	mean	419	3.9	0.4	7
June 1982		450	5.8	0.3	n.d.[1]
		346	3.2	0.3	n.d.
		449	6.8	0.5	n.d.
		305	4.6	0.3	n.d.
		349	4.6	0.3	n.d.
		294	3.5	0.4	n.d.
		317	6.4	0.5	n.d.
		351	5.0	0.4	n.d.
		324	2.4	0.4	n.d.
		329	2.3	0.4	n.d.
	mean	351	4.5	0.4	

1 n.d. = not done

APPENDIX 9

CNP and CO_3 analysis of moss-peat material dredged from moss-peat limnocorral LM81-1 two months after the addition.

TABLE 34. C, N, P, and CO_3 analysis of moss-peat material dredged from moss-peat limnocorral LM81-2 on August 23, 1981.

	C	N	P	CO_3-C
		(mg g^{-1} dry wt.)		
	392	3.7	0.5	14
	374	6.6	0.6	17
	262	4.2	0.5	11
	156	5.7	0.8	14
mean	296	5.1	0.6	14