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EFFECTS OF ACIDITY ON PRIMARY PRODUCTIVITY IN LAKES: PHYTOPLANKTON

by

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ABSTRACT

Relationships between phytoplankton communities and lake acidity in three Adirondack Mountain Lakes are being studied at Woods Lake (pH ca. 4.9), Sagamore Lake (pH ca. 5.5), and Panther Lake (pH ca. 7.0). Numbers of phytoplankton species observed as of July 31, 1979 are Woods 27, Sagamore 38, and Panther 64, conforming to observations at many other sites that species numbers decrease with increasing acidity. Peak Chl. _a_ and productivity values, respectively, were Woods 6.8 mg m^{-2} and 21 mg m^{-2} hr^{-1}; Sagamore 12.2 mg m^{-2} and 16 mg m^{-2} hr^{-1}; and Panther 23 mg m^{-2} and 52 mg m^{-2} hr^{-1}. Patterns of increasing biomass and productivity in Woods Lake may be atypical of similar oligotrophic lakes in that they develop rather slowly to maxima six weeks after ice-out, instead of occurring very close to ice-out. Phytoplankton productivity averaged from ice-out through July 31, 1979, were 12 mg m^{-2} hr^{-1}, 10 mg m^{-2} hr^{-1}, and 30 mg m^{-2} hr^{-1} for Woods, Sagamore, and Panther. Contributions of netplankton (net > 48 μm), nannoplankton (48 > nanno > 20 μm) and ultraplankton (20 > ultra >0.45 μm) to productivity per m^{-2} show that the smaller plankton are relatively more important in the more acid lakes, Woods > Sagamore > Panther ($p < .05$). This pattern could be determined by nutrient availability (lake acidification is suspected of leading to decreased availability of phosphorus). The amount of

^{14}C-labelled dissolved photosynthate (^{14}C-DOM), as a percent of total productivity, is ordered Woods > Sagamore > Panther. This is consistent with a hypothesis that microbial heterotrophic activity is reduced with increasing acidity, but the smaller phytoplankton may be more "leaky" at low pH.

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INTRODUCTION

There have been few studies of the effects of acidification on phytoplankton productivity in lakes affected by acidic precipitation and much of the work currently in progress is not generally available. This paper presents preliminary results of an ongoing investigation which is far from complete and for which much of the critical data analyses have not yet been done. The objective is to make other interested persons aware of this research effort on the effects of acidic precipitation on phytoplankton. The hypothesis behind this paper, and the work described, is that acidification alters both the structure and functioning of phytoplankton communities.

Certain lakes have become more acidic over the past one to three decades, as a consequence of deposition from the atmosphere of strong mineral acid (H_2SO_4, and HNO_3) and acidic-forming substances (e.g. NH_4^+) which result in the formation of acids when entering terrestrial or aquatic ecosystems (Likens et al., 1977). This deposition and ensuing environmental alterations are often referred to as the "acid rain" problem. Decreased alkalinity and pH values have been reported for many lakes and streams in Norway (Wright and Gjessing, 1976; Wright, 1977), Sweden (Almer et al., 1974; Dicksen, 1975; Grahn, 1976), Canada (Beamish and Harvey, 1972; Beamish and Van Loon, 1977; Watt et al., 1979) and the United States (Schofield, 1976; Davis et al., 1978). The comparison of data obtained one or more decades ago to current data has been criticized on the grounds that methods used earlier altered the chemistry of the sample or were lacking in accuracy. For example, Zimmerman and Harvey (1979) note that older data for alkalinity were determined by fixed end point potentiometric or colorimetric titrations. In systems of less than 300 micro equivalents of alkalinity per liter (where species other than those of the carbonate system are significant) these fixed end point titrations cannot be expected to give accurate results. The error is an over-estimate of about 35 micro equivalents per liter, and the error is so indeterminant "that little hope exists for any mathematical salvaging operations," according to these authors. This substantial and helpful critique of temporal comparative studies may call into question much of the chemical evidence which indicates that lakes have been acidified by acidic precipitation.

There is, however, another independent line of evidence, based on the aquatic biota. Fish have disappeared from many lakes and streams in which acidification is reported, and from many others where no chemical data from an earlier period are available (Statens Naturvårdsverk, 1975; Leivested et al., 1976; Schofield, 1976). Previously the fish were present, now they are absent, because the water is too acidic and perhaps because the concentrations of materials related to watershed acidification (e.g. aluminum) are too high (Almer et al., 1978; Cronan and Schofield, 1979). In fact, many waters formerly renowned for their good fishing are now barren and so acidic that fish cannot survive at all.

Integrated Lake-Watershed Acidification Investigations (ILWAI)

This study of phytoplankton is a component of an integrated, multidisciplinary, multiinstitutional research project being conducted in three separate lake watersheds in the Adirondack Mountains. The project known as the Integrated Lake Watershed Acidification Investigation (ILWAI), seeks to describe the effects of acid precipitation on lake-watershed ecosystems. The three lakes being studied are listed in Tables 1 and 2, and the major components of this project directly related to lake studies are listed in Table 3.

Studies of phytoplankton productivity are necessarily linked to both physical and chemical limnology. Data on pH, conductivity, temperature, dissolved inorganic and organic carbon (DIC, DOC), and seston ash-free dry-weight (AFDW) are determined by the phytoplankton project at the ILWAI laboratory, Raquette Lake, New York. In addition, chemical samples are collected from lake profiles and from inlet and outlet streams. These are analyzed by a cooperating laboratory (J. Galloway, University of Virginia) for alkalinity (acidity), NH_4, Na, K, Ca, Mg, SiO_4, SO_4, NO_3, Cl, Al, Fe, and Mn. Samples for total P analyses are frozen and stored for analysis during the winter months at BNL. All of these data obtained by this project and a closely related project on benthic plant communities are entered in a common data base maintained by Tetra Tech, Inc.

PHYTOPLANKTON

Phytoplankton Methods

Primary production is determined by ^{14}C *in situ* incubation at 5 or 6 depths in each lake. Samples are returned to the laboratory for filtration and analysis of chlorophyll *a* and phaeophyton (fluorometry), and ^{14}C activity of particulate and dissolved phases (filtration and LSC). From August

Table 1

Lakes of the integrated lake-watershed acidification investigation (ILWAI)

Name	pH range	Elevation	Coordinates	USGS Quadrangle
Woods Lake	4.7 - 5.1	615 m	43° 53' N 74° 57' W	Big Moose
Sagamore Lake	5.0 - 6.4	586 m	43° 46' N 74° 38' W	Raquette Lake
Panther Lake	5.3 - 7.8	562 m	43° 41' N 74° 55' W	Old Forge

Table 2

Areal and hydrological characteristics of the ILWAI watersheds and lakes

	Panther	Sagamore	Woods
Watershed Area, km^2	1.24	49.65	2.07
Lake Surface Area, km^2	0.18	0.72	0.23
Surface: Watershed, ratio	1:6.9	1:69	1:9.0
Volume, $10^6 m^3$	0.709	7.54	0.813
Mean Depth, meters	3.51	11.6	4.22
Outflow, 10/77-9/78, cm yr^{-1}	98.9	84.6	76.9
Outflow, 10/77-9/78, 10^6 m^3 yr^{-1}	1.19	42.0	1.59
Flushing Time ($\frac{\text{volume}}{\text{mean annual flow}}$), days	230	65	180

Table 3

Major components of the ILWAI

OWRT = Office of Water Research and Technology, Department of the interior; NYS-ERDA = New York State Energy Research and Development Authority; EPRI = Electric Power Research Institute; USGS = United States Geological Survey, Department of the Interior.

Task	Principal Investigator	Sponsor
Phytoplankton	G. Hendrey Cornell University	OWRT
Benthic Plant Communities	G. Hendrey and L. Conway Brookhaven National Laboratory	NYS-ERDA
Allochthonous Litter Decomposition	G. Hendrey and A. J. Francis Brookhaven National Laboratory	EPRI
Lake Acidification Investigation, Chemical Studies	J. Galloway University of Virginia	EPRI
Hydrologic Studies	J. Peters U.S. Geological Survey	USGS
Precipitation Studies	N. Clesceri Rensselaer Polytech. Inst.	EPRI
Data Management and Biogeochemical Modeling	C. Chen Tetra Tech. Corp.	EPRI
Watershed Vegetation and Groundwater Chemistry	C. Cronan Dartmouth University	EPRI

1978 onward, Chl. a and ^{14}C production samples were filtered through a fractionation series to determine the contributions from phytoplankton in the following size ranges: (a) netplankton > 48 μm, (b) 48 μm > nannoplankton > 20 μm, (c) 20 μm > ultraplankton > .45 μm, and the dissolved photosynthate ^{14}C-labelled dissolved organic matter (DOM). Samples of phytoplankton and of zooplankton are taken along with the primary production samples and preserved for analysis. Phytoplankton have been collected in either a van Dorn bottle or with a peristaltic pump, preserved with acid Lugol's solution, settled by the Utermöhl technique and analyzed microscopically using a Wild inverted microscope.

Phytoplankton Results and Discussion

The species of phytoplankton identified in each lake are shown in Table 4. The total number of species identified as of July 31, 1979 in each lake (Fig. 1) are Woods 27, Sagamore 37 and Panther 64, decreasing with increasing acidity. This is quite consistent with observations in numerous other locations (Almer et al., 1974; Kwiatkowski and Roff, 1976; Hendrey and Wright, 1976; Conroy et al., 1976; Yan, 1979).

Chlorophyll a

Chlorophyll a (Chl. a) concentrations are an indication of photosynthetically active algae and are used here as a measure of biomass. Problems with estimating biomass by chlorophyll are recognized. For example, algal cells are able to adjust the content of photosynthetic pigment in accordance with their light regime (Jørgensen and Steeman Nielsen, 1965). In these lakes, the light extinction coefficients are Woods 0.24, Sagamore 1.13, and Panther 0.39. Sagamore, a brown-water lake, absorbs light more rapidly than

Table 4

Phytoplankton taxa identified in Woods, Panther and Sagamore Lakes, as of August 1979. Relative frequency of accuracy indicated: 4 = dominant, 3 = common/frequent, 2 = occasional, 1 = rare/infrequent, - = absent. 8 taxa occurring in January-April samples (winter) are tabulated separately from those occurring in May-August samples. (Microscopic examinations conducted by K. Baumgartner.)

	Woods			Sagamore			Panther		
	Feb	Mar	Apr	Jan	Feb	Mar	Feb	Mar	Apr
Chlorophyta									
Ankistrodesums falcatus	-	-	-	-	-	-	-	2	-
Carteria sp.	-	-	-	-	-	-	-	-	1
Chlamydomonas	-	-	2	-	-	1	-	-	2
Oocystis novae-semliae	-	-	-	-	-	-	-	-	1
Oocystis parva	-	-	-	2	2	-	-	-	-
Staurastrum megacanthum	-	-	-	-	-	-	-	-	1
Cyanophyta									
Anabaena	-	-	-	-	-	-	-	-	1
Chroococcus minimus	-	-	-	-	-	-	-	-	1
Chrysophyceae									
Chromulina (3 or less)	3	3	3	3	3	3	3	3	4
Chromulina (6)	2	2	2	3	3	3	2	3	2
Chromulina (10)	2	2	2	3	2	-	2	2	-
Diceras chodati	-	-	-	-	-	-	-	-	3
Dinobryon bavaricum	-	-	-	1	2	-	-	-	1
Dinobryon cylindricum	-	-	-	-	-	-	2	2	2
Dinobryon divergens	-	-	-	-	-	-	-	1	-
Dinobryon sertulana	-	-	-	-	-	-	-	2	-
Chrysococcocystis ovoides	-	-	-	-	-	-	-	-	2
Kephyrion sitla	-	-	-	-	-	-	-	-	2
Ochromonas (4)	2	2	2	2	2	2	2	2	2
Ochromonas (9)	1	-	-	-	-	2	1	-	2
Ochromonas nannos	1	-	-	2	2	-	2	-	2
Ochromonas scintillins	-	-	-	-	2	-	-	-	2
Pseudopedinella gallica	-	-	2	1	1	-	-	-	2
Bacillariophyceae									
diatoms (unknown)	1	-	1	1	1	-	-	-	2
Asterionella	-	-	-	-	1	-	-	-	-
Cocconeis	-	-	-	-	-	1	-	-	-
Eunotia	-	-	-	-	-	1	-	-	-
Eunotia triodon	-	-	-	-	1	-	-	-	-
Navicula	-	-	-	-	1	-	-	-	-
Nitschia sigmoidea	-	-	-	1	-	-	-	-	-
Tabellaria	-	-	-	1	-	-	-	2	-

Table 4 (cont)

	Woods			Sagamore			Panther		
	Feb	Mar	Apr	Jan	Feb	Mar	Feb	Mar	Apr
Pyrrhophyta									
Gymnodinium	-	1	-	1	-	-	-	-	2
Gymnodinium varians	-	-	-	-	-	-	-	-	2
Peridinium inconspicuum	-	-	-	-	-	-	-	-	2
Cryptophyta									
Chroomonas acuta	-	-	-	-	-	-	1	2	2
Chroomonas pulex	-	-	-	-	-	-	-	-	1
Cryptomonas evosa	-	-	-	1	2	-	2	2	2
Rhodomonas minuta	-	-	-	-	-	-	-	-	2

Table 4 (cont)

	Woods M	J	J	A	Sagamore M	J	J	A	Panther M	J	J	A
Chlorophyta (greens)												
Ankistrodesmus falcatus	-	-	-	-	-	-	-	-	-	-	1	2
Arthrodesmus incus	-	1	-	1	-	-	-	-	-	-	1	-
Asterococcus	-	-	-	-	2	-	-	-	-	-	-	-
Ankistrodesmus convolutus, v. minutus	-	-	2	2	1	1	-	-	-	-	-	-
Botryococcus Braunii	-	-	-	-	-	-	-	1	-	-	2	-
Chlamydomonas	2	2	1	2	2	2	-	-	-	2	2	2
Closteriococcus vierheimensis (Ankistrodesmus)	-	-	-	-	2	-	-	-	-	-	-	-
Chlorococcum gigas	-	-	-	-	-	-	-	-	-	1	-	-
Coelastrum microporum	-	-	-	-	-	-	-	-	-	-	1	-
Cosmarium	-	-	-	-	-	-	-	-	-	-	1	-
Elakatothrix gelatinosa	-	-	-	-	-	-	-	-	-	2	-	1
Eudorina elegans	-	-	-	-	-	-	-	-	-	1	1	-
Gloeocystis (small)	-	-	-	-	-	-	2	-	-	1	1	-
Gloeocystis major	-	-	-	-	-	-	-	-	-	-	1	2
Gloeocystis gigas	-	-	-	-	-	-	-	1	-	-	2	1
Oocystis borgei	-	-	-	2	-	2	-	-	-	2	2	-
Oocystis novae-semliae	-	-	-	-	-	-	-	-	-	3	3	2
Oocystis parva	-	-	-	-	-	-	3	3	-	2	-	-
Oocystis pusilla	-	-	-	2	1	3	3	3	-	-	2	2
Oocystis submarina	-	-	-	-	-	2	2	2	-	2	2	-
Pediastrum tetras	-	-	-	-	-	-	-	-	-	1	-	-
Planktosphaeria gelatinosa	-	-	-	-	-	-	-	-	1	-	1	-
Quadrigula chodatii	-	-	-	-	-	-	-	-	-	-	2	-
Quadrigula closterioides	-	-	-	-	-	-	-	-	-	2	2	-
Quadrigula lacustris	-	-	-	-	-	-	-	-	-	2	-	-
Scenedesmus abundans	-	-	-	-	-	-	-	-	-	1	-	-
Scendesmus denticulatus	-	-	-	-	-	-	-	-	-	2	2	1
Scenedesmus quadricauda	-	-	-	-	-	-	-	-	-	-	1	1
Sphaerocystis	-	-	-	-	2	4	2	-	-	-	-	-
Staurastrum dejectrum	-	-	-	-	-	-	-	-	-	-	1	1
Sphaerocystis Schroeteri	-	-	-	-	-	-	-	2	-	3	4	4
Staurastrum jaculiferum	-	-	-	-	-	-	-	-	1	-	-	-
Tetraedron caudatum	-	-	-	-	-	-	-	-	2	-	-	-
Xanthidium	-	-	-	-	-	-	-	-	1	-	1	-

Table 4 (cont)

	Woods				Sagamore				Panther			
	M	J	J	A	M	J	J	A	M	J	J	A
Cyanophyta (blue-greens)												
Aphanotheca nidulans	-	-	-	-	-	-	-	-	-	-	3	3
Anabaena flos-aquae	-	-	-	-	-	-	-	-	-	2	-	-
Aphanocapsa elachista	-	-	-	-	-	-	-	-	-	2	2	2
Chroococcus limneticus	-	-	-	-	-	-	-	-	-	-	3	4
Chroococcus minimus	-	-	-	-	-	-	-	-	-	1	-	-
Coeosphaerium naegelianum	-	-	-	-	-	-	-	-	-	2	3	3
Dactylococcopsis smithii	-	-	-	-	-	-	-	-	-	-	-	2
Merismopedia tenuissima	-	-	-	-	-	3	4	4	-	-	-	-
Dactylococcopsis acularis	-	-	-	-	-	-	-	1	-	-	-	-
Merismopedia glauca	1	-	1	-	-	-	-	-	-	-	-	-
Oscillatoria	-	-	-	-	-	-	-	-	-	-	-	2
Chrysophyta												
Chrysophyceae (golden)												
Chromulina (3)	3	3	3	4	3	3	3	3	3	3	3	3
Chromulina (6)	3	3	3	3	3	3	3	3	3	3	3	3
Chrysamoeba radians	-	-	-	-	-	-	-	-	2	-	-	-
Chrysococcus radians	-	-	-	-	1	-	-	-	-	-	-	-
Chrysoikos angulatus	2	-	-	-	-	-	-	-	-	-	-	-
Chrysosphaerella longispina	-	-	-	-	-	-	2	2	1	-	-	1
Diceras-b	2	-	-	-	-	-	-	-	-	-	-	-
Diceras chodati	3	-	-	2	-	2	1	-	3	1	-	-
Dinobryon bavaricum	2	4	4	3	1	3	2	3	-	-	-	-
Dinobryon cylindricum	-	-	-	-	-	-	3	2	4	1	-	-
Dinobryon divergens	2	2	2	-	1	1	-	-	-	2	2	2
Dinobryon sertularia	2	-	-	-	1	-	-	-	-	-	-	-
Dinobryon sociale	3	3	2	3	1	2	1	-	-	-	1	-
Kephyrion valkovnovi	-	-	1	-	1	-	-	-	-	-	1	1
Kephyrion sitta	2	2	2	2	1	2	1	2	3	1	1	1
Mallomonas - A	-	2	3	3	2	2	-	-	-	-	1	1
Mallomonas - B	-	-	-	-	-	-	2	2	-	-	-	-
Mallomonas - C	-	-	-	-	-	-	-	2	-	-	-	-
Mallomonas - D	2	2	2	3	-	-	-	-	-	1	-	-
Mallomonas - E	1	1	1	-	-	-	-	-	-	-	-	-
Mallomonas - F	-	-	-	1	-	-	-	-	-	-	-	-
Ochromonas	2	2	2	2	3	2	2	2	-	-	1	1
Ochromonas nannos	-	-	-	-	2	2	2	2	3	3	2	1
Ochromonas scintillins	-	-	-	-	-	-	-	-	3	1	-	-
Pseudopedinella gallica	-	-	-	-	-	-	2	2	-	-	2	2
Uroglena americana	-	1	-	1	2	2	3	-	-	2	2	-

Table 4 (cont)

	Woods M	Woods J	Woods J	Woods A	Sagamore M	Sagamore J	Sagamore J	Sagamore A	Panther M	Panther J	Panther J	Panther A
Bacillariophycae (diatoms)												
diatoms (general)	2	3	2	2	2	1	1	2	2	2	2	2
Melosira crotonensis	–	–	1	–	2	1	–	1	1	–	1	–
Eunotia	–	–	–	–	1	1	–	1	–	–	–	–
Navicula	2	3	2	2	–	–	–	1	2	2	1	–
Stauroneis	–	–	1	–	1	–	–	–	–	–	–	–
Frustulia	–	1	2	–	–	1	–	–	–	–	1	–
Surirella	–	–	1	–	–	–	–	–	–	–	–	–
Synedra	–	–	–	–	–	–	–	–	2	2	–	–
Asterionella formosa	–	–	–	–	–	–	–	2	–	–	–	–
Cymbella	–	–	–	–	–	–	–	–	–	2	–	–
Tabellaria	–	2	1	–	1	–	–	–	–	–	–	1
Nitzchia	–	–	–	–	–	–	–	1	–	–	1	–
Fragillaria	–	–	–	–	2	–	–	–	–	–	–	–
Pyrrhophyta (dinoflagellates)												
Gymnodinium sp.	–	–	1	2	–	–	–	–	–	–	–	–
Gymnodinium varians	3	3	3	3	2	2	2	1	2	–	1	1
Gymnodinium lantzschia	–	–	–	–	2	–	–	–	–	–	–	–
Gymnodinium paradoxum	1	–	–	–	1	–	–	–	–	–	–	–
Ceratium hirundinella	–	–	–	–	–	–	–	–	–	–	1	–
Peridinium inconspicuum	2	3	2	2	–	–	1	1	1	–	1	1
Peridinium pusillum	–	–	1	1	–	–	–	–	–	–	1	–
Cryptophyta (cryptomonads)												
Chroomonas acuta	–	–	–	1	–	1	2	2	2	–	2	1
Cryptomonas erosa	1	2	3	3	2	3	3	3	3	3	3	3
Cryptomonas ovata	1	1	1	2	2	–	–	–	4	2	2	1
Cryptomonas marssonii	–	–	–	–	–	–	–	2	–	–	–	–
Rhodomonas minuta	–	–	–	–	–	1	–	–	3	3	3	3
Sennia parvula	–	–	–	–	–	–	–	–	3	2	–	–
Cryptomonas norstedtii	–	–	–	1	–	–	–	–	–	–	–	–

do either Panther or Woods so that the euphotic zone is shallower. The phytoplankton, mixing to the depth of the thermocline, will have less available light in Sagamore than in the other two lakes and the concentration of Chl. a per cell may increase. This will be described quantitatively in subsequent reports, where Chl. a will be analyzed as a function of cell volume determined by microscopy.

Chl. a concentrations integrated over the water columns (Figs. 2-4) of these lakes are typically low in winter under ice cover and increase in springtime as light begins to penetrate through the thinning ice-snow pack. In many oligotrophic lakes, such as these three, it is common to see a rapid increase in algal density just after ice-out and this did occur in Panther, and to some extent in Sagamore. The pattern in Woods Lake, however, is slightly atypical of normal oligotrophic lakes. Both productivity and Chl. a build more slowly, if steadily, to a peak in June, six weeks after ice-out, in 1979. It is not yet possible to relate the Woods Lake observations to chemical changes since nutrient data are not available (samples are frozen for analysis during the winter, when field work decreases).

Phytoplankton Productivity

Phytoplankton productivity, mg C_{fixed} m^{-2} hr^{-1}, integrated over the photic zone was averaged from ice-out (which occurred at the end of April 1979) through July 1979 and is shown in Figure 5. This average areal productivity was much greater in Panther Lake than in either of the other two lakes, while Sagamore had the lowest value (Panther > Woods > Sagamore, $p < .05$). A Li-Cor integrating PAR (photosynthetically active radiation) meter operates at each lake from April into November. Data is collected on tape and will be entered at one time into the ALP data base. When these light values become available, they will be used to calculate daily and annual production values (productivity is the hourly rate of photosynthesis, production is the mass of carbon fixed over a specified time period).

The means of the maximum volumetric productivity values observed in each lake averaged from ice-out to July 31 are shown in Figure 6 and the corresponding Chl. a values in Figure 7. These were both greater in Panther than in either of the other two lakes ($p < .05$). Mean specific productivity values (P/B = productivity /Chl. a), calculated for each of the maximum volumetric productivity observations then averaged over the corresponding time period are Woods 2.94 ± 1.29 hr^{-1}, Sagamore 3.16 ± 1.19 hr^{-1}, and Panther 3.87 ± 2.04 hr^{-1}. This may be an indication that phytoplankton photosynthesis was somewhat less effective in the two more acidic lakes for the first half of the growing season compared to phytoplankton in Panther Lake.

In Figure 8, all of the areal productivity values are plotted against pH (the average of the hydrogen ion concentrations over the 5 or 6 depths at which productivity was measured). The pH of Woods Lake is always low, so no relationship of individual productivity observations to pH is evident, except that the overall average is low. In Sagamore Lake, on the other hand, there does appear to be a relationship between productivity and pH. In Panther Lake, the lowest productivity value is associated with a single low pH values of 5.97.

The percent contributions of the netplankton (> 48 μm), nannoplankton (48 > nanno > 20 μm) and ultraplankton (20 > ultra > 0.45 μm) to areal phytoplankton productivity, from ice-out through July 31, 1979, are shown in Figure 9, and the corresponding Chl. a concentrations in Figure 10. There is an obvious shift in both productivity and biomass (Chl. a), toward smaller cell size, going from Panther to Sagamore to Woods. This certainly may be related to nutrient availability, but interpretation of these trends must be delayed until nutrient data become available.

The percent of phytoplankton productivity which appears in the filtrate passing an 0.45 μm filter, ^{14}C-labelled DOM, is presumed to have been released by the living phytoplankters during the ^{14}C-incubation, but questions have been raised as to whether this release might be influenced by the filtration process, especially from the ultra plankton (Sharp, 1977; Fogg, 1977). The percent contribution of ^{14}C-labelled DOM to areal productivity averaged from April through July is shown in Figure 12, and is significantly lower in Panther Lake ($p < .05$) than in the other lakes. There is a considerable evidence that lake acidification inhibits microbial decomposition. This topic has been previously reviewed (Hendrey et al., 1976; Hendrey, 1979). Microheterotrophs normally are able to utilize excreted algal photosynthate (DOM) and convert it into particulate material rather rapidly if environmental conditions are suitable (Paerl, 1978). Only a small portion of this algal DOM is refractory material likely to survive longer than 24 hours (Saunders and Storch, 1971). The higher percent of ^{14}C-DOM in the two acidic lakes is consistent with the hypothesis that microbial activity is reduced in this more acidic environment, but questions need to be resolved concerning the effect of filtration on the amount of ^{14}C-DOM in the filtrate (Fogg, 1977; Storch and Saunders, 1978; Sharp, 1978). This may be caused by a greater "leakiness" of ultraplankton, which are more significant in Woods Lake than in the other two lakes.

GENERAL DISCUSSION

Lakes and streams which are acidified exhibit marked alterations in the communities of phytoplankton and attached algae. Several factors related to acidification appear to contribute to these changes. Other investigations

Table 5. Variation in phytoplankton density in 58 Swedish lakes grouped by pH[a]

Number of Lakes	7	16	8	9	18
pH	< 4.5	4.5–5.0	5.1–5.6	5.7–6.2	>6.2
Phytoplankton biomass micrograms per liter	660	400	212	287	394

[a]Source: Almer, B., W. Dickson, C. Ekstrom and E. Hornshrom. 1978. Sulfur pollution and the aquatic ecosystem. pp. 271–311. IN J. O. Nriagu (ed.), Sulfur in the Environment, Part II: Ecological impacts. Wiley, New York. York. 482 pp.

have found that the numbers of species of phytoplankton occurring in lakes is related to lake acidity (Almer et al., 1974; Kwiatkowski and Roff, 1976; Hendrey and Wright, 1976; Conroy et al., 1976; Yan, 1979). Some studies have found the biomass density of phytoplankton to decrease as well.

A notable feature of many acidified lakes is their remarkable clarity. This is especially evident when viewed from a hillside above the lake or from an aircraft. Often, acidic lakes have a dark, blue-green hue. Several studies have documented increases in the transparency of lakes as they become acidified. Almer et al. (1974) noted that the transparency of Lake Stora Skarsjön increased by 7 meters while from 1943 to 1973, pH decreased from 6.2 to 4.5 and the amount of organic material in the water, measured as $KMnO_4$-demand (C.O.D.) decreased from 24 to 8 mg ℓ^{-1} in the period 1958 and 1973. Increases in transparency by as much as 10 m were observed in other acidified lakes.

There are two mechanisms generally considered to cause this increased clarity (Almer et al., 1974). The first is precipitation of humic colored substances as a consequence of decreased pH and increased aluminum concentration (Almer et al., 1978). The second is a reduction of phytoplankton density, which seems to be related more closely to phosphorus concentrations than to pH _per se_, as has been noted in several previous reports (e.g. Almer et al., 1974; Grahn, 1976; Hendrey et al., 1976; Yan, 1979).

Perhaps the most interesting report on the relationship between phytoplankton, pH and nutrients is that of Almer et al. (1978). In fifty-eight oligotrophic lakes of the Swedish west coast, the lowest phytoplankton biomass was found in eight lakes ranging in pH from 5.1 to 5.6, while biomass density was greater in lakes of both higher and lower pH as shown in Table 5. Although all of these Swedish lakes had low concentrations of phosphorus (< 10 μg/ℓ), these authors suggested that aluminum complexing of phosphorus, which they found to have a maximum near pH 5.5, might play an important role in regulating the availability of the limiting nutrient to these acidic or acidifying lakes. Transparency of six other Swedish lakes increased while pH decreased by 1.4 to 1.6 units. Similar observations have been made in Adirondack Mountain lakes (Schofield, 1973). Yan (1979) found phytoplankton biomass to be correlated to the concentration of phosphorus in an acidified lake contaminated with heavy metals, but biomass was not related to $[H^+]$. The observations of Almer et al. (1978) and others that phosphorus concentration may be linked to $[H^+]$ provides an obvious link between decreased phytoplankton biomass and lake acidification, the direct relationship between [P] and phytoplankton biomass being well established (Kalff and Knoechel, 1978). While the maximum Aℓ-P complexing occurs at about pH 5.5, the concentration of Aℓ increases with water shed and lake acidification, so that more Aℓ is available to complex phosphorus at lower pH.

Whatever the reason for the increased clarity of acidified lakes, the consequence is increased light penetration and deepening of the euphotic zone. With the resultant increased thickness of the trophogenic layer in an acidified lake, the production by phytoplankton per square meter of lake surface may be as great as, or greater than, it is in a more neutral lake. This speculation was stated by Almer et al. in 1974 and our knowledge has not yet improved much since then.

The integrated, intensive study of three Adirondack Mountain lakes and their watersheds, ILWAI, will provide an opportunity for comparing the productivity of an acidified lake, including nutrient budgets and phytoplankton removal mechanisms, to similar data from nearby lakes which are less acidic.

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FIGURE CAPTIONS

Figure 1. Number of phytoplankton species identified as of 7/31/79.

Figure 2. Woods Lake integrated chlorophyll a concentration (□) and primary productivity (O).

Figure 3. Sagamore Lake integrated chlorophyll a concentration (□) and primary productivity (O).

Figure 4. Panther Lake integrated chlorophyll a concentration (□) and primary productivity (O).

Figure 5. Productivity (mg C m^{-2} hr^{-1}) averaged over the period April 30 - July 31, 1979. (Range = –, Standard Deviation = ●.)

Figure 6. Maximum productivity value observed in each water column profile (mg C m^{-3} hr^{-1}). (Range = –, Standard Deviation = ●.)

Figure 7. Chl. a values (mg m^{-3}) associated with the maximum productivity observed in each water column profile.

Figure 8. Integrated productivity as a function of pH, the mean H^+ concentration of the euphotic zone. Panther = ●, Sagamore = Δ, and Woods = □. Arrows indicate overall mean for each lake.

Figure 9. Percent contribution to the particulate fraction of phytoplankton productivity (mg C m^{-2} hr^{-1}). (Range = –, Standard Deviation = ●.)

Figure 10. Percent contribution to areal Chl. a concentration. (Range = –, Standard Deviation = ●.)

Figure 11. Percent contribution of ^{14}C - labelled DOM to phytoplankton productivity. (Range = –, Standard Deviation = ●.)

NUMBER OF PHYTOPLANKTON SPECIES IDENTIFIED AS OF 7/31/79

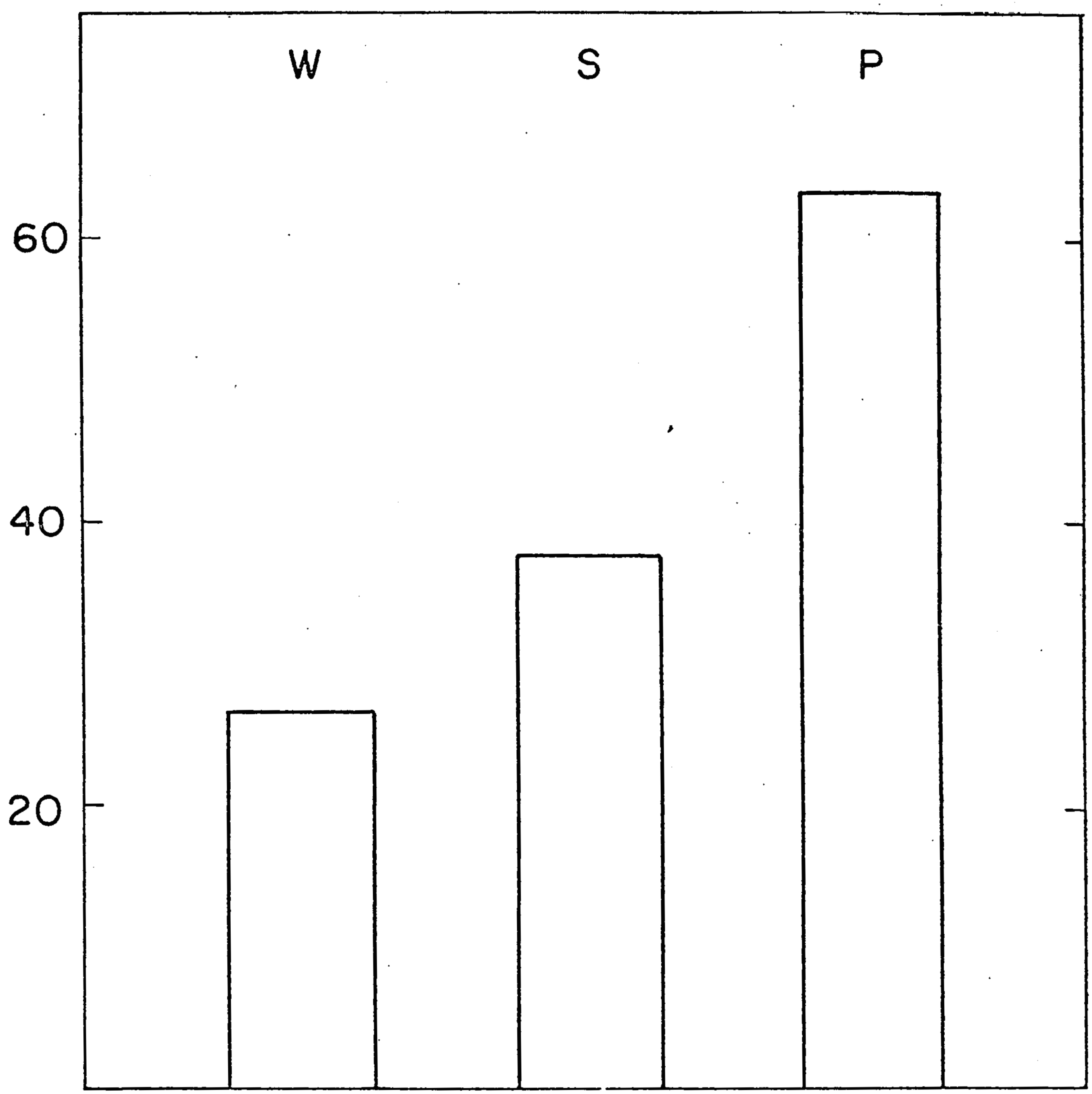
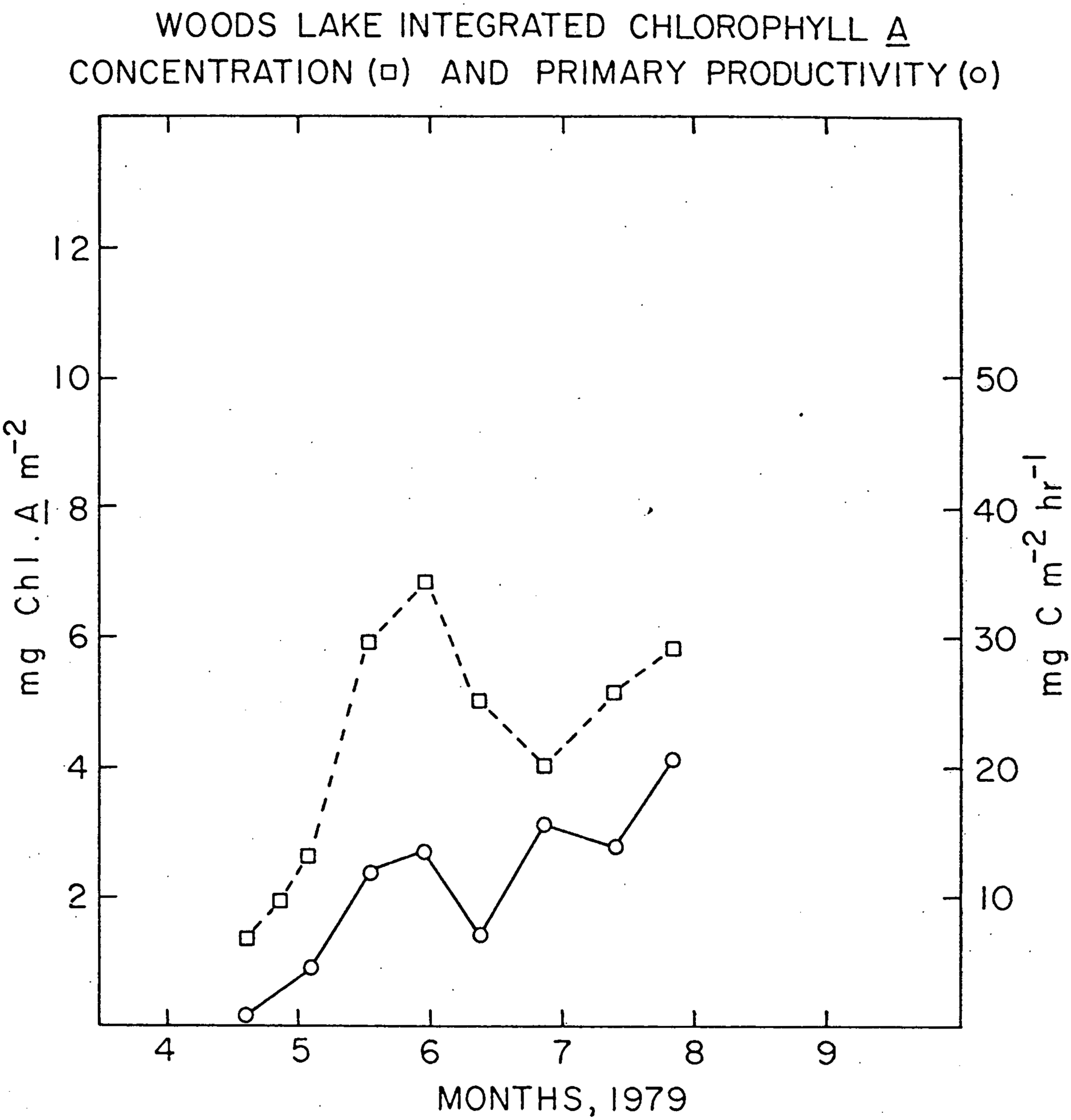


Figure 1



WOODS LAKE INTEGRATED CHLOROPHYLL A
CONCENTRATION (□) AND PRIMARY PRODUCTIVITY (○)
12
10
8
6
4
2
50
40
30
20
10
mg Chl. A m-2
mg C m-2 hr-1
4
5
6
7
8
9
MONTHS, 1979

Figure 2

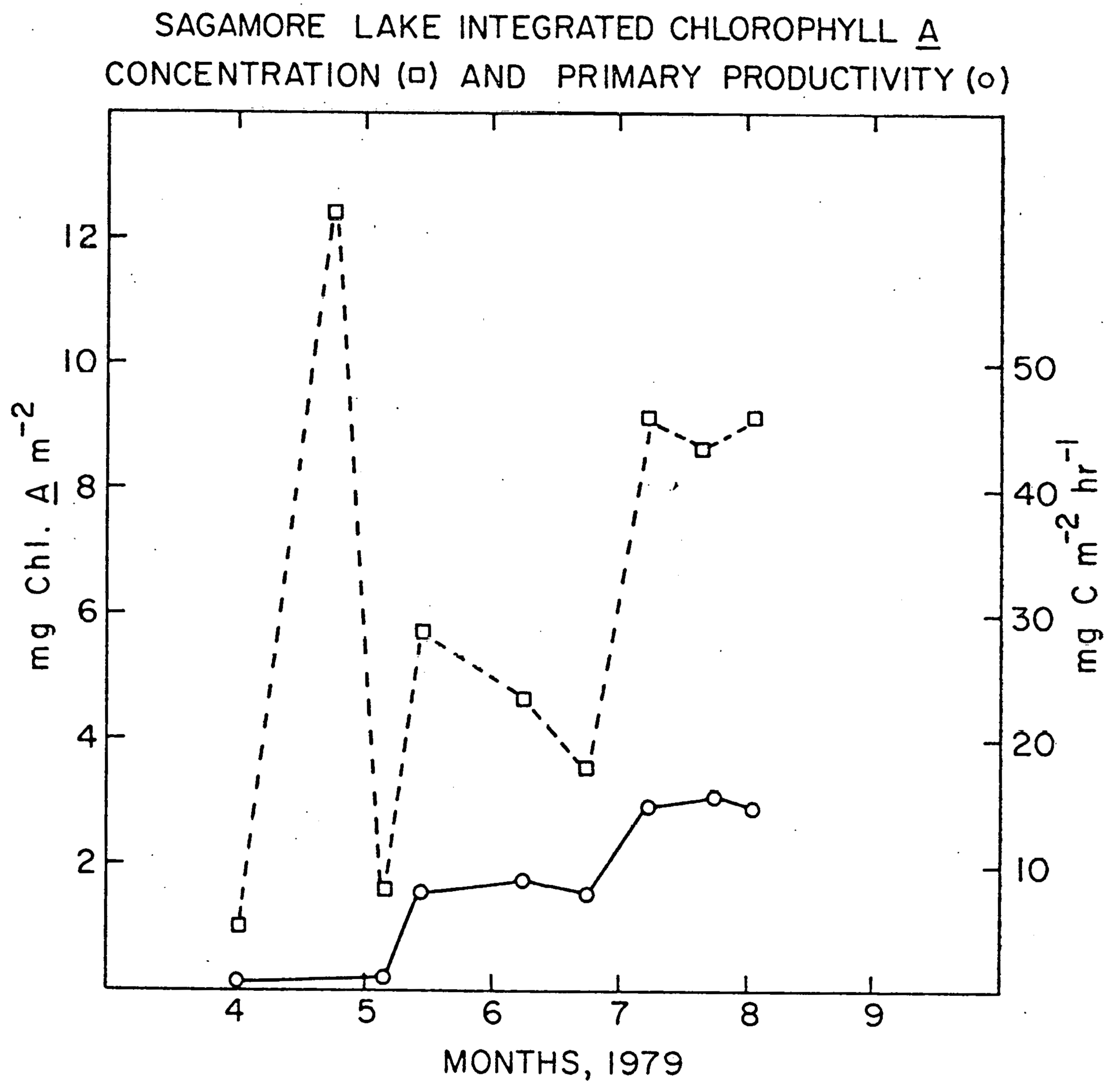

SAGAMORE LAKE INTEGRATED CHLOROPHYLL A
CONCENTRATION (□) AND PRIMARY PRODUCTIVITY (○)
mg Chl. A m-2
12
10
8
6
4
2
mg C m-2 hr-1
50
40
30
20
10
4
5
6
7
8
9
MONTHS, 1979

Figure 3

PANTHER LAKE INTEGRATED CHLOROPHYLL A CONCENTRATION (□) AND PRIMARY PRODUCTIVITY (○)

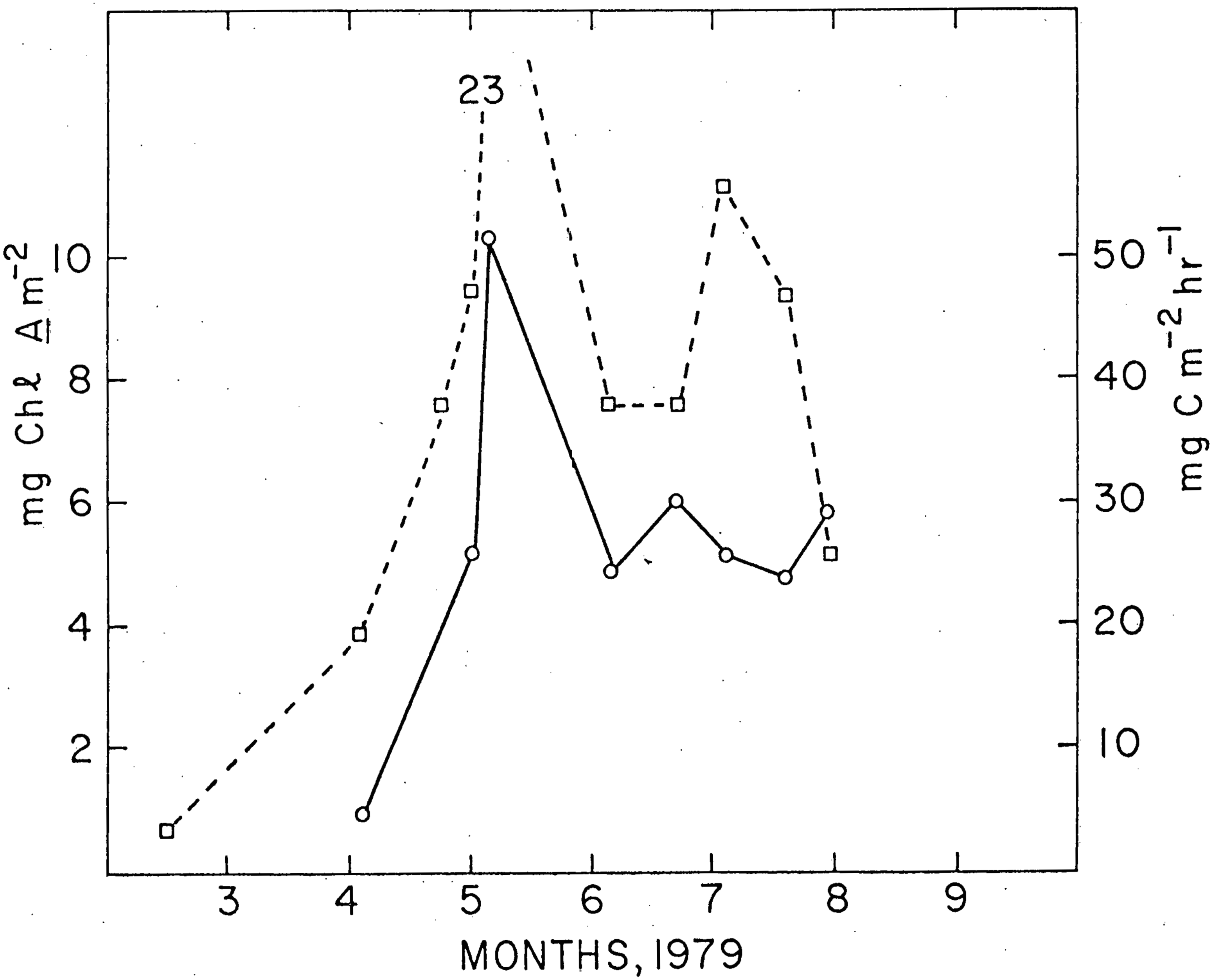


Figure 4

PRODUCTIVITY (mgC $m^{-2}hr^{-1}$) AVERAGED OVER THE PERIOD APRIL 30-JULY 31, 1979 (● = SD, – = range).

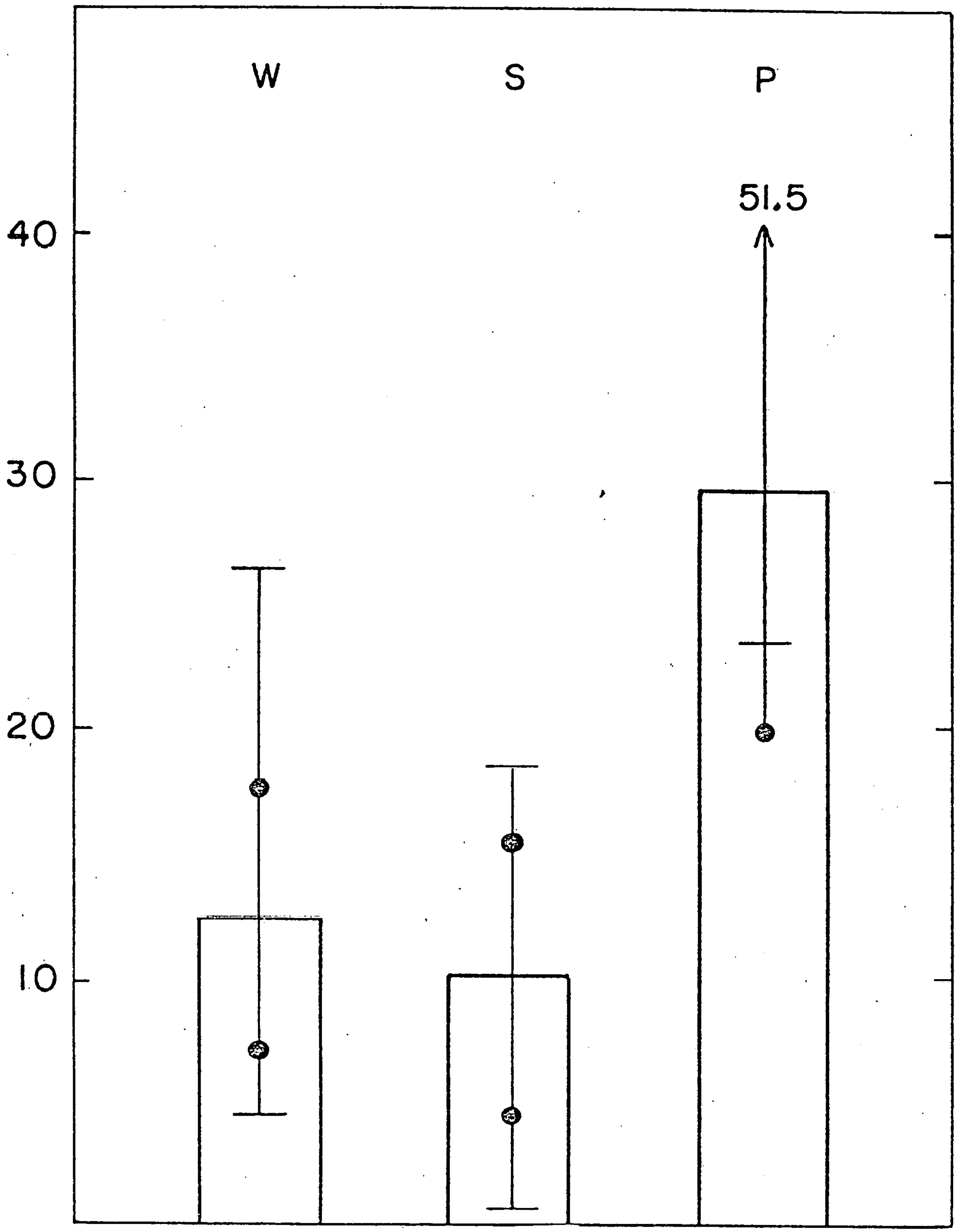


Figure 5

MAXIMUM PRODUCTIVITY VALUE OBSERVED IN EACH WATER COLUMN PROFILE (mg C $m^{-3} hr^{-1}$) (● = SD, — = range).

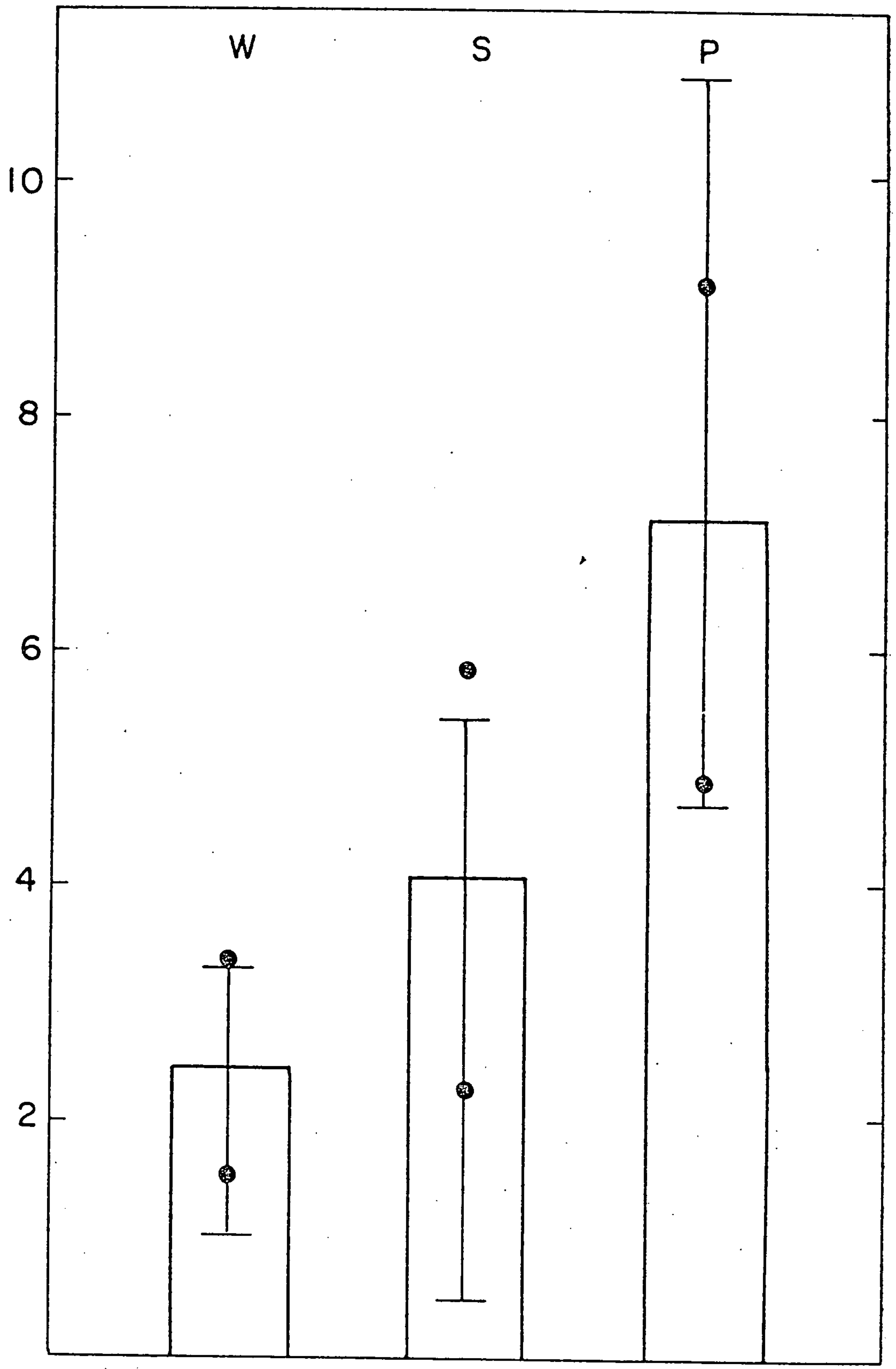


Figure 6

CHL. A VALUES (mg m^{-3}) ASSOCIATED WITH THE MAXIMUM PRODUCTIVITY OBSERVED IN EACH WATER COLUMN PROFILE (● = SD, – = range)

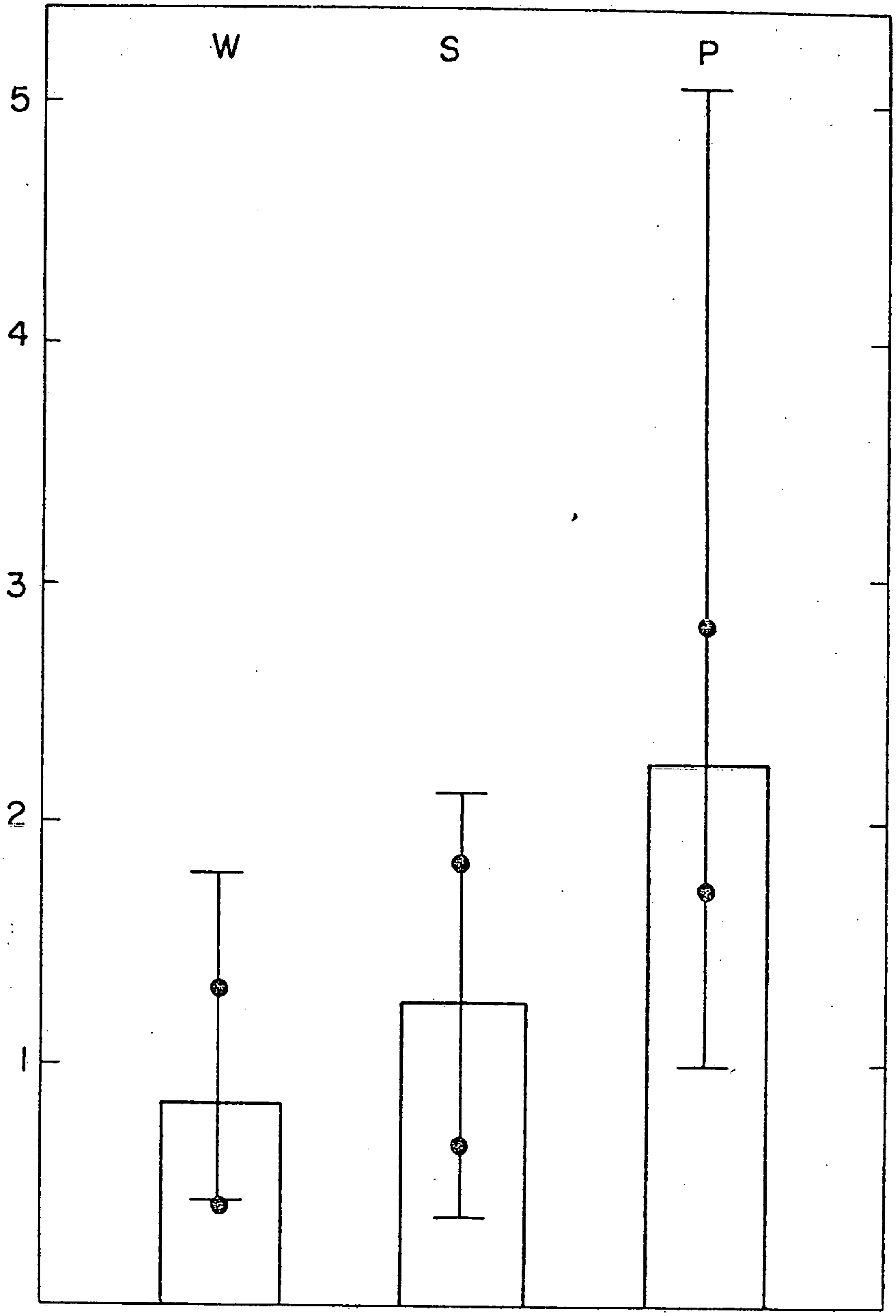


Figure 7

INTEGRATED PRODUCTIVITY AS A FUNCTION OF pH, THE MEAN H^+ CONCENTRATION OF THE EUPHOTIC ZONE. PANTHER = ●, SAGAMORE = △, AND WOODS = □. ARROWS INDICATE OVER-ALL MEAN FOR EACH LAKE.

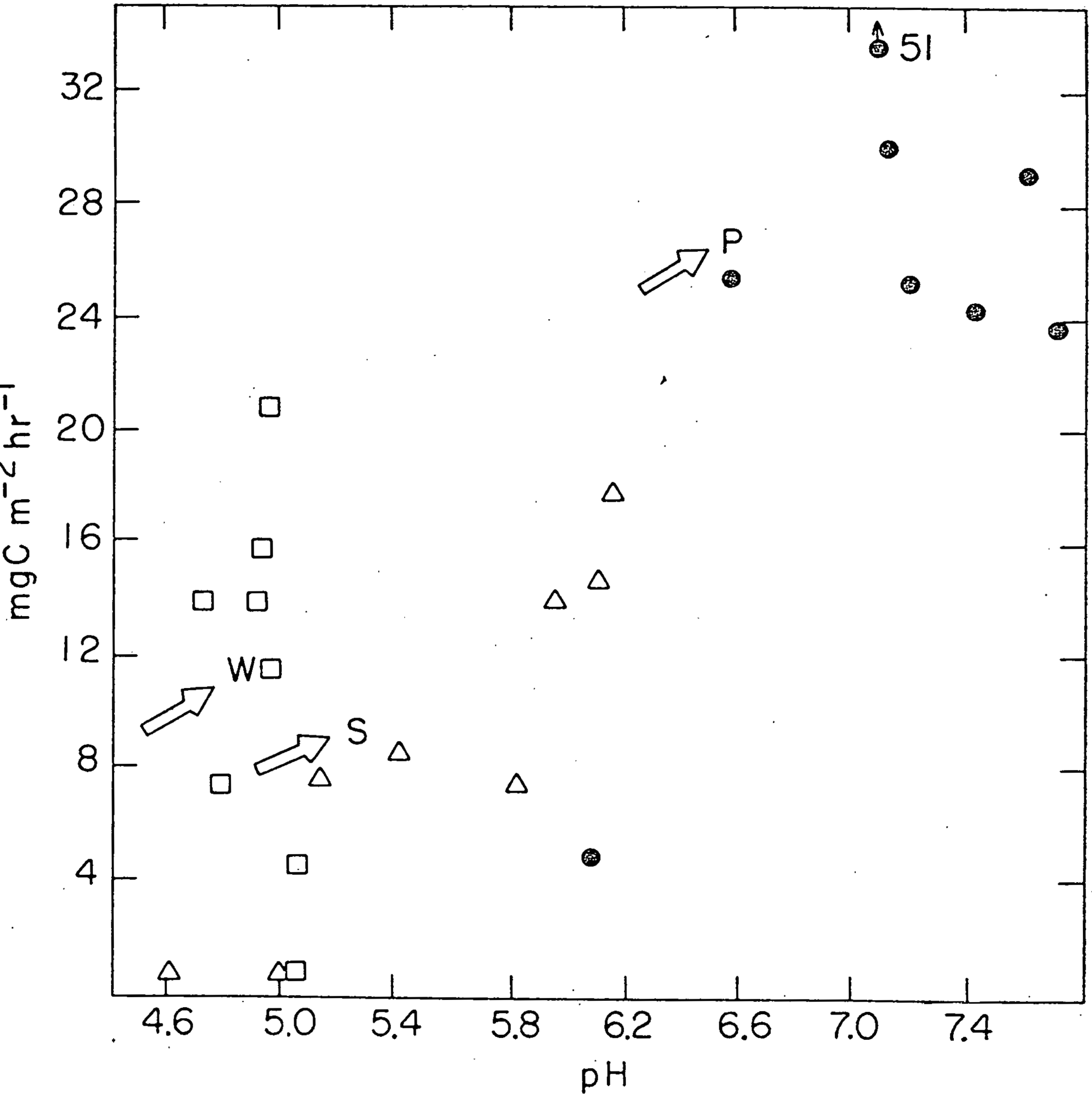


Figure 8

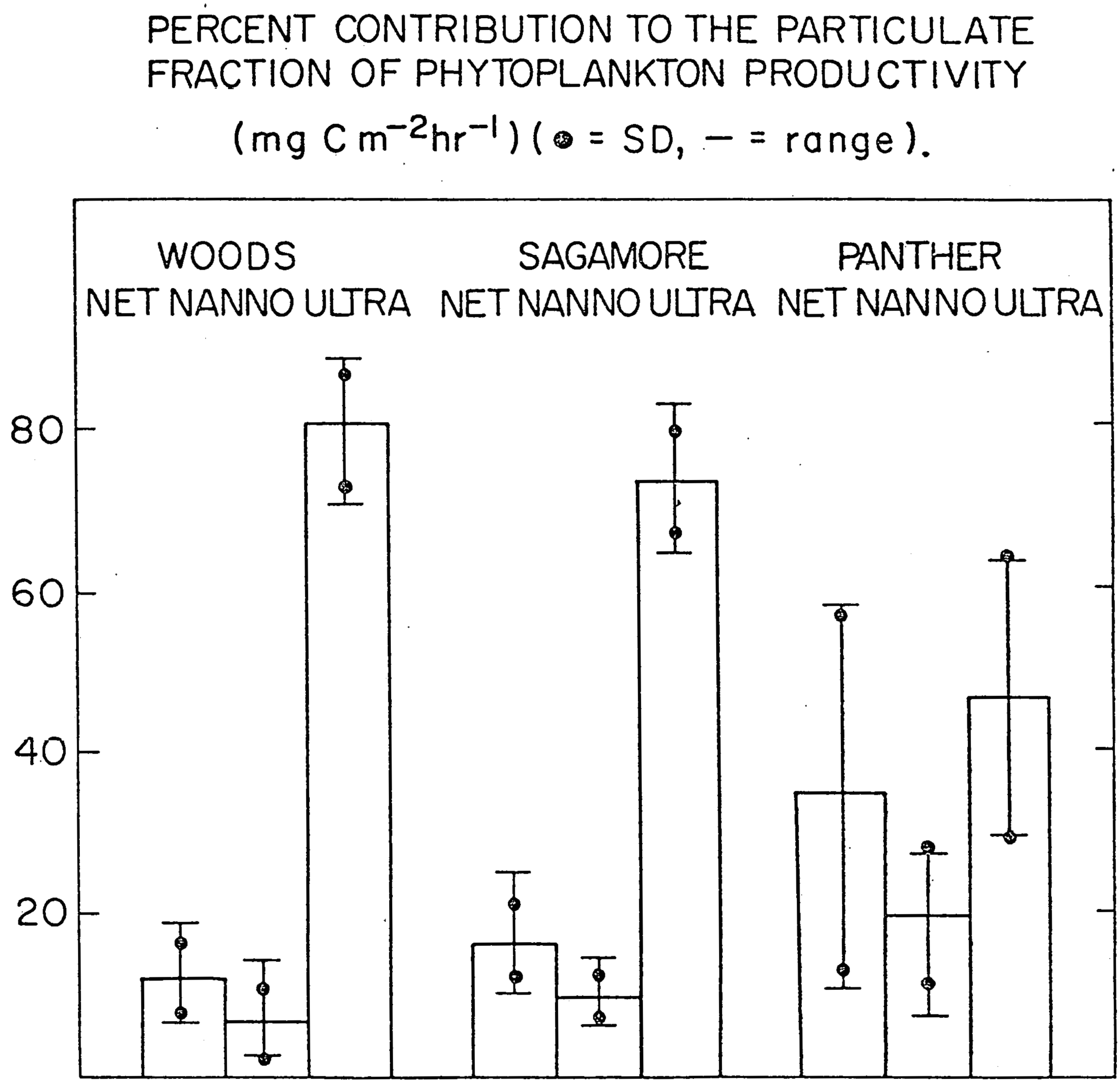
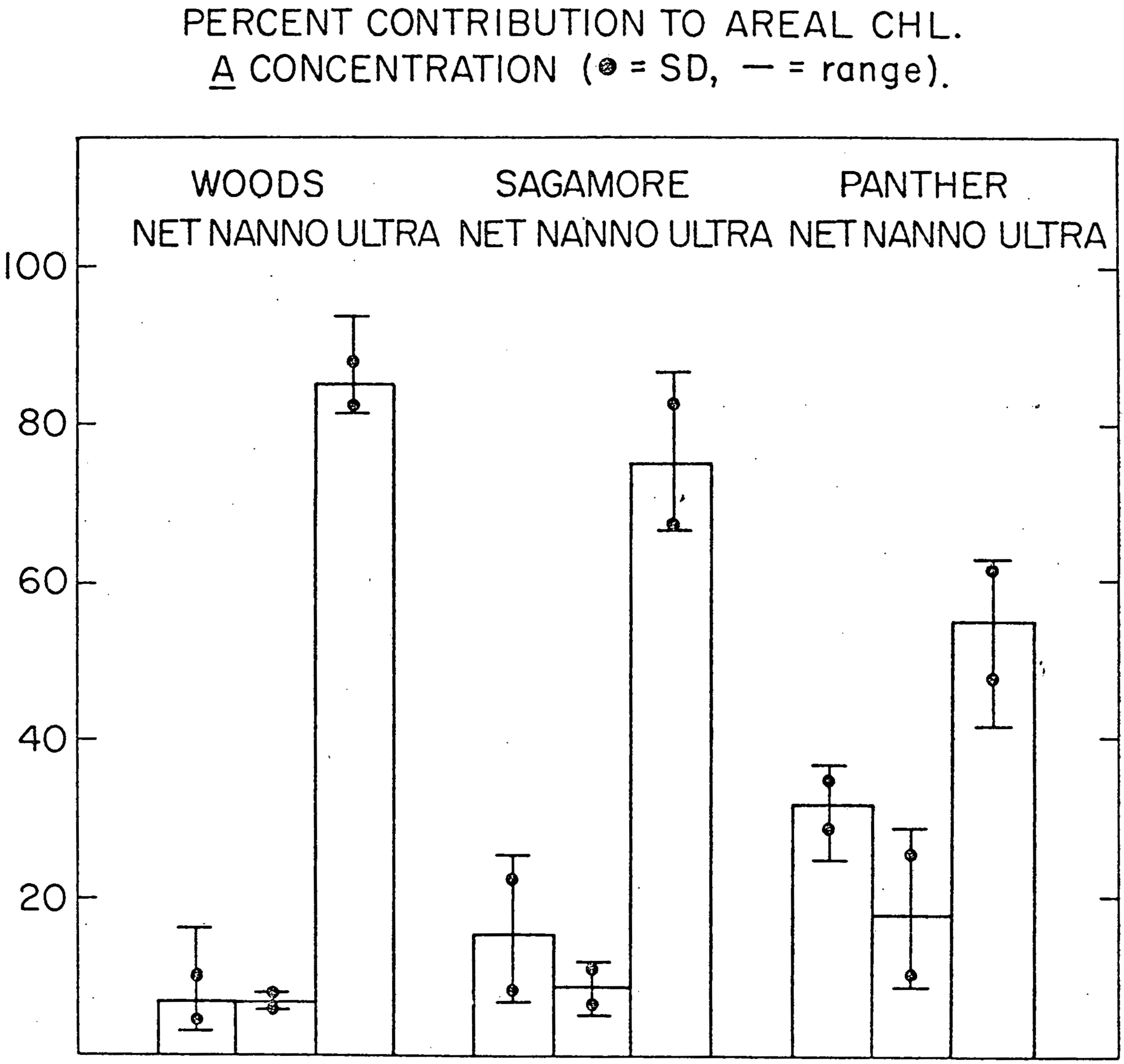

PERCENT CONTRIBUTION TO THE PARTICULATE
FRACTION OF PHYTOPLANKTON PRODUCTIVITY
(mg C m⁻²hr⁻¹) (● = SD, — = range).
WOODS
SAGAMORE
PANTHER
NET NANNO ULTRA
NET NANNO ULTRA
NET NANNO ULTRA
80
60
40
20

Figure 9



PERCENT CONTRIBUTION TO AREAL CHL.
A CONCENTRATION (● = SD, — = range).
WOODS
SAGAMORE
PANTHER
NET NANNO ULTRA NET NANNO ULTRA NET NANNO ULTRA
100
80
60
40
20

Figure 10

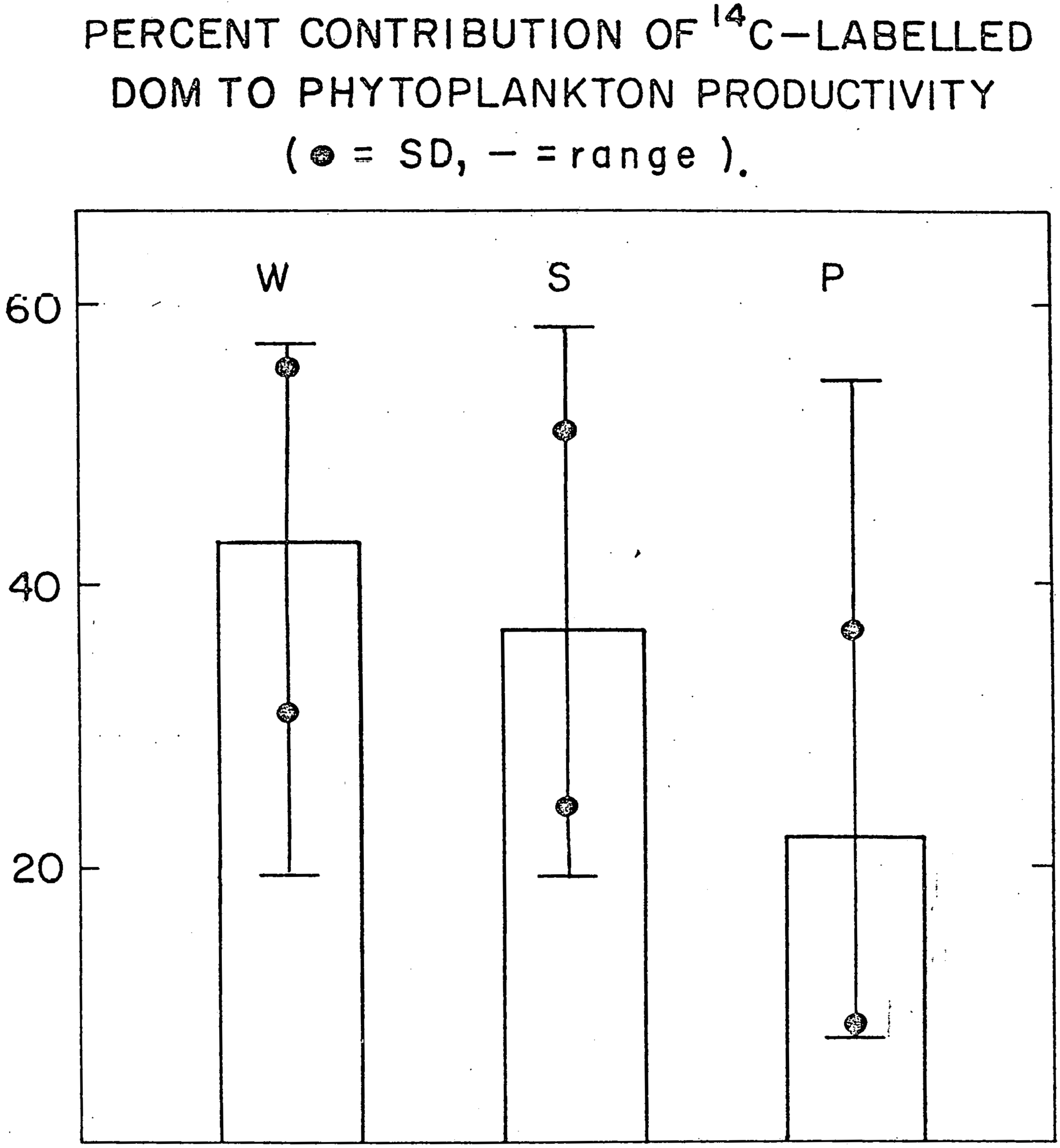

PERCENT CONTRIBUTION OF 14C-LABELLED DOM TO PHYTOPLANKTON PRODUCTIVITY
(● = SD, — = range).
W
S
P
60
40
20

Figure 11