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PREDICTING PRIMARY PRODUCTIVITY IN

WESTHAMPTON LAKE, RICHMOND, VIRGINIA

BY

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PREDICTING PRIMARY PRODUCTIVITY IN

WESTHAMPTON LAKE, RICHMOND, VIRGINIA

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ABSTRACT

Several predictive photosynthetic models were tested using light, temperature, nutrient, chlorophyll, and primary productivity data collected from Westhampton Lake, Richmond, Virginia from February-September, 1972.

A simple linear model, the Kendall rank correlation coefficient, was used to relate photosynthesis to individual meteorological, physical, chemical, and biological factors. Of the parameters measured, only the daily maximum photosynthetic efficiency ($(P/chl)_{max}$) was significantly correlated with photosynthesis.

Five multiple factor (non-linear) models were tested. In the best fitting model, primary productivity was a function of the maximum observed ratio of photosynthesis/chlorophyll concentration, light intensity, temperature, nutrient concentrations, and chlorophyll concentration. The Pearson (r) correlation coefficient between predicted and observed values of photosynthesis for this model was .58, indicating that only 34% of the variability between predicted and observed values was accounted for by the model.

Introduction

Inadequate environmental protection often results in the rapid aging of lakes in urban areas (Lee, 1970). Associated with this aging are large growths of algae (Hill, 1969). Algae form the initial link in the food web and as such exert a major influence on the ecosystem. Information concerning factors related to their growth should help provide an understanding of the aging process.

The effects of the environment on primary producers have been studied under laboratory conditions and in the natural habitat. In the former method, conditions have been controlled quantitatively and qualitatively. The application of results obtained in this manner to natural habitats has been of questionable value as possible interactions of environmental factors may not have been taken into account and the setting of the experiment may have resulted in abnormal behavior of the organisms. In the natural habitat, factors could not have been controlled. With this approach, problems arise in attempting to analytically ascertain the effects of various parameters or combinations thereof.

Mathematical models are useful for the analysis of biological systems under natural conditions. Such models can

help in understanding the relationships among the components of the system. Models may be divided into two categories, linear and non-linear. In the former, each variable appears only to the first power and no products of the variables appear (Dorn and Greenberg, 1967). An example of a simple linear model is the Kendall rank correlation coefficient, which can be used to relate photosynthesis to various individual factors. Most ecological systems cannot be fitted satisfactorily to linear models, but even so, linear models are useful as first approximations and are essential in the study of non-linear models (Dorn and Greenberg, 1967). In a non-linear model, either or both of the conditions of a linear model would not be fulfilled (Dorn and Greenberg, 1967). Several models (non-linear) which deal with the interactions of factors on photosynthesis have been developed. Fleming (1939) developed an equation to describe spring diatom blooms using phytoplankton concentrations, a constant growth rate, and a death rate due to zooplankton grazing. Riley (1946) developed a more refined model to relate the growth rate and grazing rate to incident solar radiation, temperature, extinction coefficient, nutrient concentrations and zooplankton concentrations. Riley, Stommel, and Bumpus (1949) produced equations which incorporated the spatial variation of the phytoplankton with respect to depth; also included were equations for phosphate and zooplankton concentrations. For simplification, a temporal steady-state phytoplankton population was assumed to exist; thus, the equations were most applicable during the months when the dependent variables

were not changing significantly. Steele (1956) used both
spatial and temporal variations because he found that the
temporal steady-state assumption was not applicable to the
seasonal variation of phytoplankton populations. Di Toro et
al (1970) presented a phytoplankton population model which was
based on the principle of conservation of mass, and included
as variables nutrient levels, light intensity, respiration,
grazing by herbivores, and transport of mass by dispersion or
advective flow in a body of water. Auclair et al (1971)
proposed a photosynthetic model for a cove in Lake Texoma,
Oklahoma which was a function of a maximum photosynthetic rate,
light, temperature, nutrients, and plant biomass. Photosynthesis
was estimated by direct measurements and predictive equations.
The main equation used was

$$\frac{dN}{dt} = rN, \qquad\qquad \text{(eq. 1)}$$

where $\frac{dN}{dt}$ was the change in biomass with time; r was a growth
coefficient which was a function of light, temperature, and
nutrients; and N was the biomass of plants.

In this study, an attempt was made to test the simple
linear models and the general model of Auclair et al (1971),
and to modify the latter for use with data obtained from West-
hampton Lake, an urban lake located on the campus of the Uni-
versity of Richmond, Virginia.

Methods and Materials

The simple linear models of photosynthesis based on single
factors were tested using the Kendall rank correlation coef-

ficient. The non-linear equation first used was

Primary productivity (mg C l^{-1} hr^{-1}) = $(P/chl)_{max}$ (Lcoef)

(Tcoef) (Nut. coef) (chlor), (eq. 2)

where $(P/chl)_{max}$ was the maximum daily photosynthetic effi-

ciency (mg C l^{-1} hr^{-1})(mg Chl m^{-3})$^{-1}$ observed during the sam-

pling period; Lcoef was the light coefficicent; Tcoef was the

temperature coefficient; Nut. coef was the nutrient coefficient;

and chlor was the chlorophyll concentration (mg m^{-3}). This

model and modifications of it were tested by comparing pre-

dicted and observed rates of photosynthesis.

Photosynthesis was measured by the C-14 method once a

week from March-September, 1972. Samples were taken from the

upper one meter in the south end of the lake. 20 uC of

$NaHC^{14}O_3$ in 1 ml sterile water (New England Nuclear Corp.)

were added to 2300 ml of lake water. Five sets of 125 ml

light and dark bottles were filled with the water, rinsed

externally in 2% HCl, placed in a dark box, and then taken

outside where they were exposed to five different light in-

tensities in an incubation rack. The rack consisted of five

transparent, cast acryllic tubes 63.5 cm in length (6.03 cm

I.D.) mounted on a wooden rocker assembly (Fig. 1). Two

light bottles and one dark bottle were placed in each tube.

The tubes were sealed at either end with #14 rubber stoppers

through which copper tubing was inserted. Lake water was

pumped through the tubes to maintain ambient lake water

temperature in the bottles. Temperature measurements taken

during incubation were generally consistent, seldom varying

more than 2-3 C. The rocker assembly was rotated back and

forth by a 30 rpm electric, shaded pole gear motor with a metal disc mounted off-center on the shaft to maintain the phytoplankton in suspension. The tubes allowed approximately 95% of the incident light to pass through. In order to create different light intensities within the tubes, varying layers of aluminum window screening were wrapped around the tubes. The resultant light intensities in the tubes were (in per cent incident radiation, % I_o) 95, 70, 55, 35, and 20. These figures do not include that amount of light absorbed and/or reflected by the water in the tubes and the glass bottles.

After a four hour incubation period (10 a.m.-2 p.m. or 11 a.m.-3 p.m.), the bottles were removed and injected with 1 ml of 37% formalin solution. The contents of the bottles were vacuum filtered onto Millipore filters (.45 u, HA) which were then stored in screw-capped, plastic scintillation vials in a refrigerator (10 C). The vials were filled with 15 ml of Aquasol L.S.C. cocktail (New England Nuclear Corp.) and analyzed with a Nuclear Chicago Mark II liquid scintillation system. Calculation of C-12 uptake (mg C l^{-1} hr^{-1}) was performed according to the method described by Vollenweider (1969).

Light, temperature, nutrient, and chlorophyll measurements were made twice a week from February-September, 1972. Light intensities (microamps) used for the calculation of extinction coefficients were measured at a depth just below the surface and down to one meter using a portable submarine photometer (G.M. Manufacturing and Instrument Corp.).

Daily incident radiation totals (cal $cm^{-2}day^{-1}$) were computed from hourly light intensities measured at Sterling, Virginia (National Oceanic and Atmospheric Administration). These values were used to estimate the light coefficient

$$Lcoef = \frac{L}{L_{max}}, \qquad (eq.\ 3)$$

where L was the light intensity reaching the different tubes in the incubation rack, and L_{max} was the highest daily total light intensity measured at Sterling, Virginia during the sampling period. Lcoef could range from 0-1.

Temperatures (C) were taken within the upper one meter with a battery operated thermistor probe (TNTronics) attached to the submarine photometer; this allowed for the simultaneous measurement of light and temperature. The temperature coefficient (Tcoef) was derived from Figure 2 and the following equations:

a) Tcoef = 0, when T<Tll or T>Tul

b) Tcoef = 1, when Topt1≤T≤Topt2

c) Tcoef = $\frac{T-Tll}{Topt1-Tll}$, when Tll<T<Topt1

d) Tcoef = $\frac{Tul-T}{Tul-Topt2}$, when Topt2<T<Tul,

where T was the observed temperature; Tll was the lower limit for photosynthesis (4.4 C); Tul was the upper limit for photosynthesis (40 C); Topt1 was the lower optimal limit for photosynthesis (18 C); and Topt2 was the upper optimal limit for photosynthesis (31 C). The temperature limits were taken from Auclair et al (1971). Tcoef could range from 0-1.

Nutrient concentrations were obtained for samples taken from the upper meter at the south end of the lake. Using a Hach Water Testing Kit (Hach Chemical Co.), values were obtained for nitrate, orthophosphate, silica, carbon dioxide, total carbonate alkalinity, and turbidity. Individual coefficients for nitrate (Ncoef), orthophosphate (Pcoef), silica (Sicoef), and bicarbonate alkalinity (Ccoef) were determined by the ratio of the concentration of the nutrient at time t to the optimum value (i.e., when P/chl was greatest) of the nutrient. Thus,

$$\text{Ncoef, Pcoef, Sicoef, and Ccoef} = \frac{X_t}{Xopt} \text{ if } X_t < Xopt, \text{ or}$$
$$= 1, \text{ if } X_t \geq Xopt,$$

where X_t was the nutrient concentration at time t, and Xopt was the optimum value for the nutrient. The nutrient coefficient (Nut. coef) used in equation 2 was the smallest of the individual nutrient coefficients. This approach was based on the limiting nutrient concept; i.e., the nutrient in least supply relative to its demand was assumed to be limiting to photosynthesis.

Chlorophyll "a" determinations were made by vacuum filtering 500 ml of water collected from the upper meter at the south end of the lake through a glass fiber filter (Type A, 47 mm, Gelman Instrument Co.). The filters were stored in a refrigerated desiccator (10 C). To determine the effects of time delays on the precision of chlorophyll estimates, two samples were filtered on the same day; one was analyzed immediately, the other two months later. The values were within

5% of each other. In most cases, due to excessive turbidity of the lake water, two filters were used to speed filtration. Magnesium carbonate solution was added to the water during the final stage of filtration to prevent acidic conditions from occuring and to aid in the adhesion of phytoplankton to the filter. The acetone extraction method of Lorenzen (1967) was used to determine chlorophyll and pheo-pigment (degradation products of chlorophyll) concentrations. Chlorophyll concentrations were used as estimates of phytoplankton biomass (Megard, 1972) and in the calculation of (P/chl) ratios.

Predicted photosynthetic values and Kendall rank correlation coefficients were computed with an IBM 1620 computer. A Wang Series 600 calculator was used to compute extinction coefficients, Pearson (r) correlation coefficients, standard errors of estimate, and regression equations.

Results

Air temperatures ranged from 4-27 C (Table 1). The greatest fluctuations occured from mid-February to late April. Solar radiation varied from 1.8-4.3 Kcal $cm^{-2}wk^{-1}$ (Table 1). The greatest variations occured from late May to mid-July. Precipitation varied from 0-8.7 cm wk^{-1} (Table 1). Rainfall was highest from mid-April to mid-July and there were marked week to week fluctuations.

Water temperatures ranged from 4.7-28.6 C (Table 2), and showed a generally increasing trend throughout the sampling period. The extinction coefficient varied from 1.1-6.5 m^{-1} (Table 2), with the highest values occuring from late May to mid-June. Turbidity ranged from 12-185 Jackson Turbidity Units (Table 2) and in general reflected the same trends as the extinction coefficient.

Nitrate ranged from 0.4-2.5 ppm (Table 3), with the highest values occuring from late May to early July. Fluctuations in nitrate concentrations were dramatic throughout the sampling period. Orthophosphate varied from 0.07-0.47 ppm (Table 3). As with nitrate, orthophosphate exhibited marked variability. Silica ranged from 7.7-17.9 ppm (Table 3) and showed a general trend of increase during the June to September period. Less variability in silica concentration was seen from late June to mid-September. Carbon dioxide varied from 0-8 ppm (Table 3). Between early June and mid-August carbon dioxide generally was lower than at other times; values from mid-February to late March were fairly stable. Total carbonate alkalinity ranged from 32-55 ppm $CaCO_3$ (Table 3) and with three exceptions (when carbonate alkalinity was measured) was always in the bicarbonate (HCO_3^-) form. Trends of increasing concentrations were seen from mid-February to late April, during the month of July, and from late August to mid-September. The period from early May to early June exhibited decreasing concentrations. Total carbonate alkalinity was the most stable of the chemical parameters measured.

Photosynthesis at the five light intensities on each date were weighted to give an average primary productivity (Table 4). The daily averages ranged from .037-.797 mg C $l^{-1}hr^{-1}$. Chlorophyll ranged from 7.9-91.2 mg m^{-3} (Table 4) and reflected an erratic pattern characterized by rapid changes in concentration. Pheo-pigments varied from 0-19.8 mg m^{-3} (Table 4) and also showed great fluctuations. Maximum daily photosynthetic efficiency (P/chl), in units of (mg C $l^{-1}hr^{-1}$)(mg Chl $m^{-3})^{-1}$, ranged from .001-.035 (Table 4). The values were highest from mid-June through mid-September.

Photosynthesis was lineally correlated only with the daily maximum photosynthetic efficiency (Table 5). The initial non-linear model (Table 6, #1) was constructed such that primary productivity was a function of $(P/chl)_{max}$, light, temperature, and nutrient and chlorophyll concentrations. The value used for $(P/chl)_{max}$ was the maximum ratio of productivity/chlorophyll observed during the sampling period. This value was .035 (mg C-$l^{-1}hr^{-1}$)(mg Chl $m^{-3})^{-1}$ and occured on June 15. The nutrient optima (for the calculation of Nut. coef) were those values of nitrate, orthophosphate, silica, and bicarbonate alkalinity measured on the same day as $(P/chl)_{max}$ (Table 7). These values were designated "$(P/chl)_{max}$ nutrient optima." Tcoef and Lcoef were calculated as previously described.

The predicted photosynthesis based on this model and the corresponding observed values were compared using the Pearson (r) correlation coefficient. Standard errors of estimate $(s_{x.y})$ and regression equations were also determined (Table 6).

The values of r and $s_{x.y}$ for the model (Table 6, #1) were -.05 and .2109, respectively. Thus, the initial model was not a good predictor of primary productivity. Several modifications were made to determine their effects on the model's predictive power. The modifications were divided into three categories: changes in the form of a coefficient, changes in the values of constants, and changes in the general structure of the predictive equation. The modifications by no means exhausted all possible changes which could have been made. Time limitations precluded a more comprehensive investigation of possible changes in the model.

In Model 1, the predicted values were highest at the 95% I_o level, and decreased successively at each of the lower light intensities to the lowest value at 20% I_o. This pattern was due to the structure of the light coefficient (Lcoef) in Model 1. In its original form, as solar radiation increased, Lcoef became more optimal (i.e., closer to 1). In contrast, most of the observed values of photosynthesis were highest at the intermediate light intensities. These observations indicate an inhibitory effect of strong light intensities on chlorophyll (Soeder, 1966), which would tend to decrease primary production.

The first modification of the model consisted of a restructuring of the Lcoef to account for the possible inhibition of high light intensities. Lcoef was modified to resemble the temperature coefficient (Tcoef), i.e., with an upper (Lul) and lower (Lll) limit above and below which, respectively, primary productivity would cease, and an optimal range (Loptl

and Lopt2) within which primary production would be max-
imal relative to light intensity (Fig. 3). To obtain values
for Lll, Lul, Loptl and Lopt2, the maximum observed values of
photosynthesis for each day were plotted against their corre-
sponding light intensities (Fig. 4). The lower limit (Lll)
was taken to be 0; the upper limit (Lul) was set at 450
cal $cm^{-2}day^{-1}$ (the projected value at which primary production
would be 0). Loptl, the lower limit of the optimal range, was
established at 50 cal $cm^{-2}day^{-1}$; Lopt2, the upper limit of the
optimal range, was set at 150 cal $cm^{-2}day^{-1}$. This range was
chosen because on 16 of the 20 sampling days the maximum photo-
synthesis occured at a light intensity within this range. It
was felt that this range was broad enough to be representative
of the optimal range, but narrow enough so as not to lose
sensitivity to differences in light intensities. Model 2
(Table 6) was identical to Model 1 except that the restruc-
tured Lcoef was substituted for the original Lcoef. Values
of r and $s_{x.y}$ for Model 2 were .23 and .2049, respectively.
All subsequent models used the new Lcoef.

The next modification involved the use of a different
set of nutrient optima as constants in determining the Nut.
coef in equation 2. These new optima were the concentrations
of nitrate, silica, and bicarbonate alkalinity measured on
the day when the highest photosynthetic rate was observed (the
orthophosphate value for this day was 0, so the value used
in the "$(P/chl)_{max}$ nutrient optima" was retained). This value
(.87 mg C $l^{-1}hr^{-1}$) occured on June 5 and was defined as Pmax;
the nutrient optima associated with Pmax were designated

"Pmax nutrient optima" (Table 8). Model 3 (Table 6) was the same as Model 2 except that the "Pmax nutrient optima" were substituted for the "$(P/chl)_{max}$ nutrient optima." Model 3 had the highest r (.58) and smallest $s_{x.y}$ (.1720) of the models tested.

The next modifications consisted of changes in the over-all structure of the model. In the first such modification, the nutrient coefficient was omitted. Model 4 (Table 6), without nutrients, had values of r and $s_{x.y}$ of .51 and .1810, respectively, and compared favorably with Model 3. In the second modification a maximum photosynthetic rate (Pmax) re-placed $(P/chl)_{max}$ and the biomass estimate given by the chlorophyll concentration. As in Model 4, this equation (Model 5) was used without consideration of nutrients, and had r and $s_{x.y}$ values of .41 and .1926, respectively.

Discussion

Westhampton Lake is a small, freshwater lake (.057 km^2) located on the campus of the University of Richmond. In 1971 the mean and maximum depths were 1.5 and 3.6 m, respectively (Bishop, 1971). The bathymetry has changed considerably since these measurements were taken due to siltation resulting from inadequate erosion control at points of construction in the northeast corner of the lake. Two streams feed the lake, the

major one entering from the northeast corner, the other from the northwest corner.

Westhampton Lake is small relative to its drainage basin (6.55 km^2, estimated from Va. Division of Mineral Resources Chart No. N3730-W7730/7.5). The basin is bounded approximately by Ridge Road on the west, College Drive on the south, and Three Chopt Road on the north and east. The basin lies in a well forested, residential area. The lake receives substantial runoff from precipitation. The turnover time, assuming 102 cm of rain per year and a 50% runoff, is approximately .4 month (turnover time = volume of lake/volume of runoff into lake per year = $1.1 \times 10^5 \, m^3/3.3 \times 10^6 \, m^3 \, yr^{-1}$ = .033 yr. = .4 month).

An extrinsic factor, i.e., one which originates outside the lake, such as precipitation may greatly affect qualities of the lake water, and thus photosynthesis. In Westhampton Lake only two (nitrate and total carbonate alkalinity) of the five nutrients measured were correlated with precipitation (Table 9). The correlation between nitrate and precipitation was not unexpected because of the relative ease with which nitrate is leached from soil particles (Ruttner, 1963).

Turbidity and extinction coefficient were both correlated with precipitation (Table 9); this can be visually confirmed shortly after a period of rainfall, as the lake becomes very muddy. Extinction coefficient and turbidity were highly correlated with each other, nitrate, and orthophosphate (Table 9). The correlations with nitrate and orthophosphate are a result

of runoff from precipitation which brings in soil particles and causes a rise in turbidity and extinction coefficient.

Orthophosphate was correlated with nitrate in that the levels of both increase due to precipitation and its concomitant runoff (Table 9); both would decrease due to uptake by primary producers.

Significant negative correlations were found between total carbonate alkalinity and the following parameters (Table 9): orthophosphate and precipitation. Negative correlations were also found between silica and the following factors: turbidity, extinction coefficient, nitrate, and carbon dioxide (Table 9). Further studies are needed to verify and explain these correlations.

Primary productivity in Westhampton Lake was not significantly correlated with any of the nutrients measured (Table 5). One possible explanation for the absence of correlation is that multiple factors affect photosynthesis; i.e., nutrients do not affect photosynthesis independently of other parameters (e.g., light and temperature). This is also true for the other comparisons made. Another possible explanation is that time lags may exist between nutrient levels and photosynthesis; i.e., photosynthesis may not increase until a number of days after nutrient concentrations increase (Findenegg, 1966). The finding by Bishop (1971) of significant correlations between photosynthesis in Westhampton Lake and precipitation 3, 4, and 5 days before productivity was measured lends evidence for the possible existence of time lags.

Another possibility for the poor correlation between nutrients and primary productivity is that nutrients may not usually be limiting in Westhampton Lake. There is little agreement among researchers as to optimal nutrient values for phytoplankton (Table 10). The median optimal literature values from Table 10 (.88 ppm for nitrate, .065 ppm for phosphate, and 10.5 ppm for silica) were compared with the weekly values measured in Westhampton Lake. 52% of the nitrate values, 87% of the orthophosphate values, and 58% of the silica values would be optimal relative to the literature medians. Studies involving determination of seasonal succession and nutrient optima on the species level for Westhampton Lake are needed to get accurate values for future use.

Primary productivity and chlorophyll were not significantly correlated. Experiments by Wright (1960) demonstrated that the relationship between photosynthesis and chlorophyll concentrations is not linear, and that an increase in the concentration of phytoplankton led to a lowering of the photosynthetic rate. This may be due to either a limiting nutrient, an increased light attenuation as the population densities increase (Talling, 1965), or both.

Photosynthetic rates were inhibited at higher light intensities. Bishop (1971) found the highest photosynthesis at the surface of Westhampton Lake. This contradiction may be due to differences in methods of measurement. Bishop used the oxygen evolution method and returned the BOD bottles to their original depth in the lake for an incubation period of approximately eight hours. In this study the C-14 method and an

incubation rack were used for a four hour period during that part of the day (10 a.m.-2 p.m. or 11 a.m.-3 p.m.) when sunlight was most intense. Also, in Bishop's study, the phytoplankton in the surface waters possibly were adapted to strong light intensities. In this study, a heterogeneous sample from the upper meter was used and probably not all of the phytoplankton were adapted to high intensities.

Chlorophyll concentrations were correlated with solar radiation and turbidity. The relation between chlorophyll and turbidity is probably due in part to the fact that an increase in phytoplankton biomass (i.e., as indicated by chlorophyll concentrations) results in an increase in turbidity, although in Westhampton Lake the effect no doubt is less marked than it would be in a less turbid lake.

Chlorophyll was also correlated with total carbonate alkalinity; this may be explained by the uptake of carbon dioxide during photosynthesis, which leads to an increase in pH of the lake water, hence an increase in total carbonate alkalinity (Wright, 1960).

Photosynthetic efficiency (P/chl), the maximum daily specific rate of photosynthesis as defined by Megard (1972), was correlated with water temperature. Megard reported that P/chl is strongly influenced by temperature. A strong positive correlation between P/chl and primary productivity also was found. Bishop (1971) also found this correlation in Westhampton Lake.

The P/chl ratio was inversely related to nitrate, no doubt due to the uptake of nitrate during photosynthesis.

There was also a significant negative correlation between P/chl and chlorophyll; i.e., as chlorophyll concentration decreases, P/chl increases (or vice versa). Wright (1960) and Findenegg (1965) also found the inverse relation. Megard (1972) found that maximum P/chl values were often highest where chlorophyll concentrations were highest. Wright (1960) gave three alternative explanations for the inverse relationship: 1) chlorophyll content, as analyzed spectrophometrically, is made up of increasing amounts of breakdown products with absorption spectra indistinguishable from chlorophyll, 2) photosynthetic inhibitors increase as the population increases, and 3) nutrient concentrations in the water drop to levels low enough to limit the rate of photosynthesis without a proportional decrease in chlorophyll.

The original model (Table 6, #1), as applied to Westhampton Lake was a poor predictor of primary productivity. A series of modifications were made to ascertain their effects on the predictive power of the model. These modifications included changes in the structure of a coefficient (Lcoef), changes in the values of constants (the nutrient optima), and changes in the general structure of the equation (omission of nutrients and substitution of Pmax for $(P/chl)_{max}$ x chlor). From Table 6 it can be seen that combinations of these modifications resulted in varying degrees of predictive power. The most significant changes were the restructuring of the light coefficient and the use of a different set of nutrient optima. The light coefficient was changed from a linear relationship with respect to light intensity to one which utilized an

optimal intensity range. The change of the nutrient optima
(Table 6, #3) greatly increased the predictive power of the
model. The Pmax nutrient optima agreed more closely with
the median literature (Table 10) optima used for the com-
parison with Westhampton Lake values than do the $(P/chl)'_{max}$
nutrient optima, and thus may be more reliable. The omission
of the nutrient coefficient (Table 6, #4) did not affect the
predictive power of the model to any great degree. This
indicates that nutrients may not usually be limiting in West-
hampton Lake and points out the need for further studies.
The use of a maximum photosynthetic rate (Pmax) lowered the
predictive power of the model. Thus the utilization of the
maximum photosynthetic efficiency ($(P/chl)_{max}$) and a biomass
estimate (chlorophyll concentration) resulted in a better
fitting model.

The best fitting model of the five tested, Model 3, con-
sisted of $(P/chl)_{max}$, chlorophyll concentration, the restruc-
tured light coefficient, Pmax nutrient optima, and the nutrient
and temperature coefficients used in the initial model.
Figure 5 is a scatter diagram of the predicted vs. observed
photosynthesis values for Model 3 (note: the vertical and
horizontal scales are different; i.e., the predicted values
should be moved up one complete cycle to coincide with the
scale used for the observed values). In general, the pre-
dicted values were higher than the observed values by a power
of 10. A lowering of the $(P/chl)_{max}$ ratio could bring the
predicted values more in line with the observed values; e.g.,

high chlorophyll concentrations (58-90 mg m^{-3}) resulted in high predicted productivities (1.2 mg C l^{-1}hr^{-1}). Therefore, a lowering of (P/chl)$_{max}$ would reduce the predicted values.

It is apparent that even the best fitting model does not include all of the factors which affect primary productivity in Westhampton Lake. Only 34% of the variability between predicted and observed photosynthesis is accounted for by Model 3. Future modifications of the model could include further changes in the general structure of the equation (e.g., accounting for algae being washed out of the lake, predation by herbivorous zooplankton and fishes, and the carrying capacity of the lake), changes in the structure of coefficients (to account for time lags between changes in chemical levels and biological manifestations of these levels, and luxury uptake of nutrients), and changes in the values of constants (e.g., knowledge of optimal phytoplankton nutrient values on the species level).

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Table 1. Meteorological conditions, 1972

Week of	Average weekly air temperature[1] (C)	Weekly solar radiation[2] (Kcal cm^{-2})	Weekly precipitation[1] (cm)
February 13	5	-	3.7
20	4	-	2.7
27	11	-	0.6
March 5	5	-	0.3
12	10	-	3.2
19	7	-	1.9
26	7	-	0.8
April 2	9	2.8	2.3
9	14	2.5	0.5
16	17	3.1	3.0
23	13	3.7	1.7
30	18	3.0	3.5
May 7	17	3.8	2.9
14	17	2.7	5.8
21	17	4.2	3.1
28	19	4.2	6.7
June 4	20	4.3	2.1
11	22	3.2	1.4
18	20	1.8	8.7
25	21	3.5	2.0
July 2	20	3.5	8.1
9	24	4.2	7.1
16	27	4.0	1.2
23	25	3.3	0.0
August 6	23	3.8	0.0
13	24	3.1	3.2
20	25	3.8	0.1
30	21	2.3	2.3
September 3	19	3.1	0.6
10	24	2.8	0.9

[1] National Weather Service, Byrd Airport, Richmond, Virginia

[2] National Oceanic and Atmospheric Administration, Sterling, Virginia

Table 2. Physical parameters in Westhampton Lake, 1972
(weekly averages)

Week of		Water temperature (C) (0-1 m)	Extinction coefficient (m^{-1})	Turbidity (Jackson Turbidity Units)
February	13	7	1.1	54
	20	5	4.4	61
	27	9	3.0	32
March	5	9	2.1	17
	12	11	1.5	12
	19	13	4.2	67
	26	11	2.9	30
April	2	12	2.3	15
	9	12	2.7	28
	16	20	3.4	41
	23	16	3.8	39
	30	19	5.0	65
May	7	20	3.5	42
	14	20	5.0	72
	21	20	6.4	80
	28	18	6.5	185
June	4	20	4.2	74
	11	19	2.1	45
	18	23	6.0	136
	25	24	4.0	61
July	2	23	3.2	52
	9	23	4.0	65
	16	29	1.9	27
	23	21	2.2	24
August	6	26	2.7	23
	13	26	3.2	42
	20	27	1.8	21
	30	27	1.9	43
September	3	24	3.9	73
	10	25	3.0	36

Table 3. Chemical parameters in Westhampton Lake, 1972 (weekly averages)

Week of		Nitrate (ppm)	Ortho-phosphate (ppm)	Silica (ppm)	Carbon dioxide (ppm)	Total carbonate alkalinity (ppm $CaCO_3$)
February	13	–	0.12	–	6	35
	20	–	0.13	–	5	33
	27	–	0.47	–	6	33
March	5	–	0.07	–	5	35
	12	–	0.12	–	6	40
	19	–	0.46	–	6	40
	26	–	0.11	9.0	4	44
April	2	1.1	0.03	10.0	3	45
	9	1.3	0.14	11.9	4	40
	16	1.4	0.04	13.1	6	45
	23	1.8	0.09	7.7	8	50
	30	1.4	0.11	8.9	8	46
May	7	0.7	0.09	13.2	4	50
	14	1.6	0.13	8.1	5	48
	21	2.2	0.21	8.6	6	43
	28	2.5	0.23	8.0	6	36
June	4	0.7	0.07	10.2	0	36
	11	0.4	0.06	8.4	4	48
	18	2.5	0.25	8.1	5	36
	25	2.5	0.44	14.3	3	40
July	2	1.2	0.14	13.6	2	32
	9	0.9	0.09	13.5	3	42
	16	0.5	0.08	15.4	3	48
	23	0.5	0.26	16.1	4	55
August	6	0.5	0.08	17.8	0	50
	13	0.6	0.14	14.5	6	45
	20	0.5	0.09	16.0	4	42
	30	0.4	0.11	17.9	4	50
Sept.	3	0.5	0.12	16.7	8	54
	10	0.5	0.06	17.5	2	54

Table 4. Biological parameters in Westhampton Lake, 1972
(weekly averages)

Week of	Aver. prod. ($mgC\ l^{-1}hr^{-1}$)	Photosynthesis at various % I_o ($mgC\ l^{-1}hr^{-1}$)					Chl. a ($mg\ m^{-3}$)	Pheo-pigments ($mg\ m^{-3}$)	$(P/chl)_{max}$
		95	70	55	35	20			
Feb. 13	-	-	-	-	-	-	18.5	0.30	-
20	-	-	-	-	-	-	14.7	0.11	-
27	-	-	-	-	-	-	18.1	0.00	-
Mar. 5	-	-	-	-	-	-	13.7	1.50	-
12	-	-	-	-	-	-	7.9	1.30	-
19	-	-	-	-	-	-	23.3	0.81	-
26	0.108	0.083	0.117	0.112	0.101	0.089	43.6	3.10	0.005
Apr. 2	0.037	-	0.023	0.033	0.034	0.052	33.3	4.50	0.001
9	-	-	-	-	-	-	20.2	4.50	-
16	0.213	0.045	0.201	0.252	0.300	0.307	48.8	5.60	0.004
23	0.123	0.022	0.078	0.135	0.230	0.219	25.9	0.60	0.008
30	0.149	0.052	0.140	0.190	0.203	0.205	19.4	1.40	0.010
May 7	0.325	0.330	0.348	0.331	0.276	0.248	46.1	8.90	0.007
14	0.086	0.094	0.108	0.099	0.067	0.056	25.7	3.10	0.004
21	0.142	0.060	0.108	0.183	0.197	0.205	52.8	2.20	0.002
28	0.133	0.132	0.149	0.144	0.140	0.132	61.3	9.30	0.002
June 4	0.797	0.609	0.811	0.859	0.867	0.791	91.2	0.28	0.010
11	0.412	0.279	0.381	0.454	0.478	0.451	16.7	2.90	0.035
18	-	-	-	-	-	-	20.9	1.00	-
25	0.755	0.491	0.730	0.819	0.842	0.754	37.5	1.30	0.014
July 2	0.320	0.293	0.347	0.355	0.347	0.290	15.4	3.70	0.025
9	0.120	0.088	0.120	0.134	0.140	0.128	21.1	7.30	0.007
16	0.117	0.010	0.127	0.121	0.125	0.107	13.7	3.60	0.018
23	-	-	-	-	-	-	29.0	6.90	-
Aug. 6	-	-	-	-	-	-	23.9	19.80	-
13	0.333	0.397	0.398	0.363	0.261	0.195	24.3	18.4	0.016
20	0.109	0.062	0.106	0.109	0.135	0.145	20.0	4.20	0.007
30	0.136	0.192	0.174	0.135	0.075	0.059	31.1	6.40	0.005
Sept. 3	0.324	0.234	0.340	0.351	0.399	0.368	45.2	18.90	0.008
10	0.412	0.272	0.392	0.495	0.506	0.565	48.9	14.20	0.010

Table 5. Correlations between photosynthesis and various
parameters using the Kendall rank correlation
coefficient (T), a simple linear model.

Parameter	T
precipitation	-.02
solar radiation	.16
water temperature	.20
extinction coefficient	.07
turbidity	.23
nitrate	-.14
orthophosphate	.05
silica	.18
carbon dioxide	-.03
total carbonate alkalinity	.02
chlorophyll "a"	.18
daily maximum photosynthetic efficiency $(P/chl)_{max}$	.43[*]

[*] significant at the .05 level

Table 6. Comparison of the multiple factor models tested. 1 primary productivity; 2 maximum observed value of photosynthesis/chlorophyll concentration; 3 light, temperature, and nutrient coefficients, respectively; 4 chlorophyll concentration; 5 Pearson correlation coefficient; 6 standard error of estimate; 7 predicted photosynthesis; 8 observed photosynthesis; * significant at the .05 level.

Model	Model description	r[5]	$s_{x.y}$[6]	Regression equation
1	$P.P.[1]=(P/chl)_{max}[2](Lcoef)[3](Tcoef)[3](Ncoef)[3](chlor)[4]$ (original Lcoef, $(P/chl)_{max}$ nutrient optima)	-.05	.2109	$Y[7]=.2708 - .0326\ X[8]$
2	$P.P.=(P/chl)_{max}(Lcoef)(Tcoef)(Ncoef)(chlor)$ (new Lcoef, $(P/chl)_{max}$ nutrient optima)	.23*	.2049	$Y=.194 + .0711\ X$
3	$P.P.=(P/chl)_{max}(Lcoef)(Tcoef)(Ncoef)(chlor)$ (new Lcoef, Pmax nutrient optima)	.58*	.1720	$Y=.1205 + .1544\ X$
4	$P.P.=(P/chl)_{max}(Lcoef)(Tcoef)(chlor)$ (new Lcoef, without nutrients)	.51*	.1810	$Y=.1053 + .1297\ X$
5	$P.P.=Pmax\ (Lcoef)(Tcoef)$ (new Lcoef, Pmax, without nutrients)	.41*	.1926	$Y= -.0460 + .4386\ X$

Table 7.   Nutrient concentrations ($(P/chl)_{max}$ nutrient optima) associated with the maximum (photosynthesis/chlorophyll) ratio for Westhampton Lake, measured on June 15, 1972.   Values are in ppm.

nitrate	.352
orthophosphate	.04
silica	4.66
bicarbonate alkalinity (as $CaCO_3$)	45.00

Table 8.   Nutrient concentrations (Pmax nutrient optima) associated with the maximum photosynthesis observed in Westhampton Lake, measured on June 5, 1972.   Values are in ppm.

nitrate	.88
orthophosphate	.04
silica	9.66
bicarbonate alkalinity (as $CaCO_3$)	16.00

Table 9. Kendall rank correlation coefficients for Westhampton Lake data, 1972.
          * significant at the .05 level.

		1	2	3	4	5	6	7	8	9	10	11	12	13
1	precipitation (cm per week)		-.05	-.03	.34*	.45*	.33*	.12	-.05	.19	-.26*	.02	-.13	-
2	solar radiation (Kcal cm⁻¹ wk⁻¹)			.22	-	-	-	-	-	-	-	.33*	.06	-
3	water temperature (C)				-	-	-	-	-	-.19	.36	-.09	.35*	-
4	extinction coefficient (m⁻¹)					.66*	.64*	.23*	-.52*	.16	-.12	.30*	-.21	-
5	turbidity (Jackson Turbidity Units)						.40*	.25*	-.40*	.21	-.14	.28*	-.07	-
6	nitrate (ppm)							.33*	-.60*	.21	-.24	.15	-.31*	-
7	orthophosphate (ppm)								-.07	.17	-.25*	-.04	-.08	-
8	silica (ppm)									-.29*	-.17	-.04	.25	-
9	carbon dioxide (ppm)										-.07	-.01	-.22	-
10	total carbonate alkalinity (ppm CaCO₃)											.26*	.07	-
11	chlorophyll a (mg m⁻³)												-.35*	.26*
12	daily maximum photosynthetic efficiency (mg C l⁻¹hr⁻¹)(mg Chl m⁻³)⁻¹													-
13	pheo-pigments (mg m⁻³)													

Table 10. Optimal nutrient concentrations for photosynthesis from the literature compared with ranges measured in Westhampton Lake in 1972. Values are in ppm.

Author	Nitrate	Phosphate	Silica
Auclair et al (1971)	1.32-1.98		
Di Toro et al (1970)	.0088-.88	.06	.107-.214
Hutchinson (1957)		.138[1]	
Kilham (1971)			.6-13.4[2]
Kuentzel (1969)		< .0306	
Round (1965)		.006[1]; 1.38[3]	
Sylvester (1961)	>.88		
Westhampton Lake	.418-2.53	.065-.455	7.7-17.9

[1] for Asterionella

[2] mean concentrations during dominance of different species of diatoms

[3] for blue-greens

Figure 1. Two views of the incubation rack used
for the measurement of photosynthesis.
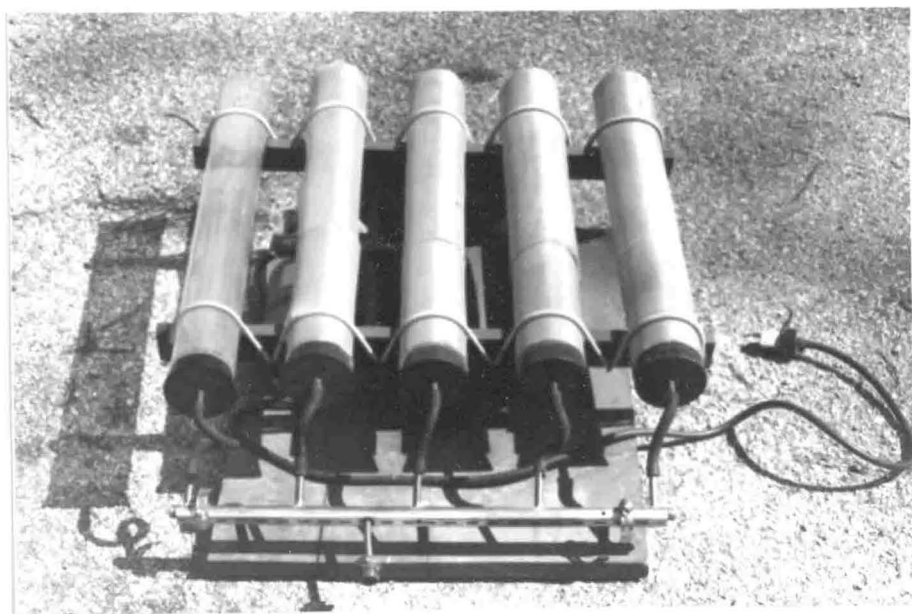
Figure 2. Structure of temperature coefficient used
in equation 2.

Tll: lower limit for photosynthesis
Tul: upper limit for photosynthesis
Topt1:   lower optimal limit for photosynthesis
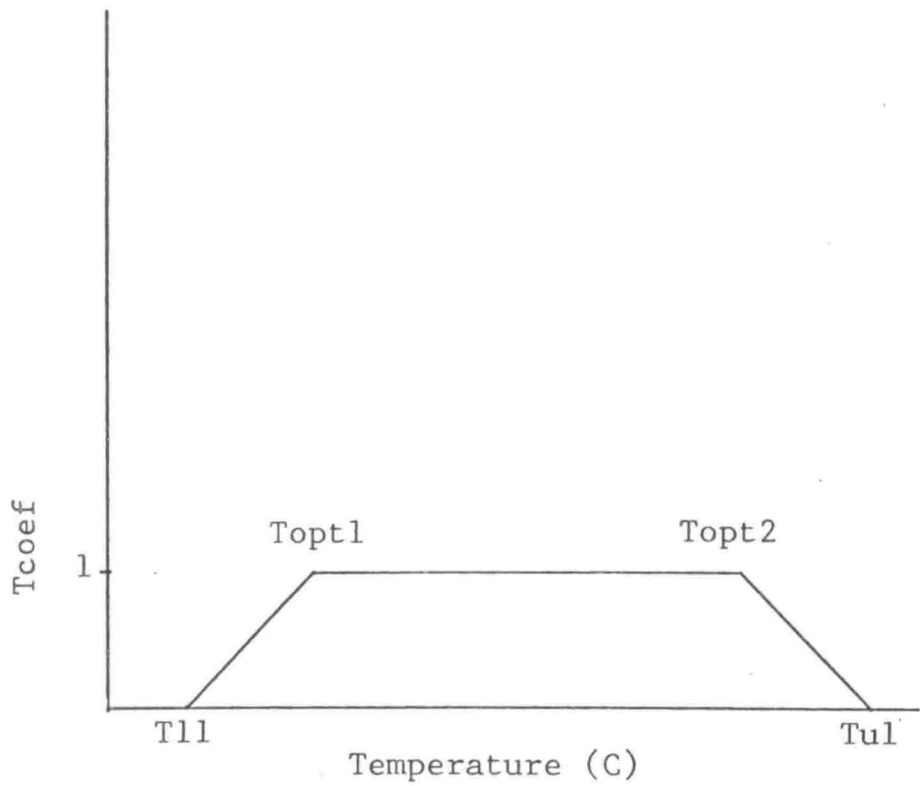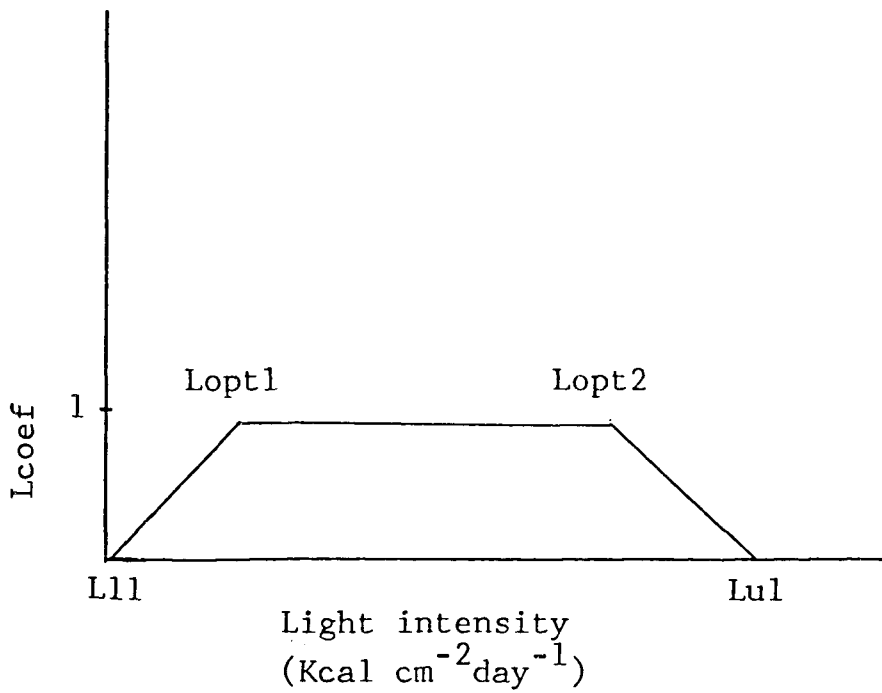Topt2:   upper optimal limit for photosynthesis

Figure 3. Structure of the modified light
light coefficient.

Lll: lower limit for photosynthesis

Lul: upper limit for photosynthesis

Loptl: lower optimal limit for
photosynthesis

Lopt2: upper optimal limit for
photosynthesis

Light intensity
$(Kcal\ cm^{-2}day^{-1})$

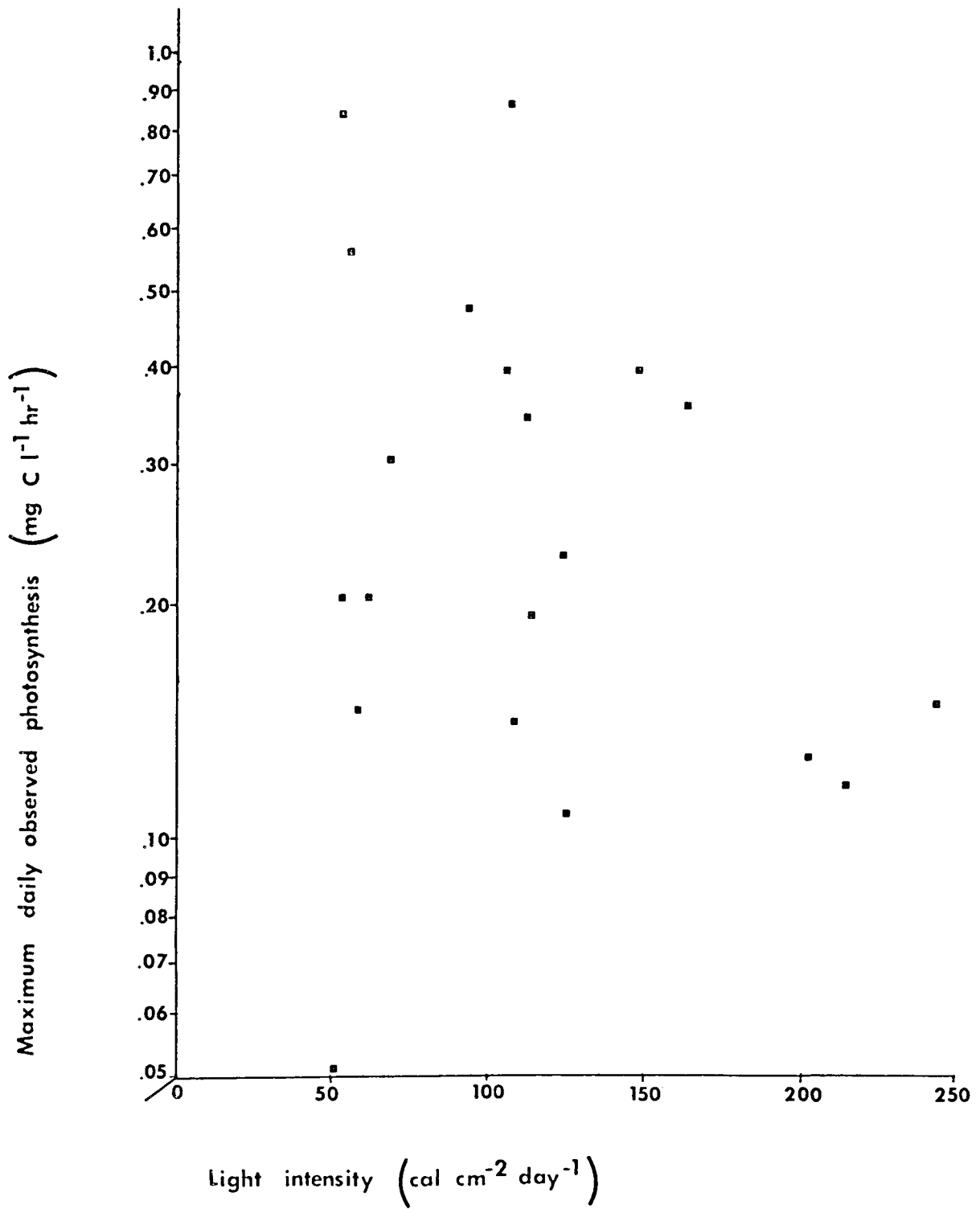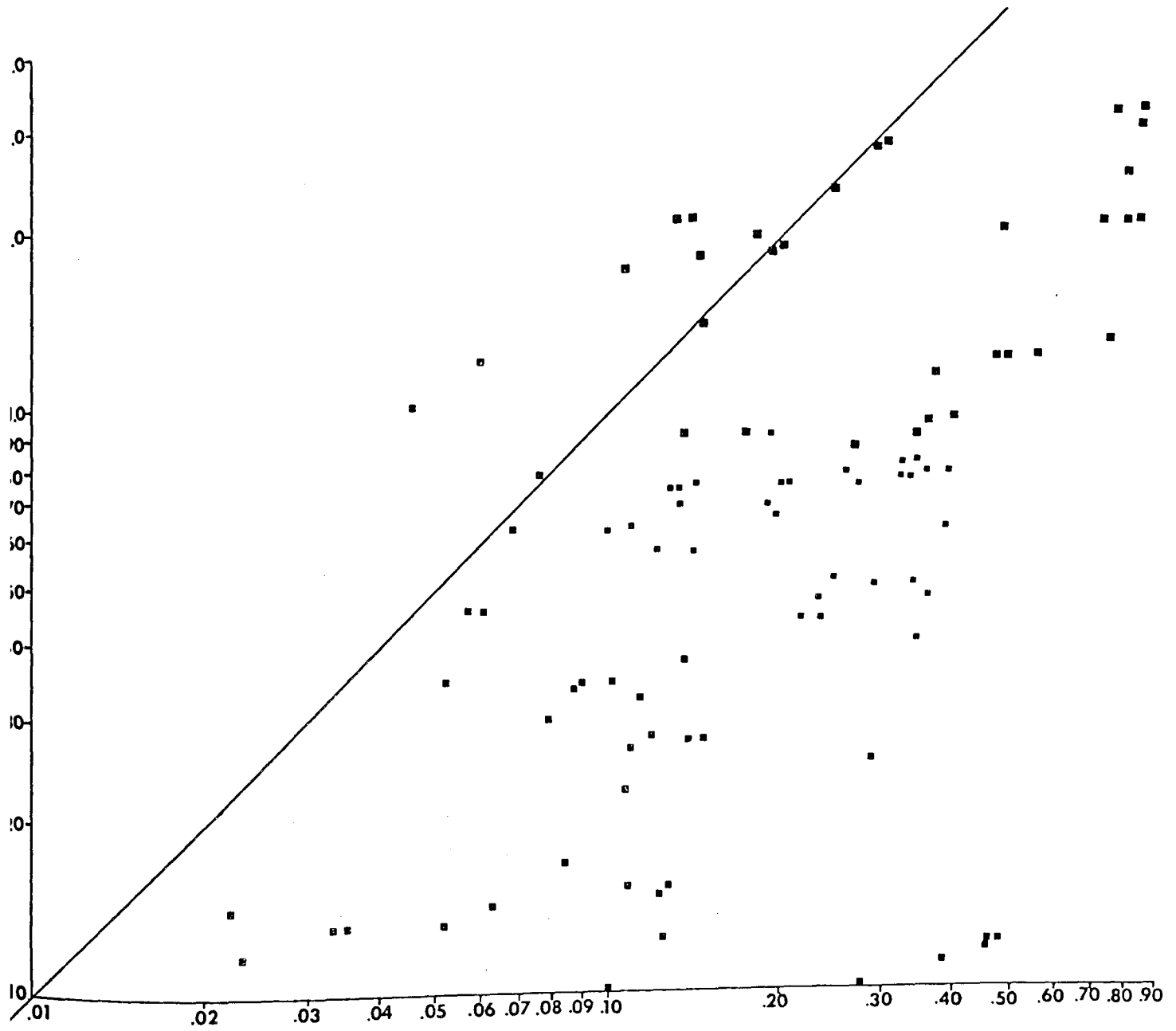Figure 4. Maximum daily observed photosynthesis vs. corresponding light intensities.

Figure 5. Scatter diagram of predicted vs.
observed photosynthesis for Model 3.

Vertical axis: Predicted photosynthesis $\left(mg\ C\ l^{-1}hr^{-1}\right)$

Observed photosynthesis $\left(mg\ C\ l^{-1}hr^{-1}\right)$

VITA

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