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## UNIVERSITY OF CALIFORNIA

# ENERGY & ENVIRONMENT DIVISION

MODELING LAKE-WATER MINERALIZATION PROCESSES

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# DISCLAIMER

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## ABSTRACT

A model for transient phenomena observed in lake-water aliquots is developed and discussed. The phenomena include directly observed rapid changes in inorganic nutrient concentrations subsequent to the addition of organic matter and deduced changes in microbial population density. An hypotheses is presented which provides a qualitatively consistent picture of the transient phenomena; this hypothesis is then incorporated into a model that is shown to provide a good quantitative description of the data. Model sensitivity, further applications, and possible procedures for further testing of the model are briefly discussed. It is concluded that within the model framework, simple experiments involving additions of organic matter to lake-water allow a

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## I. Introduction

In aquatic ecosystems, concentrations of chemical nutrients and populations of organisms can change by several orders of magnitude over periods of weeks or even days. Models of time-averaged or putative steady state properties of these systems may be misleading. In particular, while such models may be successful at describing time-averaged behavior, built in assumptions about underlying biological mechanisms cannot be considered to be tested adequately unless the models can be shown to predict transient behavior successfully. Over the past several years, experiments were performed in our laboratory to characterize transient, rapid variation in mineralization activity in lake waters (Harte and Levy, 1981). These changes were induced by additions of sizeable quantities of organic matter into lake-water aliquots. The results of these experiments provide constraints on candidate models to describe microbial mineralization

processes. In this article I show that the constraints are sufficiently tight that considerable information about the dynamics of microbial populations and mechanisms and rates of mineralization activity can be obtained by mathematical modeling of the transient phenomena.

In the following section, I summarize the major results from the experiments. In the third section, I hypothesize an explanation of these data. At the core of the hypothesis is the notion that in the presence of added organic substrate, microbes first immobilize mineralization products for their growth until the microbial carrying capacity is reached. When microbial population growth is no longer possible, then further microbial activity can lead to rapidly increased net mineralization (total mineralization minus microbial immobilization). In the fourth I describe and motivate the general structure of the selected model and explain how a number of dynamical mechanisms can be explored within this structure. To determine the best parameters within this structure use is made of both analytical and numerical methods. The procedure for so doing is described in the penultimate section and results of model simulations are presented. There follows, in the final section, a discussion of the sensitivity of the results both to parameter variation and to some alternative model assumptions, along with several speculations about possible applications of the results.

## II.  Summary of Experimental Results

A series of experiments was performed to provide insight into how inorganic nutrient concentrations in lake water change in response to sudden increases in organic substrate.  The methods, results, and relation to other studies are described in detail elsewhere (Harte and Levy, 1981). Lake water aliquots housed in 4-liter, aerated, glass beakers were subjected to increases in organic material.  The experiments were carried out at different times of the year and with waters from a variety of lakes.  The organic material consisted of dense, autoclaved, cultures of E. coli or of algae, depending on the particular experiment.  In each experiment, a wide range of levels of organic additions was studied simultaneously in initially replicate systems, corresponding to increases in total organic carbon in the range from 25% to 350%. Subsequent to the additions and for about one week the concentrations of inorganic nitrogen (ammonia and nitrate-plus-nitrite) were measured daily, while phytoplankton and zooplankton densities were monitored approximately weekly.  Closed dark- and light- bottle $CO_2$ evolution measurements were performed daily in one of the experiments.

Figures 1-5 show representative results.  Consider, first, the inorganic nitrogen (IN) data shown in Figures 1-3.  Three features are of particular interest and illustrate the variety of responses that were observed.  These features

are:

i) A threshold response in IN concentrations, characterized by negligible increase in IN concentrations below a threshold level of added substrate and a large increase beyond the threshold. For example, in Figure 2, the ratio of the maximum increase in IN in system F to that in C was about 40:1 whereas the ratio of substrate added to these two systems was approximately 6:1. We note that this threshold behavior was seen in experiments 1 and 2 but not in 3. Figure 4 displays the IN data in a different form, emphasizing the threshold effect in experiments 1 and 2 and its absence in experiment 3.

ii) An increasing delay in the time of maximum IN concentration as the amount of substrate added was increased. We note that this was seen in experiments 2 and 3 but not in 1. Because the IN measurements were only performed at daily intervals, it is possible that a small time delay in experiment 1 occurred but was not observed.

iii) A period of a day or two, between the time of substrate addition and the time at which IN increased rapidly. This was seen in those experiments that exhibited a threshold, but not in experiment 3.

In the only other experiment I am aware of in which similar phenomena were studied with large and varying amounts of added substrate, properties ii) and iii) above

were observed, but the conditions of the experiment pre-
cluded the possibility of observation of property i) (Willi-
ams and Gray, 1970; Williams, 1970). See also von Brand et
al. (1937).

A possible explanation for the threshold behavior is
that the amount of IN that can be assimilated by phyto
plankton was limited by some fixed upper bound. This could
have led to the nearly complete absence of IN associated
with low levels of added substrate and to the presence of IN
at higher levels. However, the phytoplankton volume density
measurements do not support this explanation. In Figure 5
it is seen that a threshold in phytoplankton growth occurred
between systems C and D in experiment 2. Thus it is likely
that phytoplankton uptake of IN in experiment 2 was caused
by, rather than caused, the threshold in IN production
between C and D. If assimilation of IN by phytoplankton
were the cause of the threshold, then phytoplankton densi-
ties in C would look much like those in D. In this regard,
the similarity of phytoplankton densities in D, E, and F
does suggest that saturation in IN uptake did occur, but
well above the threshold for IN production.

As discussed in detail in Harte and Levy (1981), the
closed-bottle $CO_2$ evolution measurements performed in exper-
iment 1 are incompatible with the hypothesis that the kinet-
ics of phytoplankton uptake of IN resulted in the observed
threshold effect. Other possible explanations for the

threshold involve losses of IN from the system, as for example, by release to the atmosphere of $NH_3$ or losses of $NO_3$ due to denitrification. Such effects are easily shown to be insignificant, under the aerobic and non-alkaline conditions of the experiments.

An adequate theoretical picture of microbe-detritus-mineralization phenomena must lead to a description and explanation of these data. Preferably, the differences seen in the three experiments should be understood in terms of simple parameter variations rather than by the invocation of wholly new dynamical assumptions on a case-by-case basis. In the next section, I present an hypothesis for such a coherent dynamical picture. Then in subsequent sections, that hypothesis is embodied in a mathematical model and the behavior of that model contrasted with the behavior of others not incorporating the hypothesis.

## III. An Hypothesis

I assume that subsequent to a very large increase in lake water organic substrate, the population of microbial mineralizers will increase to a limiting density and then population growth will cease. At levels of added substrate below a critical level, microbial growth is assumed to be limited by immobilization of certain nutrients, including nitrogen, mineralized from the added substrate. When the microbial carrying capacity is reached, factors other than nitrogen availability limit further growth.

An additional assumption is that when the microbial population is below its carrying capacity, microbial immobilization of nitrogen is rapid relative to other pathways by which IN is removed from the water. Thus only when the carrying capacity is reached, will inorganic nitrogen become significantly available in the water column for phytoplankton assimilation.

The qualitative connection between this hypothesis and the broad features of the data can now be sketched. The threshold seen in experiments 1 and 2 can be interpreted as arising because of a gap between the initial microbe population and the population at carrying capacity. In this picture, the initial population was below carrying capacity and an addition of about 150 μ M(C) substrate (see Fig. 4) pushed the population to its limit. In these 2 experiments, the period of a day or two between the addition of substrate and the appearance of an increase in IN concentration was the period of microbial population growth. In experiment 3, the population can be assumed to have been initially at carrying capacity; consequently no threshold was observed. Sizeable net mineralization began immediately upon addition of substrate in this case because there was no period of immobilization.

The cessation of immobilization of nutrient arises in this picture because a carrying capacity is reached and microbial growth stops. This effect is different from a

saturation effect described by Michaelis-Menten kinetics. A description of nutrient uptake by microbes in terms solely of Michaelis-Menten kinetics, with saturation of the uptake rate occuring at large concentrations of added substrate, cannot reproduce the experimental data. In particular, the threshold would not be generated.

## IV. Model Structure

The mathematical model considered here is characterized by coupled, nonlinear, first-order, time-differential equations. The dependent variables are the total nitrogen contents of the three major, rapidly varying compartments in the beakers: microbes $(X_1)$, inorganic nitrogen $(X_2)$, and organic substrate $(X_3)$. The values of the variables in the control systems are labeled $\overline{X_i}$, for i=1, 2, and 3. The value of the organic substrate in the treatment systems at t=0, immediately subsequent to the addition of detritus, is $X_3(0) = (1+\delta)\overline{X_3}$ where $\delta$ is the fractional increase in substrate. Note that $\delta$ can exceed 1. At t=0, $X_1=\overline{X_1}$ and $X_2 = \overline{X_2}$ in the treatment systems.

The variable $X_1$ refers to the total, effective population of detritivores, including those in the guts of zooplankton. I make no claim that $X_1$ is measurable or bears any simple relation to estimates of bacterial populations measured by plate counts or any other method. Indeed, both compartments $X_3$ and $X_1$ represent a gross simplification of the complexities of the detritus-decomposer structure in an

ecosystem.    My objective is to develop as simple a model as possible that can describe the experimental results and that can be subjected to further experimental tests.  More complex models, with more adjustable parameters to describe different components of substrate or different levels of dormancy of different types of bacteria,  could undoubtedly be used to fit the data, but they would not be more likely to elucidate the basic phenomena and mechanisms.   While $X_1$ cannot be directly measured, its value can be determined by fitting the models to the data.  The fact that it cannot be measured directly does not prevent experimental tests of predictions of the models.

There are two alternative ways to express the existence of a microbial carrying capacity.  In one approach, a logistic (Verhulst) term could be introduced in the equation for the time rate of change of $X_1$ (Verhulst, 1839). Instead, however, I choose to break up the time period studied into two intervals and treat the dynamics in these two intervals separately.  In the first, from $t=0$ to $t=t_o$, the microbial population increases from its initial value, $\overline{X}_1$, to its maximum, $\tilde{X}_1$, assuming sufficient substrate is added to the system to allow $\tilde{X}_1$ to be reached.  In the second interval, beginning at $t=t_o$, mineralization takes place, along with microbial maintenance, but $X_1$ is fixed at its maximum value. These two intervals have been termed the "trophophase" and the "idiophase", respectively, by Bu'Lock (1967) and that terminology will be adopted here.  The value of $t_o$ will depend on initial conditions and parameters, as well as on

the value of $\overset{\curvearrowright}{X}_1$, and has to be determined by data fitting. The reason for treating density-dependent growth in this manner is that it makes it easier to extract information from the model using analytical (non-numerical) methods.

A variable for the phytoplankton population is not included because over the time interval that will be modeled (up to 7 days from the addition of substrate) these populations are relatively unchanging. The influence of the phytoplankton population is expressed in the model as a loss term from the IN compartment. It is assumed that IN is stored by phytoplankton during this time period, preparatory to their growth (Droop, 1973). I do not assume the same storage rate constant in the trophophase and the idiophase.

The experimental control systems are taken to be in steady state over the period of interest. In a strict sense no such steady state for these quantities exists (Saunders, 1976); nevertheless, experimentally observed rates of change of the variables of interest in the control systems were fractionally small and were dwarfed by the changes we observed in the treatment systems subsequent to the sudden increases in organic substrate.

In the trophophase, in the systems to which organic substrate was added, microbial growth is assumed to occur in a manner unconstrained by carrying capacity effects. In these systems, the microbial growth equation is taken to be

(Monod, 1949)

$$\dot{X}_1 = \frac{\beta X_1 X_2}{K + X_2} \Theta (X_3 - \overline{X}_3 - \Delta); \qquad 0 \leqslant t \leqslant t_o \qquad (1)$$

The theta-function, $\Theta (X_3 - \overline{X}_3 - (\Delta)$ is equal to 0 if $X_3 < \overline{X}_3 + \Delta$ and is equal to 1 if $X_3 > \overline{X}_3 + \Delta$. $\Delta$ is an arbitrary threshold value of substrate needed to stimulate microbial growth; it is not related to the observed threshold for IN production and I assume that in all our experiments, $\Delta$ is small compared to the added substrate. Thus the $\Theta$-function is equal to 1 in the treatment systems initially, and $\dot{X}_1 > 0$ until $t = t_o$ when $X_1 = \tilde{X}_1$, unless $X_3$ is diminished by microbial activity to the extent that it drops to a value close to $\overline{X}_3$ and microbial growth stops.

The form for $\dot{X}_1$ in Eq. 1 is based on the assumption that microbes obtain their nitrogen supply from the IN pool, $X_2$. The added substrate is the source of carbon and energy for microbial growth, as well as a source of mineralizable organic nitrogen. The $\Theta$-function ensures that the carbon requirements for growth are met. In another model discussed later, microbes are assumed to derive their nitrogen directly from organic substrate.

The equation describing the rate of change of IN is

$$\dot{X}_2 = \frac{\eta X_1 X_3}{L + X_3} - \frac{\beta X_1 X_2}{K + X_2} \Theta(X_3 - \overline{X}_3 - \Delta) - \frac{\sigma X_2}{M + X_2}; \qquad 0 \leqslant t \leqslant t_o \qquad (2)$$

Here the first term on the right hand side of the equation describes the mineralization process in which microbes

digest organic substrate to produce IN. Note that built in here is the assumption that the rate of nitrogen mineralization is proportional to the total microbe population, $X_1$. The second term is just the immobilization of IN by microbes in their growth phase and the last term describes the uptake of IN by phytoplankton. For reasons discussed previously, I assume that the phytoplankton population remains constant during the trophophase and that assimilated IN is stored in algal cells.

When all $X_i = \overline{X}_i$, the $\dot{X}_i = 0$ and so the following constraint holds:

$$\frac{\eta \overline{X}_1 \overline{X}_3}{L + \overline{X}_3} = \frac{\sigma \overline{X}_2}{M + \overline{X}_2} \qquad (3)$$

Finally, to complete the description of the trophophase, the equation for the rate of change of substrate is

$$\dot{X}_3 = -\frac{\eta X_1 X_3}{L + X_3} + \frac{\sigma \overline{X}_2}{M + \overline{X}_2} ; \qquad 0 \leqslant t \leqslant t_o \qquad (4)$$

The last term in Eq. (4) represents the "death" rate of phytoplankton, balanced in the limit $X_2 = \overline{X}_2$ by the assimilation terms on the rhs of Eq. (2). It is assumed that a microbe death-rate term can be neglected during the trophophase.

During the idiophase, microbial growth has ceased, and so $\dot{X}_1 = 0$ and $X_1 = \tilde{X}_1$ (provided sufficient substrate was added to allow $X_1$ to reach carrying capacity). However, microbial metabolic activity continues and some uptake of IN

is necessary to sustain this activity and replace cell wear. This rate of uptake of IN is assumed to be proportional to $\overset{\sim}{X}_1$ and is given by $\alpha \overset{\sim}{X}_1$. Thus we have

$$\dot{X}_2 = \frac{\eta \overset{\sim}{X}_1 X_3}{L + X_3} - \alpha \overset{-}{X}_1 - \frac{\partial X_2}{M + X_2} ; \qquad t > t_o \qquad (5)$$

Finally,

$$\dot{X}_3 = - \frac{\eta \overset{\sim}{X}_1 X_3}{L + X_3} + \alpha \overset{\sim}{X}_1 + \frac{\sigma \overset{\sim}{X}_2}{M + \overline{X}_2} ; \qquad t > t_o \qquad (6)$$

The next-to-last term in Eq. 6 corresponds to the "death" of microbes, and is balanced by the maintenance term on the rhs of Eq. 5 as long as the microbial biomass is assumed to be constant.

Additional complexity can be included in this model. For example, a microbial death term could be assumed to contribute positively to $\dot{X}_3$ during the trophophase. Further complexity can arise if excretion of IN by living algal cells is taken into account. To do so, the "death" term $\overline{X}_2/(M+X_2)$ would actually be partitioned in the ratio $\gamma : 1-\gamma$ between $\dot{X}_2$ and $\dot{X}_3$. Similarly, microbial "death" could be partitioned between $X_2$ and $X_3$ in the ratio $\lambda : 1-\lambda$ . Because these complexities can be shown to alter only insignificantly the behavior of these models (given approximate input parameters taken from experiment), we ignore them hereafter.

The model presented is sufficiently flexible to allow

exploration of a number of hypotheses in addition to that presented in the preceding section. If $t_o$ is assumed to be much larger than the experimental period of interest, so that the entire experiment is assumed to take place in the trophophase and the effective carrying capacity is infinite, then Eqs. 1-4 can be used to describe the data. Or, again in contradiction with our hypothesis, $t_o$ could be assumed equal to 0, so that microbial growth is ignored, and Eqs. 5, 6, can be used to describe the data.

## V. Model Analysis

In this section, the behavior of the model is examined in some detail and compared with experiment. Some of the parameters in the model have been measured in the decomposition experiments, while others must be deduced from the data by suitable fitting procedures. Of the initial conditions, $\overline{X_2}$, $\overline{X_3}$, and $X_3(O)$ are measured directly, or determined by carbon measurements plus reasonable assumptions about C/N ratios (Harte and Levy, 1981). In contrast, $\overline{X_1}$ and $\tilde{X_1}$ have to be fit from the data. Other parameters to be fit include $t_o$, $\beta$, $\tilde{\sigma}$, $\eta$, $\alpha$, K, L, and M.

Because of the complexity of even this relatively simple model of mineralization it is sensible to attempt to determine as many of these parameters as possible by analytical rather than numerical methods. The available data include the detailed time dependence of $X_2$ and incomplete information about phytoplankton assimilation of IN. The key

features of the available data on the time dependence of $X_2$ that are used here include the lengths of time prior to the rapid increases in IN, the magnitudes of the IN maxima, the times $t_m$ at which the maxima occur, and the rate of decrease of IN concentrations subsequent to $t_m$.

In order to reduce the degrees of freedom available I proceed by first assuming that our hypothesis is correct. This procedure will allow estimation of rough values for most of the unmeasured parameters by analytical methods. In the first two experiments, in which a threshold in IN production was observed, only negligible net IN production in any system was observed during the first 24 hours following the substrate addition. In contrast, in the third experiment, in which no threshold was observed, IN production was already sizeable by 24 hours. If the hypothesis is correct, it is then plausible that in the first 2 experiments $t_o$ was greater than or equal to 24 hours. Further insight into the value of $t_o$ can be obtained by considering the rate of change of the slope of the curve $X_2(t)$. In the idiophase, Eq. (5) yields

$$\ddot{X}_2 = n\tilde{X}_1 \frac{d}{dt}\left[\frac{\tilde{X}_3}{L + X_3}\right] - \sigma \frac{d}{dt}\left[\frac{X_2}{M + X_2}\right] \tag{7}$$

Consider the early idiophase before $X_2$ reaches its peak at $t=t_m$. Because $\dot{X}_3 < 0$ and $X_2 > 0$ for $t_o < t < t_m$, it follows that

$$\ddot{X}_2 < o \; ; \; t_o < t < tm \tag{8}$$

Thus the rate of increase of $X_2$ is decreasing in the idiophase and this places a lower bound on the value of $t_o$. During the trophophase, $\ddot{X}_2$ is given by differentiation of Eq. (2). By substituting Eqs. (1,4) for $\dot{X}_1$ and $\dot{X}_3$ into the expression for $\ddot{X}_2$, it is easily shown that for $X_3(0) \gg X_1$, $\ddot{X}_2$ will start out positive, for small t, and then may or may not flip sign before $t=t_o$, depending on the sign of

$$\beta(nX_3 - \beta)/(L+X_3) - n^2 X_1 X_3 L/(L+X_3)^3.$$

As we shall see, parameter estimates suggest that $\ddot{X}_2 \geq 0$ throughout the trophophase. It can be concluded that $t_o$ is near the inflection point in $X_2(t)$. Thus, for K-1, $1 \leq t_o \leq 2$ and for K-2, $2 \leq t_o \leq 3$. For K-3, $t_o=0$.

The gap, $\overset{\sim}{X}_1 - \overline{X}_1$, in experiments 1 and 2 should be approximately equal to, $\overline{X}_3^T(0) - \overline{X}_3$, where $\overline{X}_3^T(0)$ is the value of initial organic substrate for which the threshold appears. Assuming a C/N ratio of 6 for the added substrate, the value of $\overset{\sim}{X}_1 - \overline{X}_1$ can be determined from Fig. (4) to be approximately

$$\overset{\sim}{X}_1 - \overline{X}_1 \approx \frac{1}{6} \times (150) \; \mu \, M \; (N); \; \text{experiments 1 and 2}$$

$$\tag{9}$$

$$\overset{\sim}{X}_1 - \overline{X}_1 \approx 0; \; \text{experiment 3} ,$$

Because $t_o$ is not greatly dependent on $X_3(0)$, at least for values of $X_3(0) \gg X_2^T(0)$, it follows that the parameter, K, in Eq. (1) is small compared with $X_2(t_o)$. It is reasonable to assume, as a first guess in parameter estimation,

that K=0. On the other hand, the slope of $X_2(t)$, for $1<t<t_m$, does depend strongly on $X_3(0)$, and therefore, the parameter, L, in Eqs. (2, 4) is probably large compared with $X_3(0)$. Therefore, we make the tentative assumption that $\eta/(L + X_3)$ can be replaced by a constant, $\nu$, defined by

$$\nu \equiv \eta/L \qquad (10)$$

Qualitative constraints on the model parameters resulting from the observed dependence of $t_m$ on $X_3(0)$ can also be deduced. Because $t_o$ is relatively independent of $X_3(0)$ the explanation of the large value of $\partial t_m/\partial X_3(0)$ in experiment 2 must lie in idiophase dynamics. Experiment 3 reinforces this conclusion, as a large value of $\partial t_m/\partial X_3(0)$ was observed despite the absence of a trophophase. The conditions that determine the value of $\partial t_m/\partial X_3(0)$ can be deduced as follows.

Consider, first, the pair of equations

$$\dot{X}_2 = aX_3 - b - c\,X_2$$

$$\qquad (11)$$

$$\dot{X}_3 = -aX_3 + b + c\,\overline{X}_2$$

The $X_2$-dependence here represents the behavior of the last terms in Eqs. (5, 6) when M is very large and $\tilde{\sigma}/M=c$. The constant $b=\alpha\tilde{X}_1$ and $a=\nu\tilde{X}_1$. It is straightforward to solve these equations and to show that $t_m$, given by $\dot{X}_2(t_m) = 0$, is nearly independent of $X_3(0)$ Next, consider the opposite case in which M is small, so that the dependence of the last term in Eq. (5-a) on $X_2$ disappears. In this case, the term $cX_2$

in Eqs. (11) is replaced by the constant, $\sigma$ , and explicit solution of the equations shows that $t_m$ increases with increasing $X_3(0)$.

These mathematical observations suggest that in Experiment 2, where $\partial t_m / \partial X_3(0)$ was large and positive, the constant M should be small compared with the maximum value of $X_2$. In contrast, in Experiment 1, where $t_m$ was more nearly independent of $X_3(0)$, the constant M should be comparable to or larger than the maximum value of $X_2$.

A large value of M relative to $X_2$ implies that phytoplankton assimilation of IN is proportional to the concentration of IN present, whereas a small value implies that assimilation is more nearly independent of $X_2$. This is consistent with the data on phytoplankton growth, which indicated that in Experiment 2 the rate of assimilation was relatively independent of the IN concentration, for large values of that concentration, while in Experiment 1 the rate of assimilation was roughly proportional to IN concentration.

In either of the two limits, M large or M small, and with the tentative assumptions discussed above about the values of K and L, the system of equations can be solved explicitly. Analytical insights into the values of the remaining parameters can then be obtained. For example, from Eq. (1) in the limit K=0, a relation among $\overline{X}_1$, $\tilde{X}_1$, $\beta$ , and $t_o$ is obtained. Approximate relations among $\nu$ , $\alpha$, and

$\beta$ can be obtained as well. These relations, together with the estimated value of $\overset{\sim}{X}_1 - \overline{X}_1$ and $t_o$ then allow us to fit, by numerical simulation, all of the data in Figs. 1-3. Shown in Figs. 6 and 7 are reasonable fits to the data shown in Figs. 1 and 2. Parameter values are given in the figure captions.

## VI. Discusssion

The model presented in Section IV incorporates the assumption that microbes mobilize their nitrogen from the IN compartment ($X_2$). An alternative assumption to make in decomposition models is that organic matter ($X_3$) directly supplies nitrogen for microbial growth. To explore the compatibility of that alternative assumption with experiment, consider an alternative model, in which the same fundamental assumptions concerning the trophophase and idiophase are made as in Section IV, but the equations are slightly modified. In particular,

$$\dot{X}_1 = \frac{\beta' X_1 X_3}{K' + X_3} \; \theta \, (X_3 - \overline{X}_3 - \Delta ) \tag{12}$$

$$\dot{X}_2 = \frac{\eta' X_1 X_3}{L' + X_3} - \frac{\sigma' X_2}{M' + X_2} \tag{13}$$

$$\dot{X}_3 = \frac{-\eta' X_1 X_3}{L' + X_3} - \frac{\beta' X_1 X_3}{K' + X_3} \; \theta \, (X_3 - \overline{X}_3 - D) + \frac{\sigma' \overline{X}_2}{M' + \overline{X}_2} \tag{14}$$

during the trophophase, and

$$\dot{X}_2 = \frac{\eta' \overset{\sim}{X}_1 X_3}{L' + X_3} - \frac{\sigma' X_2}{M' + X_2} \tag{15}$$

$$\dot{X}_3 = -\frac{\eta' \overset{\sim}{X}_1 X_3}{L^1 + X_3} + \frac{\sigma' \overline{X}_2}{M' + \overline{X}_2} \tag{16}$$

during the idiophase. This model differs from that in Section IV in one major respect: here the equations for the rate of change of $X_2$ do not contain a term describing a loss from the $X_2$ compartment proportional to $X_1$. The other difference between the models is in the form of Eq. 1 versus Eq. 13, but since K and K' have to be very small in order to get even an approximate fit to the data, this difference is unimportant.

In the trophophase, these equations predict a rate of build-up of IN that far exceeds that observed. Moreover, the best fits are off by more than a factor of two in the peak IN levels, $X_2(t_m)$. Thus we can conclude that within the context of our hypothesis, the direct microbial source of nitrogen is the inorganic nitrogen pool, and not organic substrate.

If the hypothesis is not assumed, and $t_o$ is taken to be either 0 in all experiments (corresponding to no increase in microbial biomass) or oo (corresponding to no limit to microbial growth), then not even a very rough fit to the data can be obtained. Of course, this does not prove that the hypothesis is correct, nor does the fact that satisfactory fits could be obtained assuming the hypothesis. To explore further the validity of the hypothesis, it is necessary to test predictions (ideally model-independent ones) of the hypothesis. The central model-independent prediction is that microbial populations should reach a plateau in systems

in which a threshold in IN concentration is observed. Unfortunately reliable total microbial counts in lake waters are notoriously difficult to carry out and are not accepted widely as quantitative indicators of the extent of nitrogen immobilization.

Model-dependent predictions offer a greater opportunity for testing. In this article, only transient responses to additions of organic matter have been discussed. It is possible to examine experimentally other transient deviations from the steady state, however, such as would be induced by additions of IN. By such means a further effort at model validation could be made.

The data of Figures 1-3 are sufficiently rich in structure that they allow a fairly precise determination of the model parameters. Although the curves shown in Figures 6 and 7 show some deviations from the data, they do capture the essential features to a good approximation. If the parameter combination, $R = \eta \, \overline{X}_1 \overline{X}_3 / (L + \overline{X}_3)$, is varied by a factor of 50% in either direction from that in the fits, and all other parameters are readjusted to yield the best fit, then that best fit is decidedly poorer than the one shown. Since R measures the gross rate of mineralization under the control (no substrate added) conditions, the model allows an approximate value of this ambient rate to be extracted from the experimentally observed transient charges in IN concentration that result from organic additions. Because

mineralization rates can be measured by other means as well (for example, by carbon-14 tracers as in Cole and Likens, 1979), it may be possible to validate the models by comparing mineralization rate estimates.

In addition to the parameter, R, determination of the gap $\overset{\sim}{X}_1 - \overline{X}_1$ is also of some interest. $\overset{\sim}{X}_1$ represents a microbial carrying capacity. Populations that generally exist close to, or far below, carrying capacity, respectively, are referred to as K or r selected. Theoretical analyses of the types of differences expected between K and r selected populations and the stabilizing role of density dependence (see e.g., May, 1973) have rarely been subjected to experimental test. Constraining any attempt to do so has been the difficulty of measuring the presence of density dependence and the nearness to carrying capacity of a population (Eberhardt, 1970; Ehrlich and Birch, 1967). One notable exception (Luckinbill, 1979) involving pure cultures of E. coli demonstrated the usefulness of overcoming these difficulties. By measuring the response of inorganic nutrient concentrations to additions of organic substrate and applying the analysis used here, the nearness of the initial microbial population to its carrying capacity can be determined.

As a final speculative application of this work, it might be interesting to classify a large number of lakes at various times of the year with respect to their response to

additions of organic substrate. Because many lakes are subjected to large seasonal influxes of organic matter from their surrounding watersheds, the experiments we performed in the laboratory are a speeded-up version of a natural phenomenon. Evidence for the types of behavior we have observed in the laboratory should be searched for in the field. A characterization of lakes according to their values of $\tilde{X}_1 - \overline{X}_1$ and $\partial t_m / \partial X_3(0)$ may provide interesting empirical relationships between these measures and measures of trophic conditions or other traditionally used limnological parameters.

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Figures

Figure 1    Inorganic nitrogen concentrations as a function of time in experiment 1.

Figure 2    Inorganic nitrogen concentrations as a function of time in experiment 2.

Figure 3    Inorganic nitrogen concentrations as a function of time in experiment 3.

Figure 4    Peak inorganic nitrogen concentrations observed in each experiment as a function of the amount of organic matter added.

Figure 5   Phytoplankton cell-volume densities as a  function of time in experiment 2.

Figure 6   A simulation of Eqs. 1-6, yielding a good description of  the inorganic nitrogen data from experiment 1. The numerical values of the parameters  in the  simulation are: $\overline{X}_1=0.002$ µM(N), $\overline{X}_2=2.5$ µM(N), $\overline{X}_3=50$ µM(N), $\overset{\sim}{X}_1=16$ µM(N), $t_0=1.5$ days, $\beta=6.0$/day, $K=0$, $\nu=\eta/L=0.1$/(µM(N) days), $\alpha=5.4$/day, $M=25$ µM(N), $\overset{\sim}{\sigma}=2.5$/day.

Figure 7   A simulation of Eqs. 1-6, yielding a good description of  the inorganic nitrogen data from experiment 2.  The numerical values for  the  parameters are:  $\overline{X}_1=0.1$ µM(N), $\overline{X}_2=4$ µM(N), $\overline{X}_3=40$ µM(N), $\overset{\sim}{X}_1=20$ µM(N), $t_0=2.35$ days, $\beta=2.25$, $K=0$, $\nu=\eta/L=0.045$/(µM(N) days), $\alpha=3$/day, $M=40$ µM(N), $\overset{\sim}{\sigma}=14$/day.
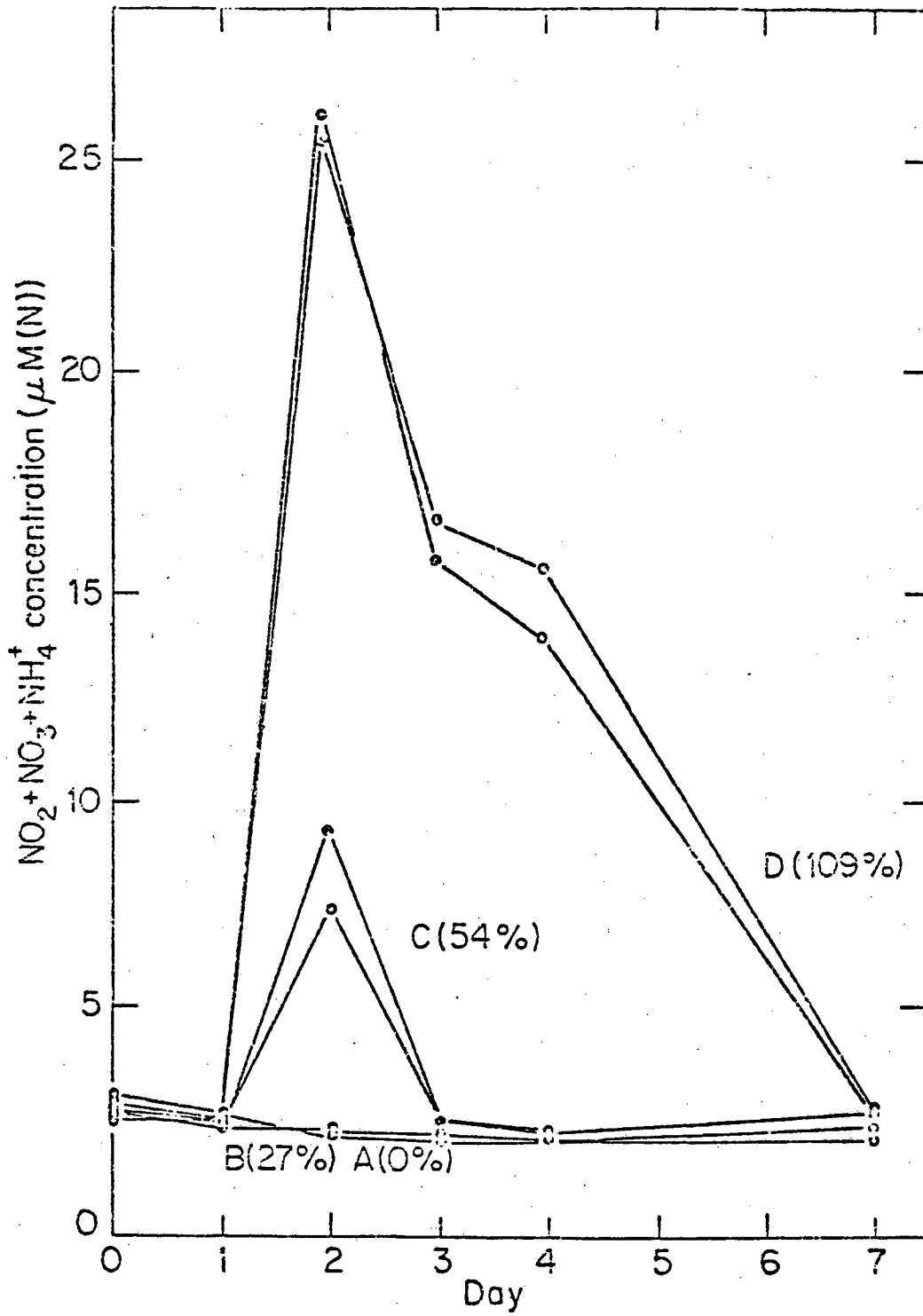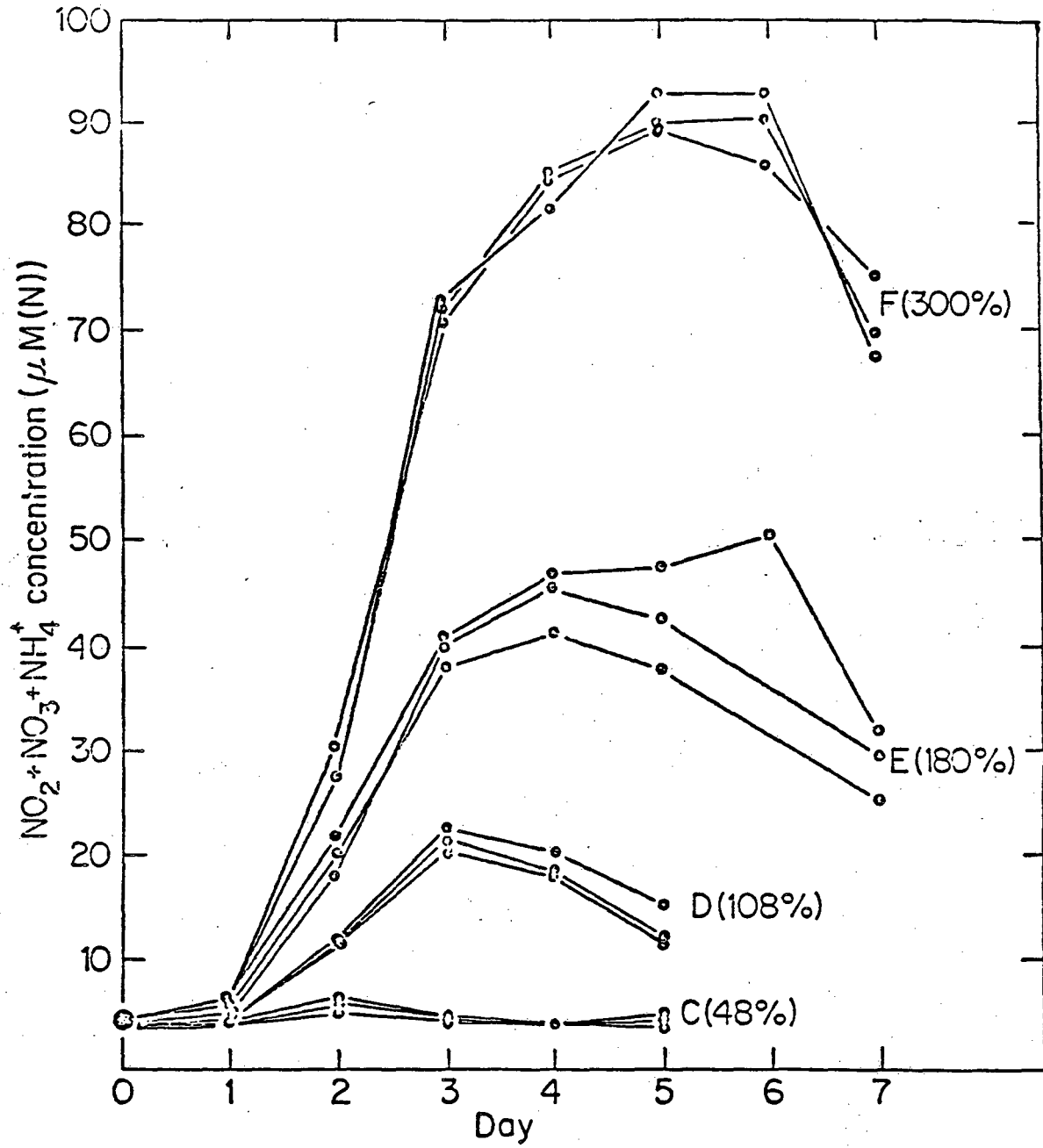
FIGURE 1

FIGURE 2

XBL 794-1355
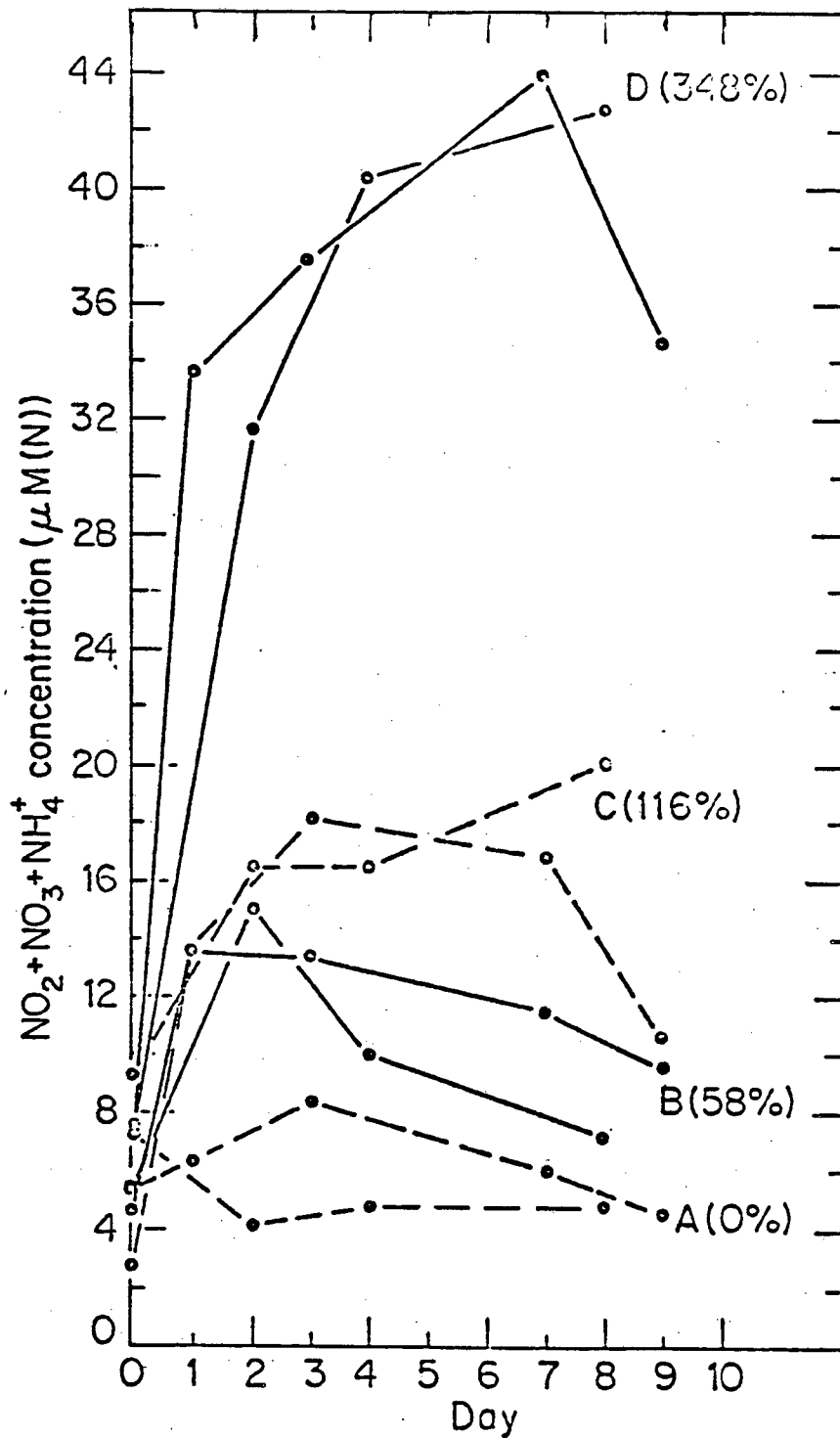
FIGURE 3

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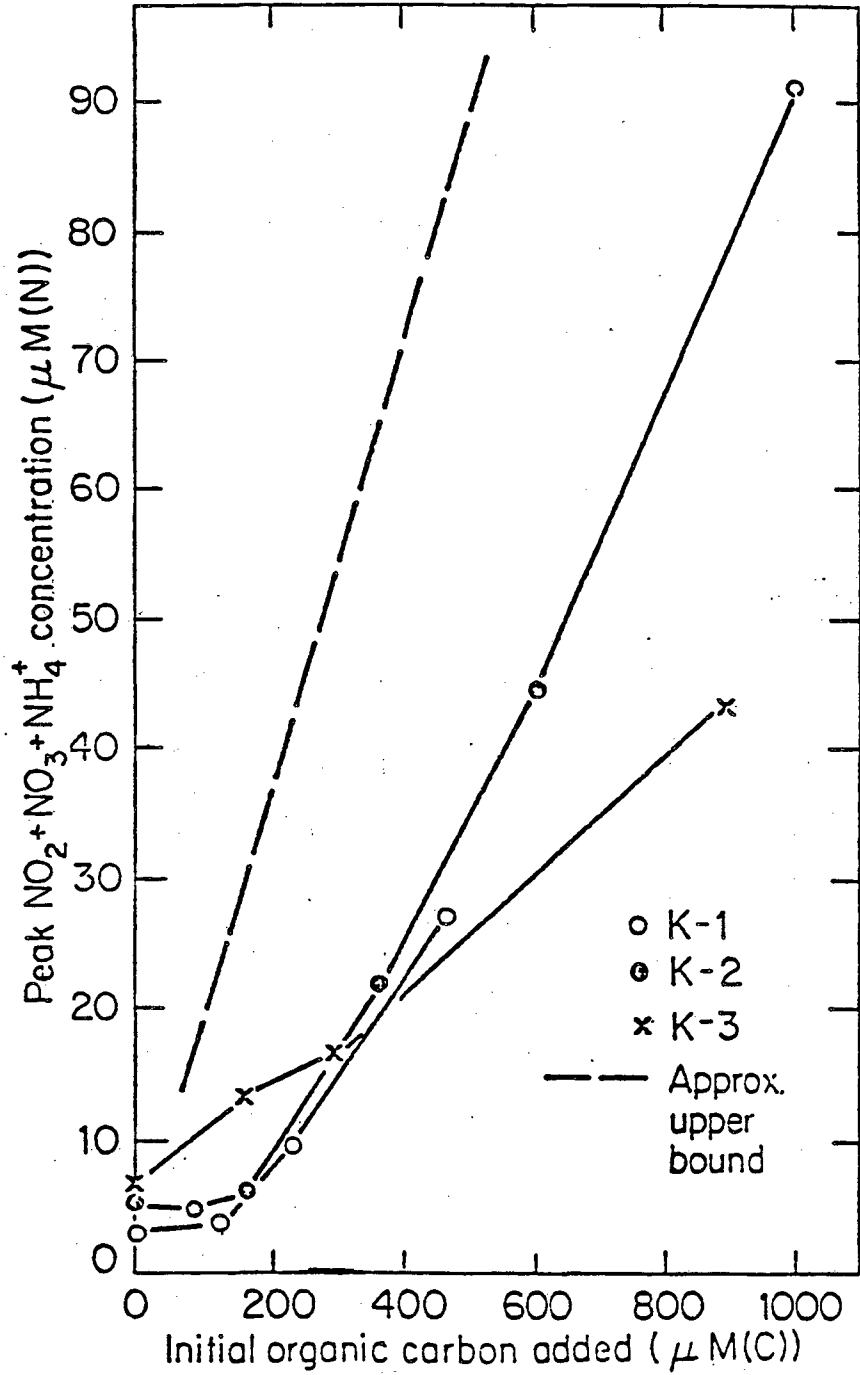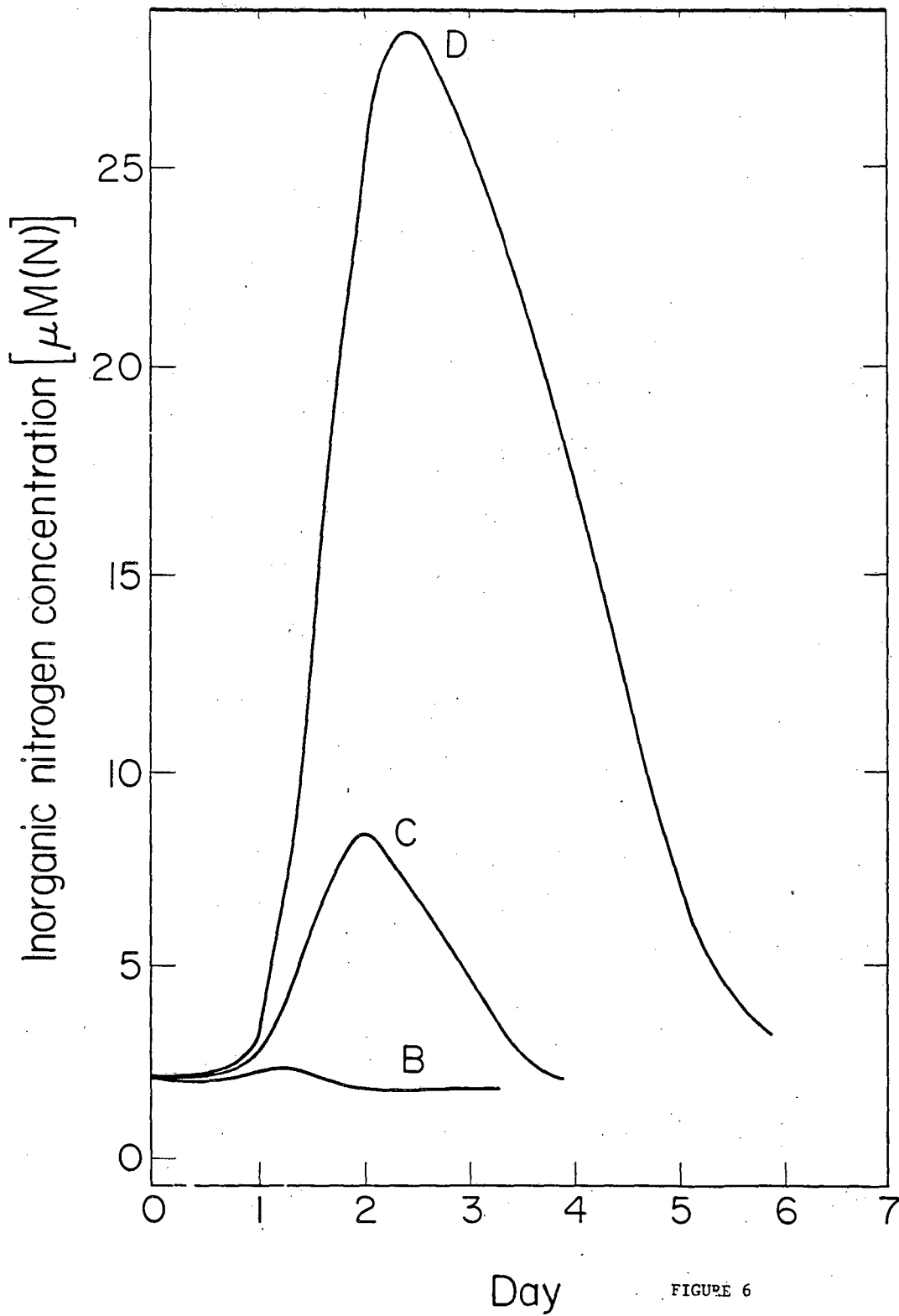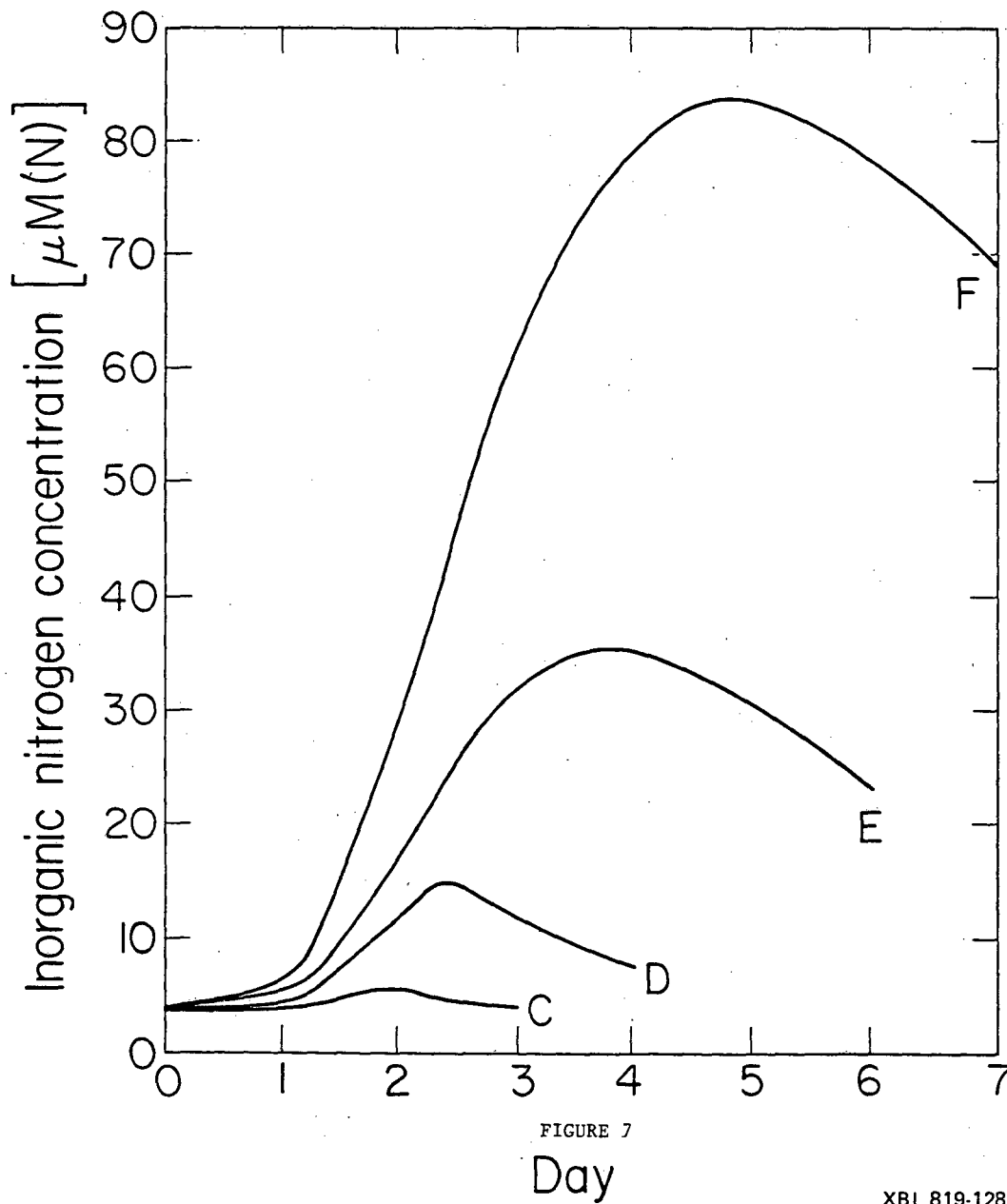
FIGURE 4

XBL 795-1490

-31-
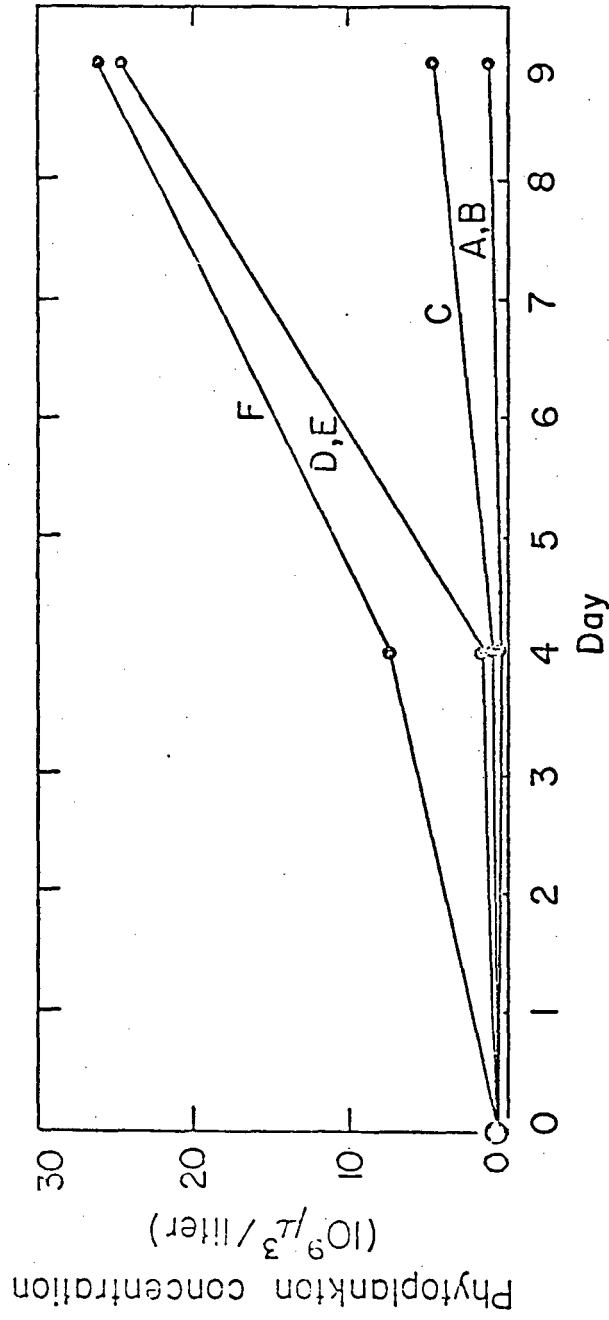


FIGURE 5

XBL 794-1358

FIGURE 6

FIGURE 7

XBL 819-1280