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Author
Harte, J.

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Lawrence Berkeley Laboratory
UNIVERSITY OF CALIFORNIA

ENERGY & ENVIRONMENT DIVISION

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John Harte and Donald Levy

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John Harte

Donald Levy

Energy and Environment Division
Lawrence Berkeley Laboratory
University of California
Berkeley, California 94720

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INTRODUCTION AND BACKGROUND

The consequences of an addition of natural detritus to an ecosystem can be anticipated in a broad qualitative sense. In a sequence of transformations induced by the additional substrate made available for decomposition, one expects an increase in decomposer populations and mineralization rates, followed by an increase in primary and then secondary production. In a series of experiments over the past two years, we have studied the short-term responses of lake-water aliquots to the addition of detritus. Results from a highly-replicable and diverse set of measurements show the expected qualitative pattern of transformations. More interesting, however, is the fact that a number of unexpected conclusions concerning the quantitative description of these transformations can be deduced, particularly when comparisons are made among the relative changes in decomposition rate brought about by different amounts of detritus added to replicate aliquots. Moreover, the results suggest that study of responses of ecosystems to detrital manipulations may enhance understanding of the kinetics of nutrient flow, allow a quantitative determination of the extent of density-dependent regulation in decomposer populations, and assist in evaluating and predicting effects of toxic substances on decomposition processes.

To our knowledge, the type of investigation described here has not been carried out before. A number of authors, however, have described related studies. Hynes (1963) discussed the generic biological and chemical changes in streams that take place as a result of the addition of organic matter at a fixed point on a stream. His concern was primarily with organic pollution and self-purification downstream from the source of pollution. The role of heterotrophs in processing organic wastes was

studied by Wuhrmann (1964), using artificial stream channels. Adding different levels of organic waste to the streams, he showed that the heterotrophs increased relative to the autotrophs as the organic levels increased. He then demonstrated that the rate of removal of additional fixed increments of organic materials (for example, glucose) was enhanced in those systems with higher heterotroph populations.

In another investigation, Wetzel and Manny (1972) studied the effects of leaf-litter loading in a hard-water stream and demonstrated that the decomposition processes could be separated into a short-term, active component and a longer-term, slow component. Warren et.al. (1964) studied changes in bacteria and trout populations in response to sucrose additions to artificial streams. Rheinheimer (1965) obtained relationships between decomposition activity on the one hand and sewage loading, temperature, and bacterial numbers on the other, for sites studied on the River Elbe. Mclaren (1973) and Alexander (1961) discussed the behavior of soil communities which have been loaded with organic and inorganic nutrients. In soils, the observed sequential pattern of changes is qualitatively similar to that in aquatic systems. Useful reviews of experimental information about decomposition processes in natural ecosystems can be found in Mann (1969), Pomeroy (1970), Alexander (1971), and Wetzel (1975).

Chemostats have been used to study bacterial growth on an organic substrate (Dicks and Tempest, 1966) and algal growth (Fuhs, 1969). Such work has been carried out under different conditions of nutrient limitation, with mixed populations of bacteria, protozoa, and yeast, and on a variety of substrates (Yoon et. al., 1977). The development of reliable mathematical models for substrate uptake is one major goal of chemostat studies (Nyholm, 1976; Dabes et. al., 1973).

A number of tracer experiments using ^{14}C-tagged organic acids have been conducted to study the uptake of these organic materials in lake-water samples. Robinson et. al. (1973) found that Michaelis-Menten kinetics characterized the uptake and that maximum uptake velocity rank-ordered with bacterial populations for 6 out of 8 organic acids studied. Wright (1975) added different amounts of ^{14}C-labeled glycolic acid to lake-water aliquots, to achieve initial concentrations of 250 and 500 µg/liter, and showed that the rate of disappearance of the added substrate in the treatments was independent of the initial concentration. Moreover, the bacterial counts showed no significant difference between treatments and control. The objectives of these studies are similar to ours - to investigate properties of decomposition by studying the response of lake waters to different levels of added substrate. One important difference in our approach is that we use natural detritus rather than simple, isolated constituents of detritus. The advantage of working with realistic substrate is offset, to some extent, by the disadvantage of not being able to employ tagged substrate.

In some decomposition studies carried out with a substrate consisting of a particular organic acid, evidence is seen for a simple relation between bacterial numbers and mineralization rates (Rheinheimer, 1965; Robinson et.al., 1973). Were this generally true, bacterial counts would suffice for measuring decomposition rates. However, in other studies it was found that measured bacterial populations do not provide a reliable indication of decomposition (Wright, 1975); it has been stressed that even if all bacteria could be counted accurately, their numbers or growth rates are not necessarily in proportion to their decomposition activities (Hobbie, 1972). For that reason we have not relied on measurements of populations of decomposers for determination of decomposition rates; with tracer techniques

also ruled out, we have emphasized direct measurements of mineralization products from decomposition.

In order to quantify the short-term decomposition activity in our systems, we have measured chages in water-column inorganic nitrogen levels (NH_4^+ and $NO_2 + NO_3$) over the seven days subsequent to the detrital addition. This time period was always sufficient to detect a rise and then a fall in the inorganic nitrogen levels. The major advantages of these measurements are threefold. First, ammonia production and its possible subsequent oxidation to nitrites and nitrates is usually an end stage of the decomposition pathways for organic materials. Second, the presence of soluble-inorganic-nitrogen products reflects detrital decomposition taking place anywhere in the system, whether on the surfaces of the container or in the water column. Finally, inorganic nitrogen can be measured with relative ease and precision and thus a good statistical basis is obtained for identifying, and developing models for, systematic decomposition phenomena.

There are also disadvantages to relying solely on measurements of changes in inorganic nitrogen for decomposition studies. First, they do not allow a separation of inorganic-nitrogen production from inorganic-nitrogen uptake by phytoplankton, and for that reason we made a number of supplementary measurements, including dark- and light-bottle CO_2 exchange and phytoplankton cell volumes. Second, to a poorly known extent, NH_4^+ produced during decomposition will be absorbed onto particulate materials and thus can be difficult to detect (Hutchinson, 1957). Finally, in a variety of natural circumstances inorganic nitrogen is not a limiting nutrient and in such cases interest in decomposition may be directed toward other mineralization products.

METHODS

The experiments reported here were carried out in 4-liter glass beakers housed in a temperature-controlled room at 19±1°C. Illumination was provided by a bank of 8 4-ft high-output fluorescent lights on a 12h:12h light:dark cycle; the light irradiance on the water surface of the microcosms was 7.0±.3 watts/m^2 PAR. The water in each microcosm was agitated gently by air pumped at a rate of about 1 liter per minute through a capillary tube extending 15 cm below the water surface.

The water samples investigated were taken from a number of lakes in the San Francisco Bay area. Initially, lake water was brought into the laboratory and placed in large microcosms, ranging from 15 to 700 liters in volume. After periods of time ranging from 1 to 4 months, depending on the experiment, 4-liter samples were taken from the larger microcosms and transferred to the beakers where the detritus additions were carried out.

The detritus was prepared in several different ways, depending on the experiment. In two of the sets of experiments, E. coli grown specifically for the purpose were used. These dense cultures reached concentrations of 5 mM (C) (5 millimoles of carbon per liter of water). The E. coli were harvested, sonicated for 30 minutes effectively breaking cell walls, and then autoclaved for 40 minutes at 110°C and 25 psi. To prepare detritus for three other sets of experiments, algae consisting primarily of Scenedesmus, Chlorella, Gleocystis, Ankistrodesmus, and LRGT's were grown under nutrient-rich conditions, harvested, and then sonicated and autoclaved. In one of these three sets, the soluble portion of the detritus was separated and used for investigation of DOM additions, while in the other two the DOM and the particulate organic materials (POM) were not separated.

Table 1 summarizes the conditions of each of the five sets of experiments carried out (labeled K-1 to K-5). In each set of experiments, the

replicate 4-liter beaker systems were initiated from the larger laboratory microcosms three days prior to the addition of detritus, and background values of all monitored quantities were then determined. On day-zero of each experiment, organic carbon was measured in all 4-liter systems and in the concentrated detritus spike. The detritus was then immediately added to all treatment systems, at relative concentrations shown in Table 1. With the exception of water-column phytoplankton and zooplankton (number and volume), which were measured approximately weekly, monitoring was carried out daily for periods ranging from one to several weeks. Measurements were made from water samples taken from the 4-liter systems at approximately 4 hours after the onset of light each morning, at 11:00h. Table 2 lists the methods used for monitoring chemical and biotic parameters.

RESULTS

Our primary interest is in the relationship between the quantity of detritus added and the fraction rapidly mineralized. One particularly striking feature of two of the five experiments (K-2 and K-3) that we will emphasize below is a threshold-like behavior in the mineralization activity, signalled by a near absence of mineralization below a critical initial concentration of detritus. In this section we present the results of each of the five experiments, while in the following section we discuss possible dynamical origins of the major results.

The quantities monitored in the experiments are not all expressed in the same units, such as phytoplankton volume density (cubic microns/liter) and NH_4^+ concentration (micromoles/liter). In order to develop approximate nitrogen budgets, we occasionally use conversion factors allowing reduction of all

measurements to common units of nitrogen concentration. For living biomass and freshly prepared detritus, we assume a molar C/N ratio of 6, and for phytoplankton, protozoa, larger zooplankton, and bacteria volumes, we assume 10^9 cubic micron per liter equals 1.3 micromoles of nitrogen per liter (denoted μM(N)). Graphs of the data presented below are expressed in directly-measured units, but phytoplankton volumes and NH_4^+ concentrations are drawn to a scale such that they can be compared directly within each experiment. It must be emphasized that these conversions are approximate and can depend on stage of growth and nutrient conditions.

Table 3 lists the major organisms other than bacteria present in the 4-liter systems prior to the addition of detritus. In each of the five experiments, nearly all of the organisms listed in Table 3 were present in treatments and controls, although in numbers which varied considerably from one experiment to another, and which varied during the course of each experiment. In K-2, for example, a ciliate protozoan dominated (by volume) the animal population, while in K-3, a rotifer (Lecane sp.) and a cladoceran (Alona guttata) dominated. In K-4 and K-5, the dominant phytoplankton were Mougeotia sp. and Phacus sp., while in K-1, Cryptochrysis sp. dominated.

K-1: Only one level of added detritus was studied in K-1, corresponding to a 50% increase in organic carbon. Initial levels of organic carbon in both treatment and control were 150 μM(C). Figure 1, shows NH_4^+ and total phytoplankton volume in the water column plotted as functions of time with day-0 the day of detritus additions in the treated systems. Over the first 3 days subsequent to the spike, NH_4^+ levels in the treated systems (B) showed a marked increase, ∿5.5 μM(N), relative to the control systems (A) indicating initial decomposition of the added detritus. The small increase of NH_4^+ in A during the first 4 days is unexplained. The detritus spike raised

the total nitrogen level of B by about 12.5 μM(N) relative to A, and therefore the observed increase of 5.5 μM(N) NH_4^+ in the treatments relative to the controls represents about 45% of the maximum possible.

Subsequent utilization of released materials for secondary production is demonstrated by the phytoplankton bloom on days 8-17 in the treated systems and its absence in the controls. At the height of the algal bloom the total phytoplankton volume in the water column in B corresponded to about 13 μM(N), using the conversion factor mentioned above. Even considering the uncertainties in this conversion, the amount of phytoplankton growth in B suggests that more inorganic nitrogen was produced than actually appeared in the peak NH_4^+ measurements.

Figure 2 shows the daily fluorescence data from K-1. For the first 3 or 4 days, fluorescent levels were steady, differing between treatment (B) and control (A) by an amount which can be entirely accounted for by the added detritus, itself. Subsequently, fluorescence levels in B increased substantially, peaking on day-17, and then fell rapidly. Replication among the three treatments and among the three controls was excellent. The fluorescence levels and phytoplankton volumes were in qualitative agreement.

Nitrate + nitrate concentrations in both A and B were below 1 μM(N) throughout the experiment and showed a small increase from day-1 to day-4. The low levels of NO_2 + NO_3 compared with NH_4^+ at their peak in the treated systems suggest that uptake of NH_4^+ or NO_2 + NO_3 by phytoplankton was more rapid than uptake of NH_4^+ by nitrifying bacteria. For the concentrations of NH_4^+ seen here, such relative rates are consistent with observations of others (Goering, 1972; Knowles et al, 1965).

The dark- and light-bottle CO_2 production data were consistent with the NH_4^+ and phytoplankton data. A rise in both dark- and light-bottle CO_2 production

in B was observed on day-1, followed by a negative value for light-bottle production indicating increasing photosynthesis. The controls did not replicate as well as the treatments, showed slight evidence for a dark-bottle peak, and showed considerably less light-bottle uptake. Total phosphorus levels were quite constant during the first 5 days of the experiment, averaging about 1.4 μM(P) in the treatments and 0.3 μM(P) in the controls. Phosphatase levels replicated well, were similar in A and B during the first 2 days of the experiment, and then dropped in B, but not A. By day-5 phosphatase levels in the treatments were about one-half the initial level.

Total zooplankton volumes decreased in both controls and treatments from day-0 to day-22. The initial volume of zooplankton corresponded to $\sim$ 1.5 μM(N). Evidence was obtained for slightly higher values of bacteria and zooplankton counts in the treatments relative to the controls. Bacterial counts replicated poorly, and we attach little significance to them.

K-2: NH_4^+ concentrations during the first week of K-2 are shown in Fig. 3, plotted as a function of time. NH_4^+ concentrations in A and B were identical within experimental error and only their average values are shown. As in K-1, replication of NH_4^+ data was excellent. Note that the day on which NH_4^+ concentration peaked was the same for systems C and D, namely day-2.

An important feature of Fig. 3 is the fact that the peak concentrations of NH_4^+ are not linearly related to the amount of detritus added. Explicitly, in D the peak NH_4^+ value was $\sim$ 25 μM(N) whereas in C it was $\sim$ 7 μM(N), even though the amount of detritus added to D (470 μM(C)) was only double the amount of detritus added to C (235 μM(C)). Furthermore, comparing the peak level in C with that in B, there is evidence of a threshold effect, since systems B with 117 μM(C) of added detritus showed no significant peak in NH_4^+ levels. We call this phenomenon the "nonlinear, threshold effect",

the name intended to suggest the observation of both a near absence of NH_4^+ concentration below a certain level of increase in detritus, and a faster-than-linear increase beyond the threshold. This effect characterizes not only the maximum NH_4^+ concentrations reached (on day-2), but also the rate of production of NH_4^+, as deduced by comparison of NH_4^+ concentrations on days 1 and 2.

Fig. 4 shows the peak NH_4^+ concentrations (averaged over replicates) for all 5 sets of experiments, plotted as a function of the amount of organic carbon added in the form of detritus. In K-2 the nonlinear, threshold effect is clearly seen, with peak NH_4^+ concentration increasing rapidly only beyond a certain initial increase in orgainic material. The peak $NO_2 + NO_3$ concentrations in K-2 also showed a threshold behavior, as shown in Fig. 5. Note that the peak $NO_2 + NO_3$ concentrations were low compared with peak NH_4^+ concentrations in systems C and D. Peaks in $NO_2 + NO_3$ ocurred 1 to 2 days subsequent to day-2 when NH_4^+ levels were maximum.

Phytoplankton volumes are shown in Fig. 6. The scale is such that approximate nitrogen levels can be inferred directly by comparison with the scale in Fig. 3. For purposes of later discussion it is important to note that these measurements were taken only from the water column and did not include phytoplankton that were growing on the surfaces of the beakers or had settled to the bottom. It can be observed that only a portion of the peak NH_4^+ levels in C and D can be accounted for in these phytoplankton measurements. No evidence exists for a nonlinear or threshold effect in these data, but they do indicate that algal growth was promoted by the added detritus. The non-protozoan zooplankton volumes for K-2 were consistently lower by at least a factor of three than the phytoplankton volumes during the 17-day period in which monitoring was carried out. Thus only a very small portion of the total-nitrogen budget is represented by these zooplankton , although they may

have played an important role in detrital processing. The protozoa were more likely to have played such a role, however. A sharp rise in protozoa volume was seen between day-0 and day-5 in all the treatment systems but not in the control, with a subsequent drop back to very low levels between day-5 and day-10. The protozoa volumes recorded on day-5 were roughly comparable to the phytoplankton volumes measured on day-17 (see Fig. 6), with C and D reversed. Unfortunately protozoa data were not obtained daily between day-0 and day-5 so that the peak values were probably missed.

The dark- and light-bottle CO_2 production data are shown in Figures 7 and 8. The qualitative patterns are consistent with our other results. The increase (relative to the control) in the dark-bottle CO_2 production peak rate in system D was considerably more than twice that in C. Beginning on day 2, the light-bottle measurements suggest increasing CO_2 uptake in the order $D > C > B$, but with no evidence of a threshold effect. The replication in these data was within ±20%, which was not as good as the replication in the NH_4^+ data. Further interpretation of these closed-bottle measurements will be given in the Discussion Section below.

The dark- and light-bottle ammonia-evolution rates are consistent with the data on ammonia levels in Fig. 3; production dominated during the first 2 days, balanced by a roughly equal rate of ammonia uptake from the water column during the following two days. The rates of production and uptake were comparable to those deduced from the slopes of the graphs in Fig. 3.

K-3: Fig. 9 shows the major result from K-3: the peak ammonia levels displayed the same nonlinear threshold effect as in K-2 and indeed the two sets of data as plotted in Fig. 4 are nearly overlapping. It should be emphasized that K-2 and K-3 were run nearly 8 months apart and were performed with different sources of lake water. The detritus spike was identical in the two

experiments, however. An interesting and unexpected feature of the data in Fig. 9 is the increasing delay in the time at which peak ammonia levels were reached as the detritus spike was increased. This was not observed in K-2.

Phytoplankton data from K-3 are shown in Fig. 10. The scale again is drawn so that corresponding nitrogen concentrations can be inferred directly by comparison with Fig. 9. The zooplankton levels in all systems were below an equivalent of 2 μM(N).

K-4, K-5: In these two experiments, which utilized a detritus spike comprised of algae rather than E. coli, no nonlinear or threshold effects were observed, and the fraction of the detritus spike mineralized during the course of the experiment was considerably less than in K-1, 2, or 3 (see Fig. 4). K-4 and K-5 were carried out simultaneously, using identical lake-water samples. The higher NH_4^+ levels reached in K-4 compared with K-5 suggest that DOM was more effectively ammonified than was an equivalent concentration of DOM + POM.

DISCUSSION

Our discussion focuses on possible mechanisms that might give rise to the nonlinear, threshold effect seen in the peak NH_4^+ concentrations in the two experiments, K-2 and K-3. Three broad categories of causes can be identified. First, the observed effect could arise if some biological process that removes NH_4^+ from the water column (for example, uptake by algae or by nitrifying bacteria) saturated at some critical NH_4^+ concentration so that the fractional amount removed decreased with increasing NH_4^+ production. A second possibility is that the nonlinear, threshold effect characterizes the decomposition process, itself. Finally, physical processes for removal of NH_4^+ might give rise to the effect.

If the explanation involves saturation of NH_4^+ uptake in the process of formation of some product (such as NO_2 + NO_3, or algal biomass), then a clear signal would be the observation of an amount of product that does not increase as fast as linearly in the amount of detritus added. On the other hand, if the amount of product seen also exhibits the nonlinear, threshold effect, then the biological uptake rate is reflecting, not causing,the observed NH_4^+ phenomenon and the first category of explanation is ruled out. This basic argument is easily extended to the case in which a chain of products is formed, such as $NH_4^+ \rightarrow NO_2 + NO_3 \rightarrow$ algae.

Consider, first, the possibility that in the nitrification process, the uptake of NH_4^+ by nitrifying bacteria saturated, or became independent of the amount of NH_4^+ present, above a certain NH_4^+ concentration. Neglecting, for the moment, complications arising because of algal uptake of NO_2 + NO_3, then the NO_2 + NO_3 concentrations should increase less rapidly than linearly with increasing detritus. Instead, however, the NO_2 + NO_3 data, themselves, exhibited a threshold behavior (Fig. 5), indicating that the nitrification rates reflected, rather than caused, the NH_4^+ threshold.

Consider, next, the possibility that the observed nonlinear, threshold effect in NH_4^+ production resulted because the uptake of NH_4^+ or NO_2 + NO_3 by algae saturated for large inputs of detritus. The data shown in Figs. 6 and 10 lessen the possibility that nutrient uptake for water-column phytoplankton growth caused the effect. The phytoplankton growth rates and absolute levels in K-2 (Fig 6) suggest that with increasing detrital additions, a roughly proportional increase in phytoplankton production took place. In K-3, the water-column phytoplankton data (Fig. 10) even show a threshold effect, in the sense that production in D was considerably greater than that in C, suggesting that phytoplankton growth reflected, rather than caused, the threshold-like large difference in inorganic nitrogen between C and D.

On the other hand, the bunching effect observed for phytoplankton growth in D, E, and F suggests that saturation kinetics in inorganic-nitrogen uptake by phytoplankton might have caused the slightly greater-than-proportional increase in peak NH_4^+ levels as the detritus input increased from D to E to F.

If all of the uptake of inorganic nitrogen that occured showed up as phytoplankton growth in our water column measurements, then saturation of inorganic nitrogen uptake could be ruled out as an explanation of the nonlinear, threshold effect in K-2 and the threshold effect in K-3. But it is likely that considerably more uptake of inorganic nitrogen occurred, as deduced from the following rough nitrogen-budget estimation. In systems C and D of experiment K-2 there was a large gap between, on the one hand, the amount of nitrogen in the form on NH_4^+ which disappeared between day-2 (when NH_4^+ levels peaked) and day-7 (when they had returned to initial levels) and, on the other hand, the amount which subsequently showed up in the form of water-column phytoplankton. This suggests that either inorganic nitrogen was stored in pre-growing phytoplankton cells and would have been observed in phytoplankton measurements had they continued beyond day-17, or that more nutrient uptake and algal growth occurred, even by day-17, than was reflected in the water column phytoplankton data. In the latter case, the additional algae most likely ~~was~~ were growing on the surfaces or had sunk from the water column to the bottom of the beakers. Saturation of NH_4^+ uptake by this additional algae might then have produced the observed threshold phenomenon.

Evidence against these possibilities can be obtained from the dark- and light-bottle CO_2 production data for K-2, shown in Figs. 7 and 8. In fact, from this data an argument can be advanced to suggest that the nonlinear, threshold phenomenon characterized the pelagic decomposition process, itself.

We write:

$$L = Q + P$$

and

$$M = Q + R$$

where L and M are the light- and dark-bottle CO_2 production rates respectively, Q is the actual decomposition rate, P is the net primary production contribution to CO_2 exchange in the light, and R is the dark-period respiration contribution to CO_2 exchange. It is then straightforward to show that on day-1, when CO_2 production was maximum, the Q's are a faster-than-linearly increasing function of added detritus for any fixed P/R ratio satisfying $0 \leqslant R \leqslant -P$. This is illustrated in Table 4, which gives the value of Q on day-1 for 3 different assumed values of P/R. We cannot estimate reliably from the closed-bottle data what the net amount of algal growth actually was, as that quantity is very sensitive to the value of P/R.

The closed-bottle NH_4^+ production measurements in K-2 provide further evidence against the possibility that the kinetics of uptake of ammonia by algae on the surfaces of the 4-liter vessels was a significant cause of the threshold effect. The closed-bottle measurements utilized water-column samples from the 4-liter systems and the bottles could not have developed appreciable surface growth over the 4-hour period of measurment. Nevertheless, these closed-bottle NH_4^+ production rates clearly exhibited the threshold effect and were consistent with the data in Fig. 3. We note that these measurements were made in water-column samples that did not include any of the added detritus which may have sunk to the bottom of the 4-liter containers. The fact that the threshold effect was seen suggests that it reflects water-column activity and was not due to the proportionally greater amount of detritus which may have settled to the bottom of D or C as compared with B.

One other possible explanation of the threshold phenomenon deserves mention. Some NH_4^+ is known to adsorb onto the surfaces of particles (Hutchinson, 1957), and this fraction of the produced NH_4^+ would escape detection by our measurement procedures. If particle-surface-area were adequate to adsorb a relatively large fraction of the NH_4^+ produced in system B, but not in the systems with larger amounts of added detritus, then a threshold effect would appear. The difficulty with this explanation is that the amount of particle-surface-area added to each of the systems in K-2 and K-3 was proportional to the amount of organic carbon added, and therefore such a saturation effect is unlikely.

We have argued that the nonlinear, threshold effect characterizes the decomposition process. An intriguing possibility is that density-dependent effects in the population of decomposers are responsible. To explore this possibility consider a population of decomposers which is in the presence of an increased food supply in the form of added detritus. Suppose, further, that because of crowding or some other density-dependent mechanism the decomposers are limited in their ability to mobilize the additonal nutrient for biomass growth. Then the ratio of the mobilization rate to the mineralization rate will be lower than it would be if the population were at a lower value where mobilization was not inhibited. We hypothesize that at levels of added detritus below the threshold seen in K-2 and K-3, the decomposers were able to mobilize detritus effectively, at the expense of mineralization, while above it, density dependence led to the more rapid rate of mineralization.

CONCLUSIONS

Observation of the response of lake-water aliquots to sudden additions of detritus appears to be a potentially useful starting point for analysis of decomposition dynamics. In a series of preliminary investigations of this type, we have learned the following:

i) Highly replicable responses to the added detritus can be obtained, with the primary exception being bacterial counts.

ii) The qualitative pattern of succession triggered by the added detritus is in accord with traditional ideas about decomposition and nutrient flow.

iii) Interesting quantitative responses occur in the levels of inorganic nutrients, particularly the nonlinear, threshold effect observed in K-2 and K-3, and the increasing delay in the time at which peak ammonia levels were reached in K-3.

iv) Significant differences exist between system response to DOM and to a mixture of DOM and POM (K-4 vs. K-5), between system response to a detritus spike consisting of algae and one consisting of *E. coli*. (K-2 and K-3 vs. K-4 and K-5), and between an identical spike administered to different types of lake water (K-2 vs. K-3).

The nonlinear, threshold effect was unexpected. A saturation mechanism in the uptake of detritus by decomposers (described, for instance, by Michaelis-Menten kinetics) would be expected to give rise to curves in Fig. 4 with a nonlinearity opposite to that seen in K-2 and K-3 (that is, they would be expected to have a negative second derivative). The phytoplankton data and the closed-bottle CO_2 measurements suggest that the phenomenon is intrinsic to the deomposition process, itself. To resolve the question of the role of phytoplankton uptake, it will be useful to supplement detritus-addition experiments with ammonia-addition experiments under otherwise-identical conditions.

The investigations reported here do not allow a determination of whether the threshold is characterized by a particular percentage increase or a particular absolute increase in the concentration of detritus. Nor do they point to possible components of the detritus (e.g., particular organic forms of nitrogen or phosphorus) whose concentrations characterize the effect. Further studies with lake-water samples containing a wider range of background detritus concentrations will provide additional information, particularly about the former issue.

In addition to the threshold effect, the relation between the amounts of added detritus in K-3 and the times at which peak NH_4^+ levels were reached challenges our understanding of the kinetics of nutrient mineralization and mobilization. Simple mathematical models of detrital decomposition and subsequent uptake of mineralization products are being investigated by us in order to determine how the kinetics has to be constrained in order for the model predictions to match our experimental results. The behavior observed experimentally is sufficiently unusual that the results severely restrict the range of permissable assumptions built into simple mathematical models for their description. This work will be reported in detail later.

The success of efforts to develop and confirm models of decomposition is hampered by a paucity of firm information about kinetics and mechanisms. Model predictions for decomposition behavior are strongly affected by the form of the model as well as by the numerical value of the parameters used (e.g., rate constants). Observations of unmanipulated natural systems can provide only limited insight into both model form and model parameters. For example, even with the use of tracers, experimental determination of non-linear or non-donor-controlled terms in mathematical models is impossible when the amount of tracer is a small fraction of each compartment's material and the compartment levels are not altered. In contrast, carefully selected

and executed manipulations of a system (such as by addition of detritus) can augment efforts to develop, quantify, and validate models.

Further experimental and theoretical studies of the effects of detritus manipulations in laboratory systems may help clarify a number of important issues involving nutrient flow in aquatic, and possibly terrestrial, ecosystems. In particular, the technique of detritus-spiking may provide a means of measuring the degree of density-dependent regulation in decomposer populations. Considerable debate has taken place in ecology as to whether the notion of density dependence is useful and empirically testable. Under the assumption that the concept is operations, Hairston et. al. (1960) argued that decomposers are generally food-limited in nature, while Potter (1964) stated that in aquatic systems the number of benthic bacteria present limit the rate of decomposition (presumably because factors other than food limit their numbers and activity). Later discussion has centered on whether density dependence can be measured; see, for example, Ehrlich and Birch (1967), Slobodkin et. al. (1967), and Lidicker (1978).

Much of the debate on this topic has taken place within the context of attempts to search for and quantify density dependence by correlation analysis, in which the change in a population over a fixed time-period is examined to see whether that change depends nonlinearly upon the population itself. As shown by Eberhardt (1970), this approach is beset with statistical traps. From a theoretical viewpoint, there is little question about the important potential role of density dependence - it exerts a stabilizing influence on populations, as described in May (1973) and references therein. For example, the presence of a Verhulst term (or, more generally, any faster-than-linear loss rate in a population) is likely to render practically any mathematical model of interacting populations both more resistant and resilient to externally

imposed disturbances. For that reason it is important to develop methods of measuring such effects in nature. It is suggested here that appropriately-chosen detritus manipulations, rather than correlation studies on undisturbed systems, offer a possible means of identifying and quantifying density-dependent effects in populations of decomposers.

The measurement of density dependence may also be of interest in studies of community succession of microorganisms. Luckinbill (1978) has demonstrated in laboratory studies that pure cultures of E. coli grown under density-dependent controls (K-selected) are superior competitors to ones adapted to conditions permitting log-phase growth (r-selected), whether the comparison is made under crowded or non-crowded conditions. The significance of investigating such effects in natural systems can be inferred.

Other possible applications of the technique of detritus-spiking are:

i) Quantifying the rate of mineralization of DOM in the nutrient cycles of aquatic systems. Richey et. al. (1978) and Wetzel (1975) observed that the contribution of DOM to the overall mineralization rate in lake water is poorly understood today. Moreover, the importance of rapid turnover of DOM in the seasonal production cycle is not well known and therefore little can be deduced at present about the damage to that cycle resulting from alteration by toxic substances of the rate of utilization of DOM.

ii) Assessing the effects of toxic substances upon decomposition rates, by developing standard procedures for comparing the response to detritus manipulations of lake-water aliquots which have been treated versus controlled for toxic-substance inputs.

iii) Setting standards, based on natural threshold phenomena, for allowed levels of organic loading into natural aquatic systems.

Admittedly, laboratory aliquots do not behave precisely like the lakes from which they are derived and thus results of laboratory studies cannot be applied blindly to natural water bodies. However, during bloom periods the similarity is closest, and therefore by restricting attention to periods of rapid growth, distortions induced by the laboratory environment are minimized (Harte et. al., 1978). Moreover, by confining these detritus-manipulation studies in the laboratory to a period of a few weeks, problems of surface growth generally do not become serious. The admitted shortcomings of this approach must be weighed against the intrinsic difficulties of determining toxic-substance effects in natural lakes under natural conditions. For example, the presence of hundreds of potentially-toxic constituents in coal-conversion effluent makes enormous the task of assessing, under completely realistic conditions, the effects of the effluent from each of a large number of possible water treatment methods. Rapid, semi-realistic, assessment methods may play an important role in the future; planned manipulations of lake-water aliquots can provide useful information supplementary to that obtained from field studies, with a high degree of statistical reliability and at relatively little expense or difficulty.

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FIGURE CAPTIONS

Figure 1. Phytoplankton volumes in units of 10^9 cubic microns per liter (right-hand scale) and NH_4^+ concentrations in units of micromoles per liter (left-hand scale) in treatment and control systems in experiment K-2.

Figure 2. Fluorescence levels in the treatment (B) and the control (A) systems in experiment K-1.

Figure 3. NH_4^+ concentrations in the treatment (B, C, and D) and the control (A) systems in experiment K-2. Shown in parentheses next to each system label is the percent increase in organic carbon.

Figure 4. The maximum NH_4^+ concentration plotted versus the increase in organic carbon for each system in each of the 5 experiments. The dashed line shows the approximate upper bound for the NH_4^+ concentration assuming that the C/N ratio is 6, that all of the nitrogen present in the added detritus is converted to NH_4^+, and that all of the produced NH_4^+ is present at the time NH_4^+ concentrations reach their peak value. The control systems' NH_4^+ levels were all within the error bar indicated at zero μM(C).

Figure 5. The maximum nitrite + nitrate concentrations measured in the treatments and controls in experiment K-2. The error bars simply reflect the spread of values measured in the replicate systems.

Figure 6. Phytoplankton volumes measured in experiment K-2.

Figure 7. The daily dark-bottle CO_2 production rates for K-2. The control value has been subtracted from each of the treatment systems' values here in order to display directly the relative effects of the detrital additions. Replicate measurements have been averaged. For reference, the control system measurements for the 5 days of measurement presented here were -2.35, 2.7, 1.3, 2.2, and .75 μM(C)/hour respectively.

Figure 8. The daily light-bottle CO_2 production rates for K-2. The control value has been subtracted from each of the treatment systems' values here in order to display directly the relative effects of the detrital additions. Replicate measurements have been averaged. For reference, the control system measurements for the 5 days of measurement presented here were -4.75, -.15, .1, -.05, and -.65 μM(C)/hour respectively.

Figure 9. NH_4^+ concentrations in four of the treatment systems in experiment K-3. Results for systems A and B are not shown; their concentrations were consistently below that of system C. Shown in parentheses next to each system label is the percent increase in organic carbon for that system.

Figure 10. Phytoplankton volumes measured in experiment K-3. Where two systems are represented by a common line, the results of for those systems were indistinguishable within estimated measurement error.

TABLE CAPTIONS

Table 1. Summary of the configurations of the 5 detritus-addition experiments.

Table 2. Methods used for measuring chemical and biological parameters.

Table 3. List of organisms in the 4-liter systems used for the detritus-addition experiments.

Table 4. Values of Q (the contribution of decomposition to the rate of CO_2 exchange) on day-1 of K-2, for 3 assumed values of the ratio of P to R (see text).

Experiment	Initial organic carbon concentration	Detrital material	Quantities monitored	System	Amount of detritus added, expressed as percent increase in organic carbon	Number of replicates
K-1	150 µM(C)	algae (DOM+POM)	NH_4^+, NO_3+NO_2, fluorescence, phytoplankton and zooplankton species (number and volume), bacteria plate count, dark- and light-bottle CO_2 evolution, total phosphorus, phosphatase	A B	0%(control) 50%	3 3
K-2	430 µM(C)	*E. coli* (DOM+POM)	NH_4^+, NO_3+NO_2, organic and inorganic carbon, dark- and light-bottle CO_2 and NH_4^+ production, phyto-plankton and zooplankton species (number and volume)	A B C D	0%(control) 27% 54% 100%	2 2 2 2
K-3	340 µM(C)	*E. coli* (DOM+POM)	NH_4^+, NO_3+NO_2, phytoplankton and zooplankton species (number and volume)	A B C D E F	0%(control) 24% 48% 108% 180% 300%	3 3 3 3 3 3
K-4	260 µM(C)	algae (DOM)	NH_4^+, NO_3+NO_2, phytoplankton and zooplankton species (numbers and volumes), fluorescence	A B C D	0%(control) 58% 116% 348%	2 2 2 2
K-5	260 µM(C)	algae (DOM+POM)	NH_4^+, NO_3+NO_2, phytoplankton and zooplankton species (number and volumes), fluorescence	A B C D	0%(control) 61% 122% 366%	2 2 2 2

TABLE 1

Parameter	Method	Special equipment	Reference
O_2	polarography	O_2 meter (YSL 57)	--
pH	electrometry	pH meter (Orion)	--
IC	infrared absorbanch	IR analyzer (Beckman 865)	--
OC	combustion to IC	TOC analyzer (Beckman 915A)	--
NH_4	blue indophenol reaction	spectrophotometer (Zeiss PM2 DL)	Solorzano, 1969
NO_3 + NO_2	reduction, diazotization	"	Golterman, 1969
IP	ascorbic acid reduction	"	APHA, 1971
TP	persulfate digestion to IP	"	APHA, 1971
fluorescence	fluorometry	fluorometer (Turner 111)	Strickland and Parsons, 1968
CO_2 evolution	equilibria kinetics	pH meter (Orion 601) IR analyzer (Beckman 865	Truesdell and Jones, 1974
phytoplankton	tube chamber	5 ml tube chamber (Wild) inverted microscope (Lietz)	--
zooplankton	counting chamber	100 ml count. chamber (Wild) binocular microscope (Lietz)	--

TABLE 2

CHLOROPHYTA

- Ankistrodesmus
- Chodatella quadriseta
- Closterium sp.
- Mougeotia sp.
- Rhizoclonium sp.
- LRGT I (<5μ)
- LRGT II (>5μ)
- Nephrocytium sp.
- Gleocystis sp.
- Planktosphaera gelatinosa
- Quadrigula sp.
- Scenedesmus bijuga
- Scenedesmus quadracauda
- Schroderia setigera
- Staurastrum sp.
- Treubaria trippendicula

BACILLARIOPHYCEAE

- Coscinodiscus lacustris
- Cyclotella Menenghiana
- Fragilaria sp.
- Navicula spp.
- Synedra radians
- Synedra ulna
- Anomoeneis sp.
- Gomphonema sp.

CYANOPHYTA

- Anabaena sp.
- Oscillatoria sp.
- Spirulina sp.

CYPTOPHYCEAE

- Cryptochrysis sp.

EUGLENOPHYTA

- Phacus sp.
- Unid. flag. I
- Unid. flag. II

PYRROPHYTA

- Unid. Dinoglagellate I

PROTOZA

- Paramecium sp.
- Vorticella sp.
- Actinosphaerum sp.
- Monas sp.

ROTIFERA

- Ascomorpha sp.
- Dicranophorus sp.
- Keratella quadrata
- Lecane sp.
- Philodina sp.
- Polyarthra sp.
- Trichotria sp.
- Voronkowia sp.
- Unid. rotifer I

ANNELIDA

- Pristina sp.

CLADOCERA

- Daphnia pulex
- Simocephalus vetulus
- Alona guttata

COPEPODA

- Cyclops vernalis

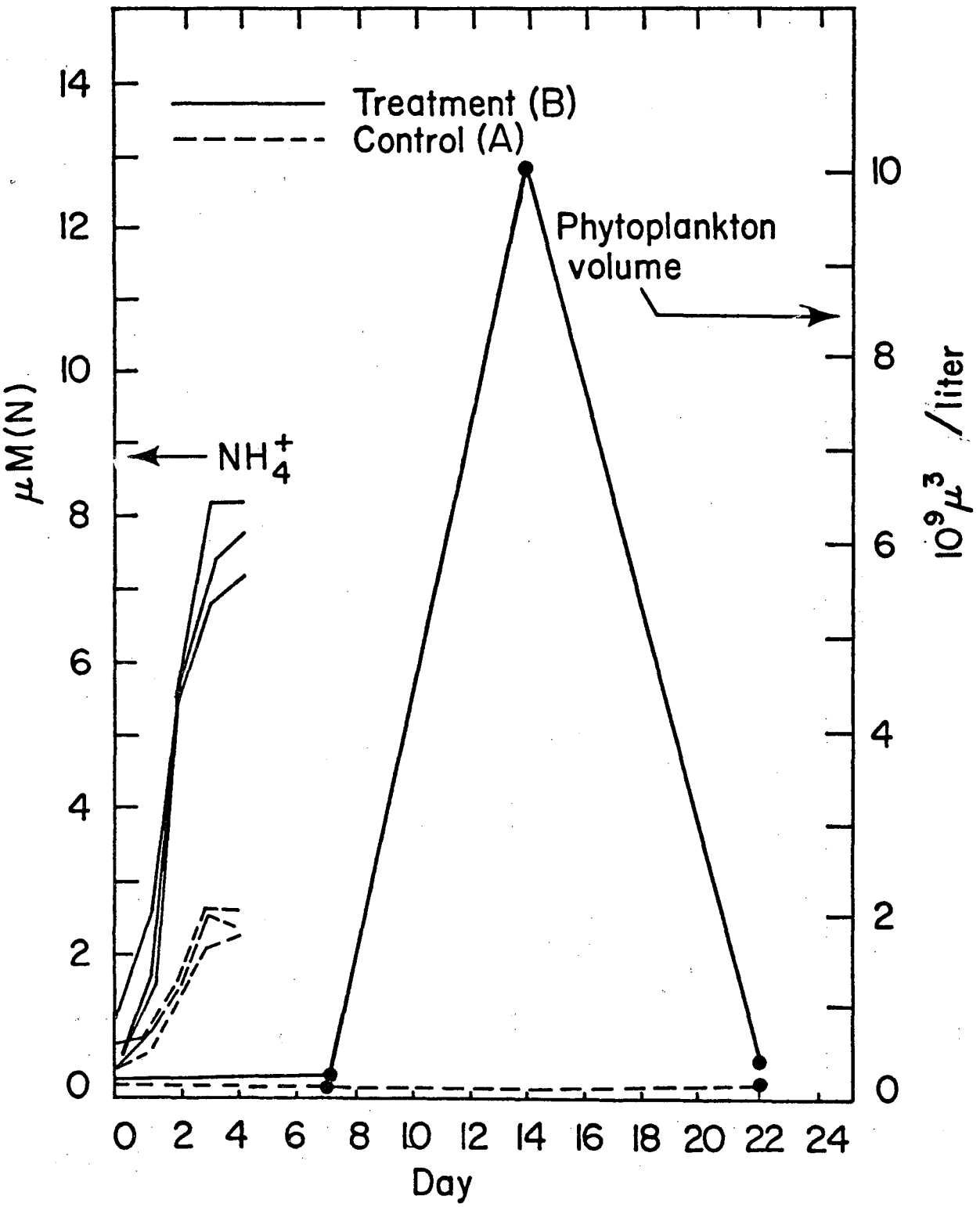
OSTRACODA

- Cypridopsis sp.

TABLE 3

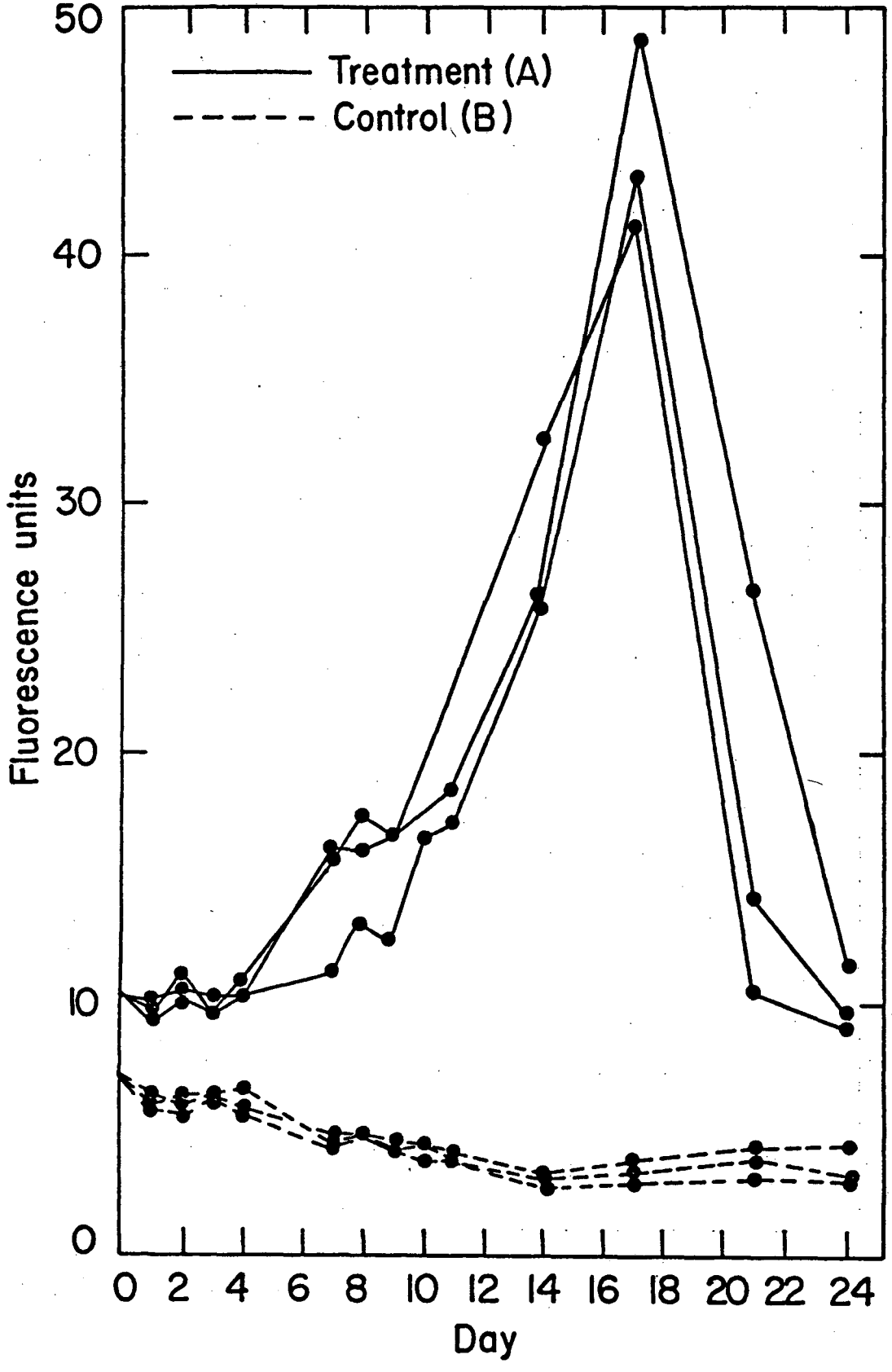
	R = 0	R = -P/2	R = -P
$Q_D - Q_A$	6.05	4.75	4.35
$Q_C - Q_A$	1.90	1.20	0.85
$Q_B - Q_A$	1.15	0.55	0.25
Q_A	2.70	1.75	1.27

TABLE 4



XBL 794-1353

FIG. 1



XBL 794-1354

FIG. 2

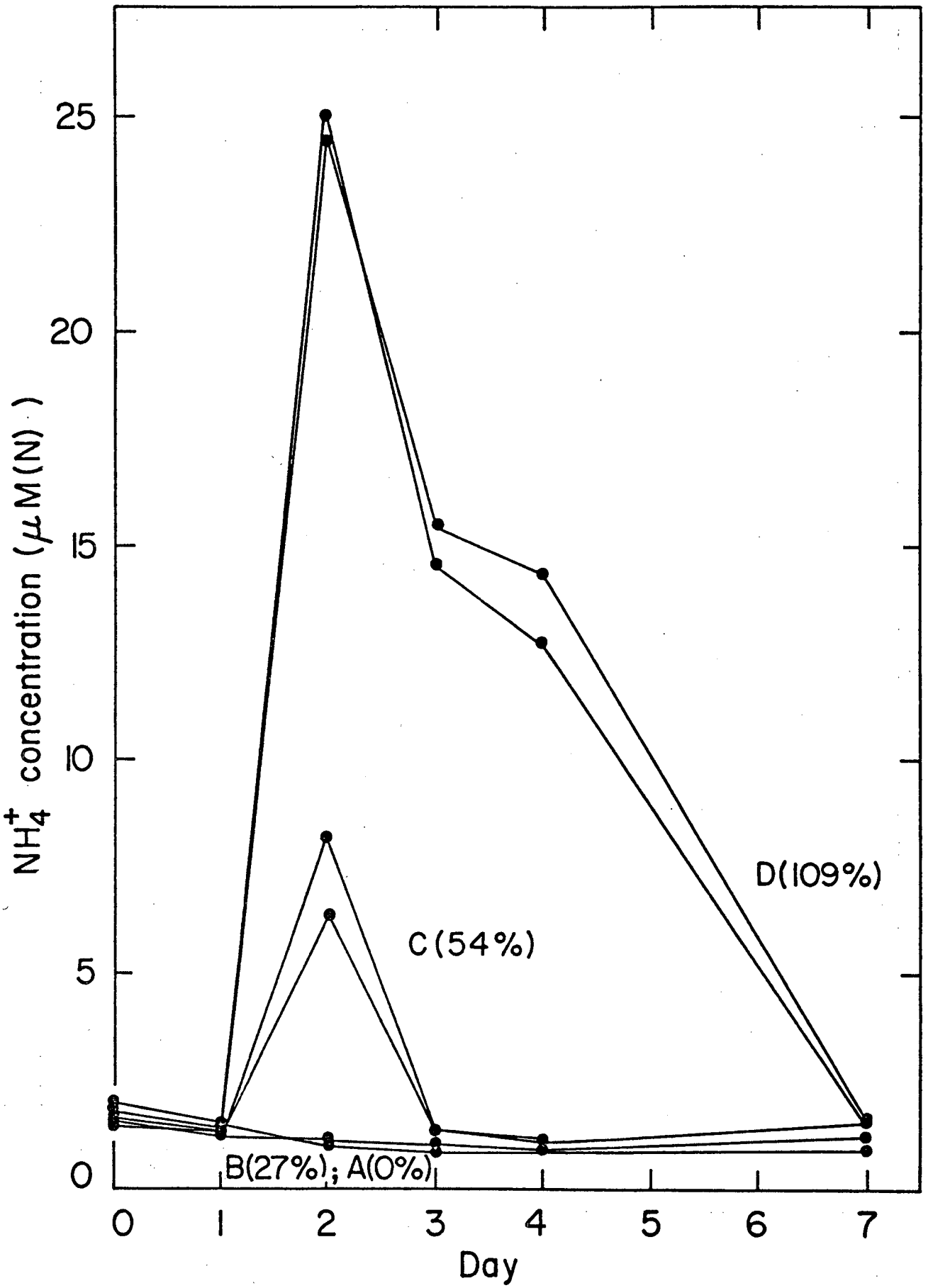


FIG. 3

794-1356

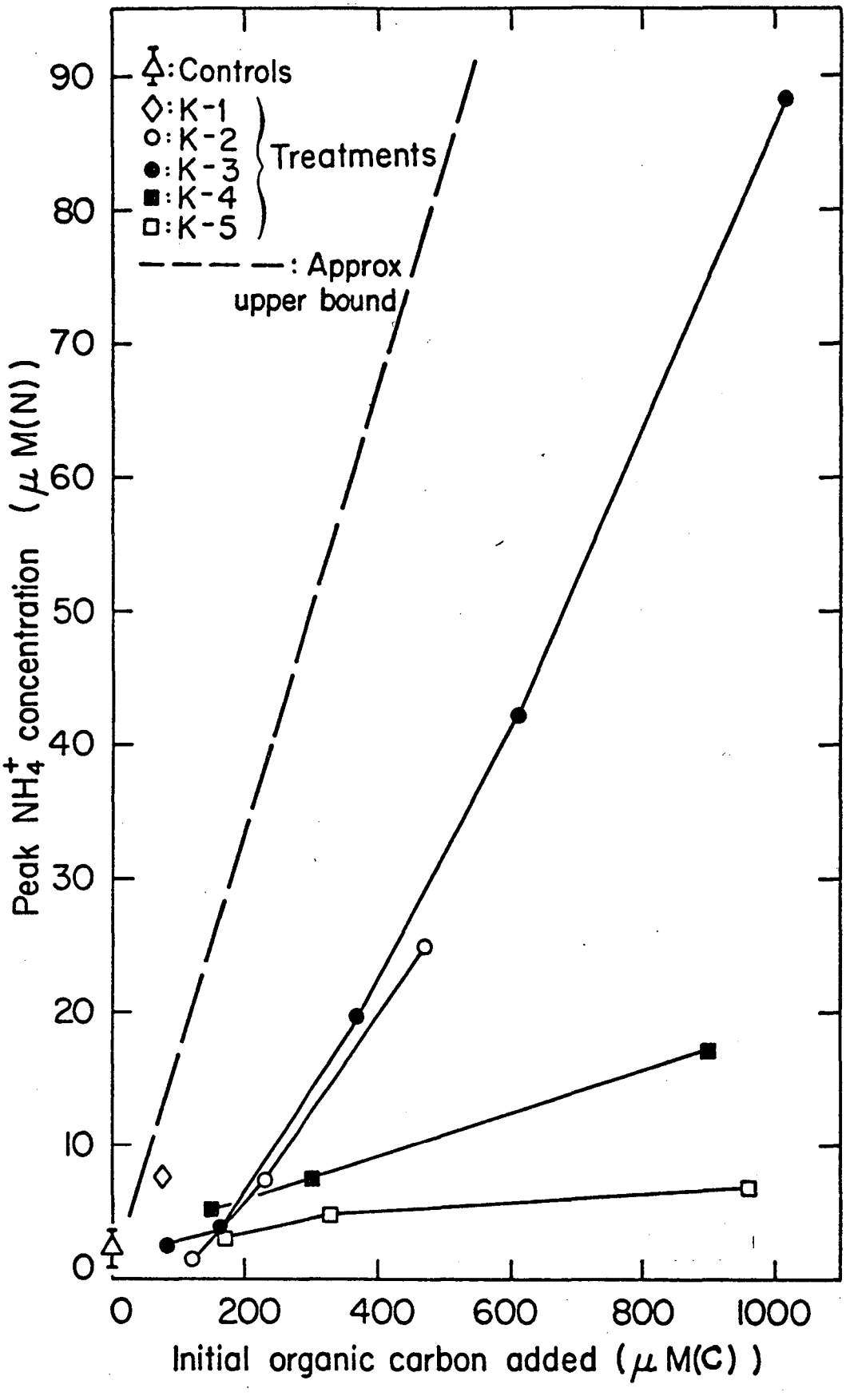
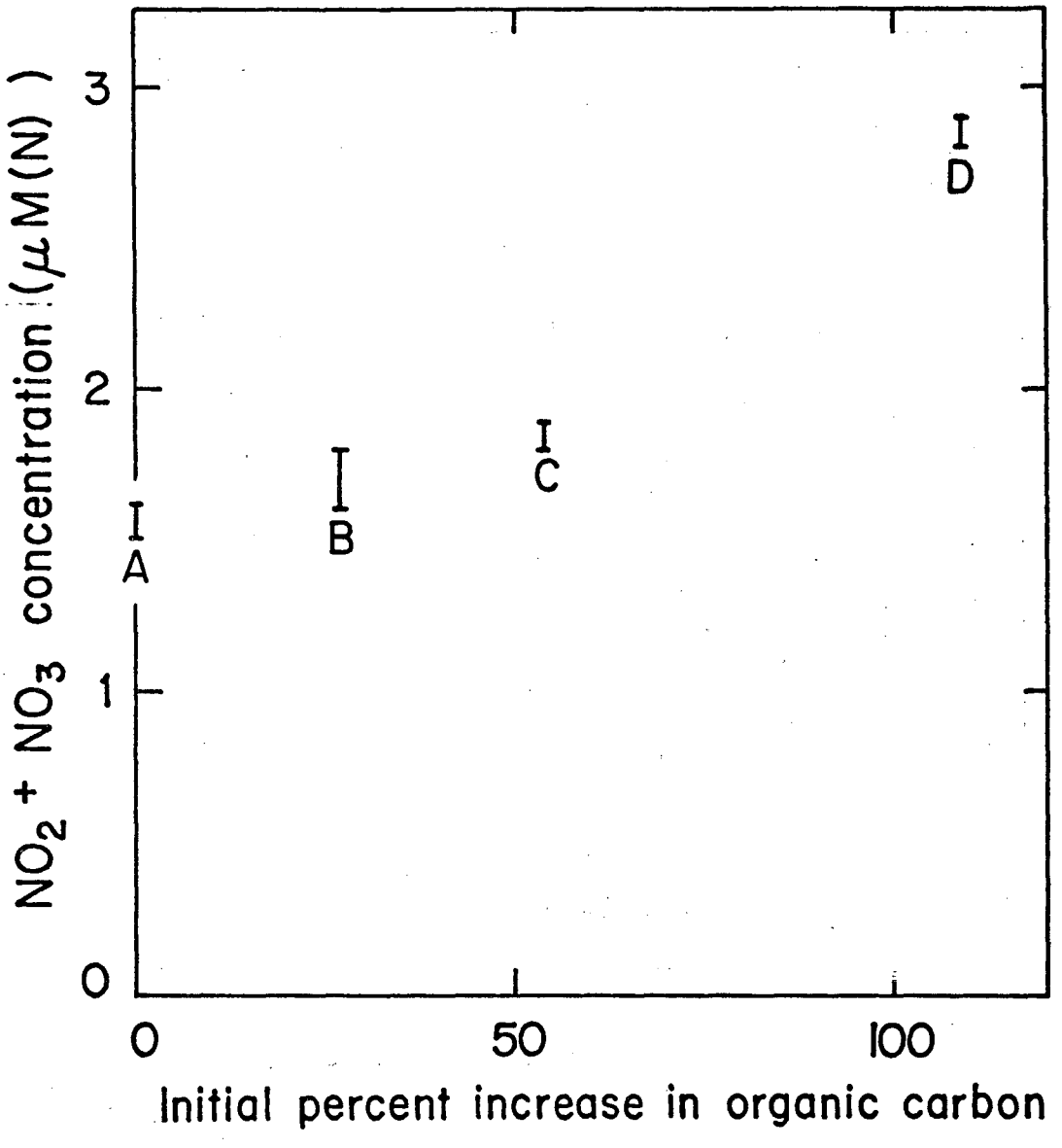


FIG. 4

XBL 795 - 1490



XBL 794-1359

FIG. 5

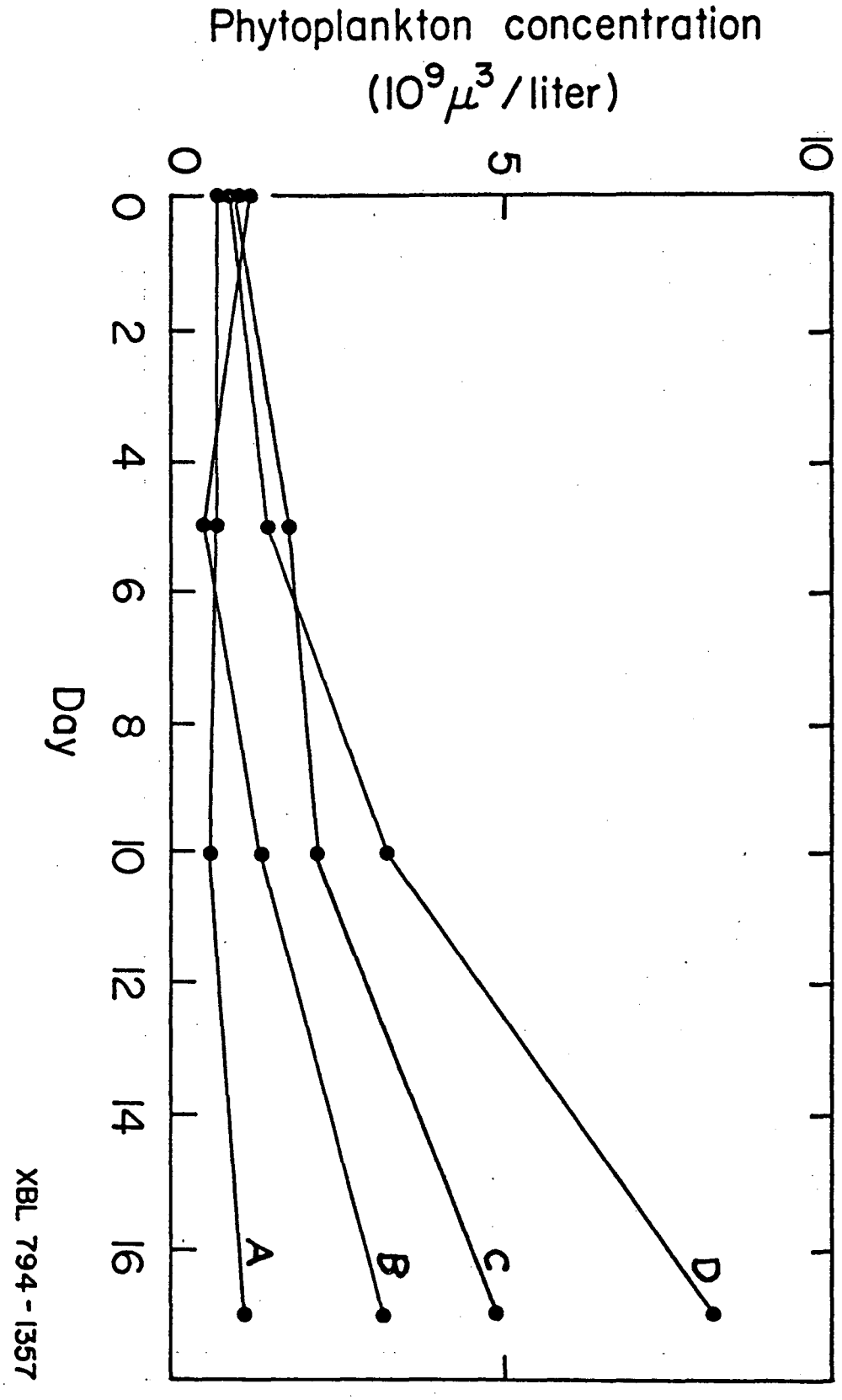

Phytoplankton concentration
(10⁹μ³/liter)
0
5
10
Day
0
2
4
6
8
10
12
14
16
A
B
C
D
XBL 794-1357

FIG. 6

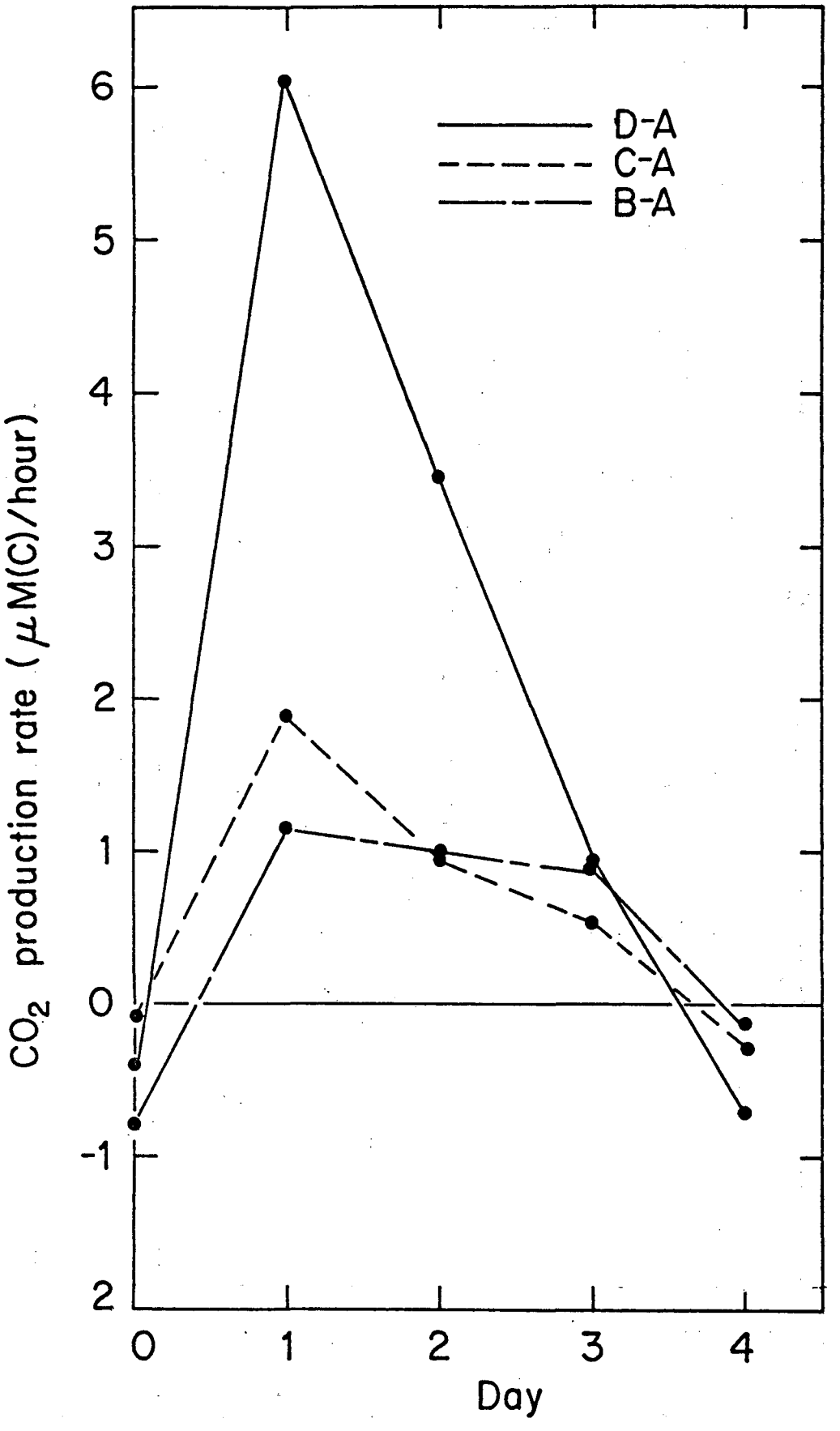

D-A
C-A
B-A
CO_2 production rate (μM(C)/hour)
6
5
4
3
2
1
0
-1
2
0
1
2
3
4
Day
XBL 795-1428

FIG. 7

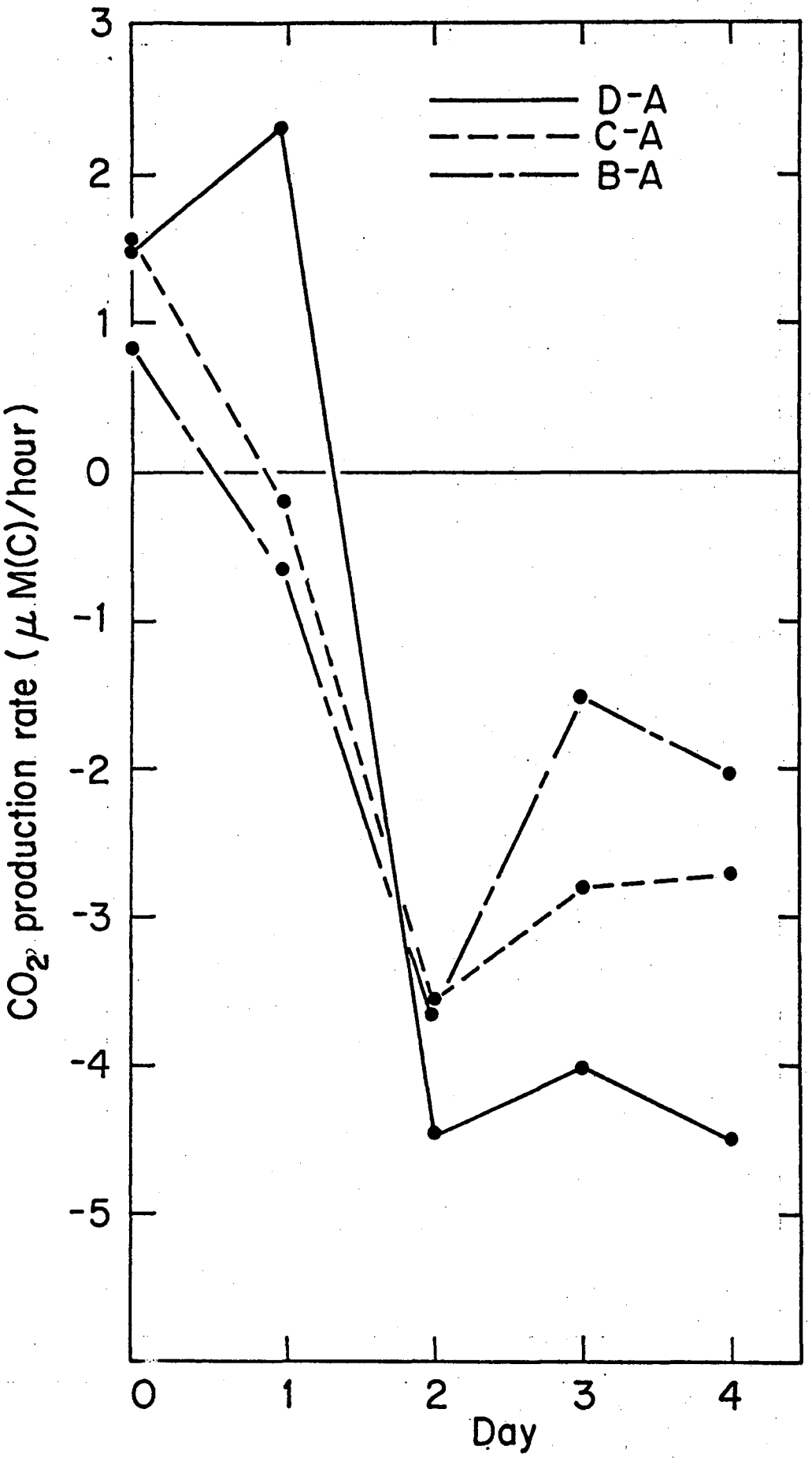


FIG. 8

XBL 795-1427

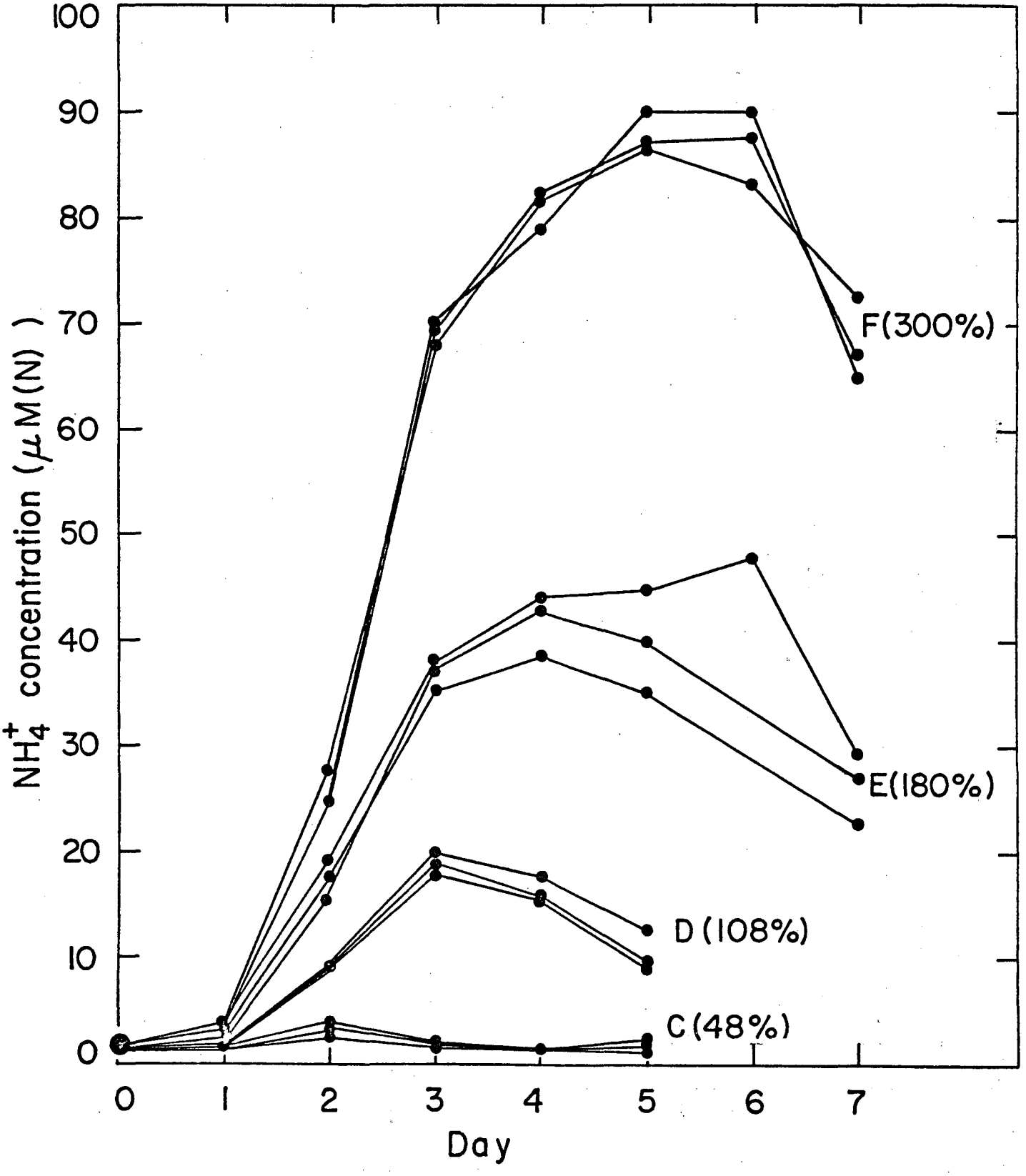


FIG. 9

XBL 794-1355

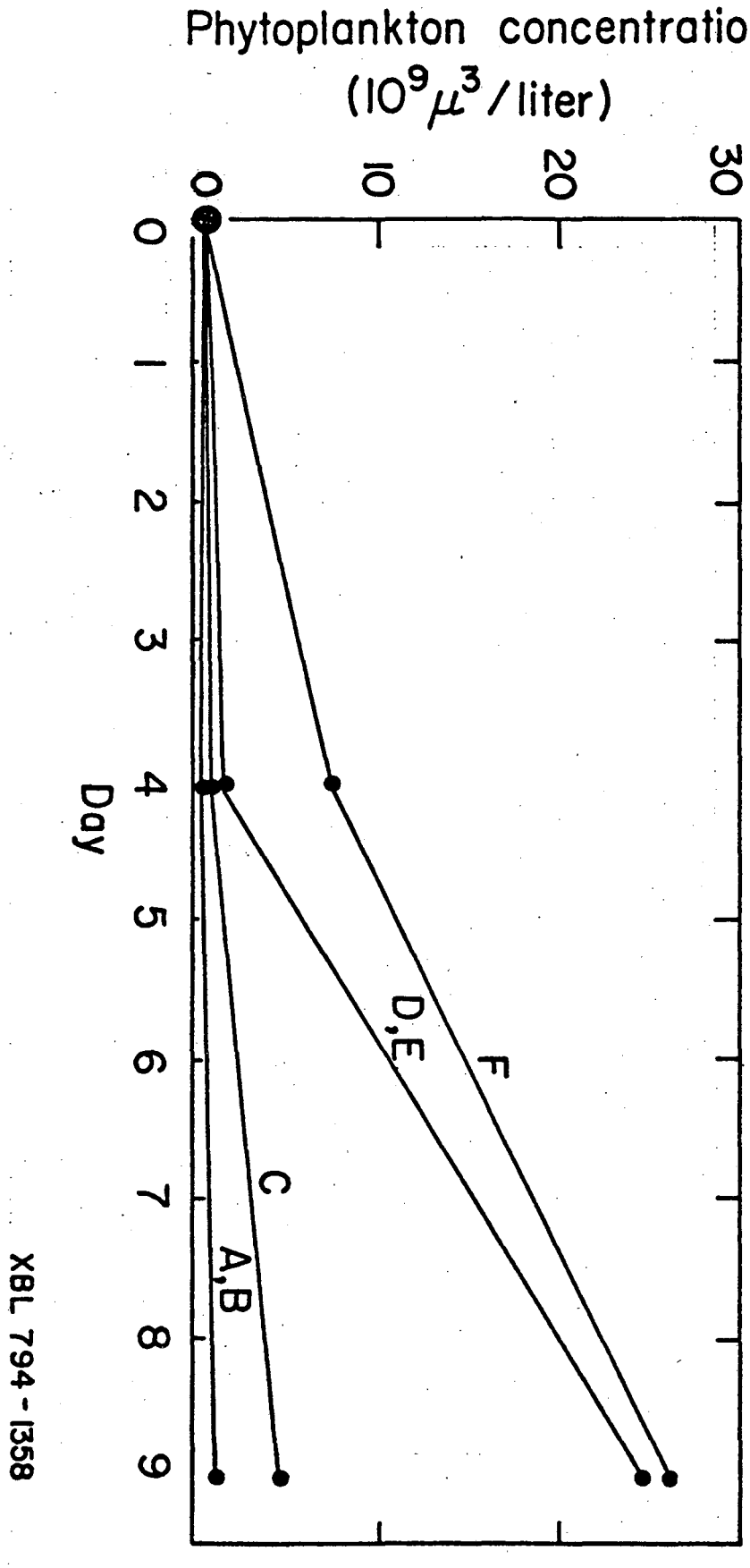

Phytoplankton concentration
(10⁹μ³/liter)
0
10
20
30
Day
0
1
2
3
4
5
6
7
8
9
A,B
C
D,E
F
XBL 794-1358

FIG. 10

FOOTNOTES

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