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Microcosms as Test Systems for the Ecological Effects of Toxic Substances An Appraisal with Cadmium

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MICROCOSMS AS TEST SYSTEMS FOR THE ECOLOGICAL EFFECTS OF TOXIC SUBSTANCES: AN APPRAISAL WITH CADMIUM

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16. ABSTRACT

A two-phase set of experiments was conducted to address some of the problems inherent in ecological screening of toxic substances in aquatic microcosms. Phase I was a 4 x 4 factorial experiment (four levels of cadmium versus four levels of nutrient enrichment) on the intereactive effects of cadmium and nutrients using static microcosms. Phase II was a 2 x 4 factorial experiment (continuous and pulsed cadmium inputs versus phosphorus limited and non-limited inputs) using flowthrough microcosms to study temporal aspects of system behavior in response to nutrient limitation and chronic versus acute cadmium perturbations. Generally, as cadmium concentration increased, parameters changed to indicate more system stress, except that high nutrient levels reduced somewhat the stress effect of cadmium.

Of the variables measured, community metabolism, community composition by trophic groups, and output/input ratios for NO_3-N, Mn, and Fe provided the best indicators of system response to cadmium. Nutrient enrichment and phosphorus limitation significantly influenced cadmium effects on most of the variables studied. Pulsed cadmium inputs early in succession significantly affected system response to cadmium pulses later in succession.

A bibliography of microcosm literature is included.

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FOREWORD

Environmental protection efforts are increasingly directed towards preventing adverse health and ecological effects associated with specific compounds of natural or human origin. As part of this Laboratory's research on the occurrence, movement, transformation, impact, and control of environmental contaminants, the Environmental Systems Branch studies complexes of environmental processes that control the transport, transformation, degradation, and impact of pollutants or other materials in soil and water and assesses environmental factors that affect water quality.

Concern about environmental exposure to toxic substances has increased the need for accurate information on the transport, fate, and effects of trace contaminants in natural waters. In developing this information, interest is currently being shown in the use of microcosms for toxicant screening and predictive model validation. This report evaluates microcosms as research tools for providing accurate and reliable data on ecological effects of a toxic substance.

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ABSTRACT

A two-phase set of experiments was conducted to address some of the problems inherent in ecological screening of toxic substances in aquatic microcosms, and to test two hypotheses concerning the response of ecosystems to perturbations. Phase I was a 4 X 4 factorial experiment (four levels of cadmium versus four levels of nutrient enrichment) with static microcosms designed to test the "subsidy-stress" hypothesis (Odum *et al.* 1979), and focused on the interactive effects of cadmiun and nutrients. Phase II was a 2 X 4 factorial experiment (continuous and pulsed cadmium inputs versus phosphorus limited and non-limited inputs) with flowthrough microcosms designed to test the "biomass increment" hypothesis (Vitousek 1977), and focused on temporal aspects of system behavior (especially out/input for several elements) in response to nutrient limitation and chronic versus acute cadmium perturbations.

Phase I results supported the subsidy-stress hypothesis with respect to cadmium inputs: Increasing cadmium concentrations (0, 1, 10, 100 ppb) caused a decrease in the P/R ratio, a decrease in grazing herbivores, increase in nighttime respiration and fungi, all indicators of system stress. Since net daytime production and nighttime respiration increased with nutrient enrichment, there was no nutrient stress effect even at the highest level. There was a significant interaction effect of cadmium and nutrients with high nutrient levels reducing somewhat, stress effect of cadmium. Phase II results generally supported the biomass increment hypothesis and suggested a retention pattern for continuous, low concentration cadmium inputs similar to that of essential elements. Cadmium may have accumulated to a toxic threshold in some of the microcosms. Pulsed, high concentration cadmium inputs had significant effects on system behavior, depending on timing of inputs.

Conclusions relevant to toxicity screening in microcosms are: 1) Of the variables measured, community metabolism, community composition by trophic groups, and output/input ratios for NO_3-N, Mn and Fe, provided the best indicators of system response to cadmium. 2) Nutrient enrichment and phosphorous limitation significantly influenced cadmium effects on most of the variables studied. 3) Pulsed cadmium inputs early in succession significantly affected system response to cadmium pulses later in succession.

Recommendation: For screening a suspected toxic substance, we recommend a hierarchy of microcosm experiments including: 1) static microcosms (with and without sediments), 2) flowthrough microcosms (with and without sediments), and 3) microcosm subsamples from specific natural ecosystems. Each step results in increased information about effects of a toxicant and each step more closely approximates natural ecosystems.

A bibliography of microcosm literature is presented at the end of the report.

This report was submitted in fulfillment of Grant No. R805860010 by the University of Gerogia under the sponsorship of the U.S. Environmental Protection Agency. The report covers the period 22 May 1978 to 31 September 1980, and work was completed as of 30 September 1980.

CONTENTS

FIGURES

TABLES

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SECTION 1

INTRODUCTION

The release of toxic substances into the environment has become a serious problem, especially in industrialized nations. Toxic substances amount to over 43,000 different compounds totaling 51 million tons annually in the U.S. according to a report issued by the Council on Environmental Quality (1979). These chemicals enter the environment from all phases of industrial and commercial activity, including extraction, production, storage, transportation, utilization and disposal. The "once-through" nature of the production-consumption process with little waste removal at source imposes a heavy burden on natural systems, which in the past have been called upon to absorb and assimilate the wastes of civilization. As a result, many compounds remain in the environment for long periods of time increasing the chances for exposure to humans and other components of the biosphere. The human and ecological effects of many of these compounds are unknown or have been discovered tragically through accidental contamination.

In accordance with the Toxic Substances Control Act of 1976 (TSCA), the U.S. Environmental Protection Agency is developing testing standards for evaluating potential hazards of chemicals before they are manufactured and released into the environment. In 1979 methods were proposed for human health-effects testing (oncogenicity, acute and subchronic toxicity, and reproductive teratogenic and metabolic effects); standards for evaluating ecological effects and environmental fate and transport have not yet been developed (Council on Environmental Quality

1979), but interest is currently being shown in the use of microcosms for toxicant screening and predictive model validation (Haque et al. 1980).

The use of microcosms for these purposes is somewhat controversial due to the uncertainty involved in extrapolating results to natural conditions. However, when considered as generalized models of ecological processes, small scale microcosms might provide a means for evaluating gross effects of toxic substances on ecosystems because such microcosms do mimic certain properties of ecosystems. For example, a number of studies have demonstrated similarities between temporal processes in natural systems and microcosms, including species succession (Gorden et al. 1969, Kurihara 1978), biomass accumulation (Wilhm and Long 1969, Odum 1971), net production and community respiration (Beyers 1962, Odum 1971), and radioisotope uptake and distribution (Whittaker 1961, Leffler 1977a). In addition, similar responses have been suggested in natural and microcosm systems to various perturbations, including radiation (Ferens and Beyers 1972), temperature (Leffler 1978), heavy metals (Asmus et al. 1978, Giesy et al. 1979), arsenic (Giddings and Eddlemon 1978), organic toxicants (Bryfogle and McDiffett 1979, Asmus et al. 1979), and nutrient enrichment (Wilhm and Long 1969, Fraleigh 1971). Thus, while quantitative extrapolation of microcosm results is not currently possible (but see Shirazi 1979), qualitative behavior of microcosms under controlled laboratory conditions may provide a preliminary basis for evaluating the ecological effects of toxic substances.

The development of standardized testing procedures will require answers to several important questions, including the following:

1) Which ecosystem properties are most sensitive or best reflect ecosystem response to toxicant perturbations?

2) What influence will other environmental variables (e.g., pH, nutrient enrichment, light intensity, etc.) have on ecological effects of a toxic substance?

3) Will ecosystem response be a function of the timing or frequency of toxicant inputs with respect to stages of ecosystem development?

4) What degree of realism (biotic and abiotic complexity) should be incorporated into microcosms for use in toxicity screening?

In an effort to address these questions and to further evaluate the potential utility of microcosms as ecological screening tools, we have conducted a series of experiments in which aquatic laboratory microcosms were exposed to a toxic substance. Because most of these questions are important, not only for screening protocol development but for ecosystem analysis in general, we have designed the experiments to test two hypotheses which have been developed to explain ecosystem behavior in response to stress (toxic substances being a specific form of stress). The experiments were conducted in two phases, each addressing a different hypothesis.

PHASE I

Odum et al. (1979) have suggested that ecosystems respond to environmental perturbations in a "subsidy-stress" fashion (Fig. 1). At low to moderate levels of intensity system inputs often act to subsidize or increase overall system function (e.g., the effects of nutrient enrichment or increase in temperature on productivity). Conversely, high levels of the same input can stress or decrease system function or result in development of an entirely different system (replacement).

The overall pattern is a unimodal, bell-shaped curve of system response along a gradient of increasing perturbation intensity. It also is hypothesized that relative variance of system response increases monotonically along the perturbation gradient. The response of system function to a toxic or lethal input is hypothesized to be a stress at all levels of input. Complicating these general response patterns are the influences of environmental and developmental gradients, such that system response to a given level of perturbation might vary with environmental conditions or successional stages. These interactive effects are especially important considerations for toxicity screening, since test results will be unavoidably biased by standard testing conditions. An alternative to single factor experiments (i.e., varying levels only of a toxicant) might be a multifactor or factorial experimental design which would allow for consideration of the interaction of several factors simultaneously.

Phase I of our experiments was designed to test the subsidy-stress hypothesis and to evaluate the influence of an environmental variable (nutrient enrichment) on aquatic microcosm response to a toxic substance (cadmium). The experiment was arranged in a 4 X 4 factorial design with increasing levels of nutrient enrichment superimposed on increasing cadmium levels. Of particular interest were the interactive effects of nutrients and cadmium on several system level variables.

PHASE II

A number of ecosystem studies have suggested that nutrient output/input ratios are sensitive system level measures of ecosystem

behavior and stress response (e.g., Woodwell and Whittaker 1968, Bormann et al. 1974, Jordan and Kline 1972, Rykiel 1977). These studies indicate that the loss of essential elements from ecosystems often increases significantly after disturbance. Vitousek and Reiners (1975) and Vitousek (1977) have summarized information from the literature into a set of hypothesized patterns of output/input behavior for essential and non-essential elements (Fig. 2). This is called the "biomass increment" hypothesis, since it suggests that nutrient output is an inverse function of the rate of biomass production within an ecosystem. Briefly, the hypothesis is as follows for an essential nutrient: Prior to biotic colonization of an area nutrient outputs are equal to inputs (barring abiotic uptake or loss). As biota become established and ecosystem development proceeds, nutrient output becomes less than inputs due to biotic uptake and storage in growing tissues. At the time of peak net ecosystem productivity the ratio of nutrient output/input is at a minimum, thereafter gradually increasing to unity as net productivity approaches zero at ecosystem maturity (steady state). A pulsed perturbation to the ecosystem (i.e., one time "destructive event") results in an increase in nutrient output/input followed by secondary succession and an abbreviated repeat of the initial patterns of productivity and nutrient uptake. For non-essential elements output/input remains near unity throughout the entire sequence of events; for limiting quantities of essential elements deflection of the output/input curve is related to the degree of limitation.

Efforts to empirically evaluate these patterns in natural ecosystems have not been conclusive (e.g., Haines 1978, Martin 1979,

Johnson and Edwards 1979) probably due to long successional time scales, indistinct ecosystem boundaries and potentially large sampling errors. Laboratory microcosms provide a partial solution to these problems and a potential means for evaluating nominal and stressed ecosystem nutrient flux patterns. For example, Confer (1972) found that phosphorus output from continuous flow aquatic microcosms decreased (relative to input) during early succession but increased to approximately equal input after prolonged operation. The introduction of snails and ostracods after two months of succession resulted in a significant increase in phosphorus output. Evans (1977) showed that elevated phosphorus inputs into flowthrough marine reef-flat microcosms resulted in increased ammonia-nitrogen uptake, whereas elevated ammonia-nitrogen inputs caused increased output of phosphorus, suggesting that ammonia is toxic to reef-flat communities.

Studies in terrestrial microcosms have shown that systems respond to heavy metal perturbations with increased outputs of essential elements (Asmus et al. 1978, Van Voris et al. 1980). However, Giesy et al. (1979) found no significant changes in nitrate, phosphate and sulfate outputs from stream channel microcosms exposed to cadmium; they suggested that future studies include measures of ammonia and potassium dynamics as possible indicators of heavy metal stress in microcosms.

In addition to the input-output dynamics of essential elements, the temporal patterns of uptake and release of toxic elements by ecosystems is an important consideration for toxicity screening in microcosms and for ecosystem analysis in general. Little is known of the long term input-output behavior of toxic elements. Henderson (1975) suggested

that ecosystems must have a finite capacity to accumulate toxic elements and as that capacity is approached, increasingly greater proportions of input should appear in system outputs. He proposed that temporal patterns "should fall somewhere between the curves for non-essential, not accumulated, and limiting elements" (Fig. 2). If this is true, then the potential for an ecosystem to become a source of (rather than a sink for) toxic elements increases as the system approaches maturity. Further, if the accumulation capacity could be estimated a priori, then this potential might be predictable.

Phase II of our experiments was designed to test Vitousek's (1977) and Henderson's (1975) hypotheses and to evaluate the utility of output/input ratios of several elements as indicators of microcosm response to toxic element (cadmium) perturbations. Several other factors were incorporated into the experiment to determine: 1) the influence of pulsed versus continuous toxicant inputs on system response, 2) the effects of toxicant exposure early in succession on system response to the same toxicant applied later in succession (i.e., the influence of system "history" on stress response), and 3) the influence of nutrient limitation on system response to toxicant exposure. The experiment was arranged in a 2 X 4 factorial design with phosphorus-limited (N:P = 100) and non-limited (N:P = 10) input regimes superimposed on four modes of cadmium input (zero input, continuous input, cadmium pulses early and late in succession, and a cadmium pulse late in succession).

In addition to the objectives discussed above, both experimental phases were coordinated to provide a comparison between the responses of static and flow-through microcosms to a toxic substance. To accomplish

this, both experiments incorporated the same inoculum, microcosm containers and laboratory conditions, and most of the same response variables. Due to differences in experimental design, however, rigorous statistical comparisons between Phase I and II were not possible.

SECTION 2

MATERIALS AND METHODS

GENERAL

Experimental Design

Phase I and Phase II both consisted of factorial experimental designs with various combinations of nutrient and cadmium treatments, as shown in Figures 3 and 4. Phase I employed three replicates per treatment combination (48 microcosms), all arranged in a completely randomized design in the growth chamber. Supporting tables were rotated every four weeks to minimize variability due to possible gradients of temperature, light, etc. Phase II employed four replicates per treatment combination (32 microcosms) arranged in two randomized complete blocks (two replicates of each treatment combination in each block) in the growth chamber. These systems remained in place throughout the experiment because of attached input and output tubing. No significant differences in light intensity or water temperature were detected between the two blocks.

Experimental Containers

Polypropylene animal containers 26cm X 20cm X 15cm (with a seven-liter capacity) were chosen for both experiments based on National Bureau of Standards data (Struempler 1973) which indicate that this material does not adsorb heavy metals, and on a preliminary adsorption experiment which indicated no significant retention of the elements of interest. Containers were filled to six liters with nutrient solution.

Experimental Conditions

A 2.8m X 2.8m animal room at the Institute of Ecology, University of Georgia, was modified for use with the installation of a bank of 40-watt Gro & Show lights with an average intensity of 79-86 μeinsteins cm^{-2} sec^{-1} at the water surface, and a twenty-four hour timer set for a twelve hour light - twelve hour dark cycle. Temperature and humidity were under thermostatic control through the building system; air temperature varied between 19°C and 30°C. Water temperature varied from 19°C to 21°C (Phase I) and 19°C to 25°C (Phase II).

Nutrient Medium

The medium used in Phase I was a modified Taub and Dollar (1964) #36 with the nutrient gradient (Appendix A) spanning a wide range of concentrations intended to approximate levels found in natural systems, ranging from oligotrophic to hypereutrophic (Wetzel 1975). Each level had a nitrogen to phosphorus ratio of ten (N:P = 10). Phase II used two levels of modified Taub #36 medium (Appendix A), one with a nitrogen to phosphorus ratio of ten (N:P = 10) and the other with N:P = 100 to impose phosphorus limitation. This level of Taub #36 was chosen on the basis of results from Phase I.

Toxic Substance

Cadmium was selected as the toxic chemical for the following reasons:

1) Cadmium is on the EPA's list of toxic substances of immediate concern.

2) Cadmium is toxic at some concentration to all organisms (Bowen 1966).

3) Cadmium possesses physical properties which result in a certain degree of persistence in aquatic systems.

4) Cadmium concentrations can easily be measured with available instrumentation.

Cadmium was added in the form of cadmium chloride because of its solubility even at high concentrations (Giesy et al. 1977). The range of cadmium concentrations in Phase I (0, 1, 10 and 100 ppb Cd) included one level below and one level above that of the EPA (1971) recommended allowable cadmium concentration of 10 ppb in drinking water, and was chosen to cover the wide range of toxicity levels found for different aquatic organisms (Warnick and Bell 1969, Patrick et al. 1968, Stapleton 1968).

In Phase II, 10 ppb cadmium was chosen for the continuous input based on the drinking water standard and on a preliminary study which indicated that higher concentrations (for example, 100 ppb) severely depressed system metabolism after only a few weeks of continuous input. Pulsed inputs were pipetted into appropriate systems to achieve total concentrations of 100 ppb (day 28), 500 ppb (day 64), 750 ppb (day 100) and 750 ppb (day 190).

Inoculum

Inoculation of both phases was 50 ml from stock microcosms originally derived from a natural pond, and self-maintaining in the laboratory. Cross inoculation among replicates was done during the

first week of each experiment to reduce initial variability and, thereafter periodic reinoculation from laboratory stock systems was conducted to provide a continuous input of genetic material. The stocks contained bacteria, fungi, blue-green algae, green algae, protozoa, nematodes, annelids, rotifers, ostracods, cladocerans, and copepods.

Community Metabolism

Metabolic activity in both experimental phases was assessed through net daytime production and nighttime community respiration based on diel changes of dissolved oxygen concentrations, as measured by the three-point oxygen method of McConnell (1962). This consisted of a dissolved oxygen reading taken before the lights went on, a second reading just before the lights went out and a third reading the next morning before the lights went on. All measurements were made with a YSI model 54 A oxygen meter equipped with a self-stirring probe. Net daytime production (P_D) is the difference between the first and second reading, while nighttime community respiration (R_N) is the difference between the second and third reading. Gross production is the sum of P_D and R_N and net community production the difference between P_D and R_N. Results are presented in terms of net daytime production and nighttime community respiration in mg O_2/l/12 hr.

Corrections for oxygen diffusion were calculated several times according to McConnell (1962). It was found that diffusion over any given 12-hour period was generally less than 6% of corresponding P_D and R_N values. Therefore, diffusion corrections were not applied to the data. This probably resulted in underestimation of both P_D and R_N, since dissolved oxygen concentrations were slightly above saturation during

the day and below saturation at night.

Statistical Analyses

All data analyses were conducted on an IBM 360 computer using methods from the Statistical Analysis System package (Barr et al. 1979). Analyses included Means, GLM, and ANOVA (Duncan's Multiple Range option). The Plot Procedure was used to plot means and 95% confidence bars against time for most of the variables; overlapping confidence intervals indicated no significant difference between two values, while non-overlapping intervals indicated significant differences at $p = 0.05$. Results of statistical analyses are presented in Appendix C.

PHASE I

The aquatic systems used in Phase I were static (non-flowing) systems and ran for 119 days in 1978. Cadmium and nutrient solution were applied at the time of the first inoculation (day zero).

Sample Collection and Analysis

In addition to net daytime production and nighttime respiration, measurements were made of: (1) total biomass (all particulate matter), (2) plant pigments (chlorophyll a and phaeo-pigments), and (3) taxonomic composition. All samples were collected as aliquots of suspended matter following thorough mixing of the microcosms (very little attached growth occurred). Biomass estimates were based on the change in filter weight after a 20-ml sample of the microcosm was filtered through a glass fiber filter. Presample and postsample weight was determined after drying in

an oven (60°C) for 24 hours. Chlorophyll a and phaeo-pigment concentrations were measured as 663 nm wavelength absorbance of acetone-extracted solutions of filtered matter, according to Strickland and Parsons (1968). Samples for biomass, plant pigment analysis, and production and respiration were taken twice weekly.

Taxonomic composition was quantified when qualitative examinations of samples indicated a major shift in community structure. The fungal population density was estimated by plating two dilutions (10^0 and 10^{-1}) of each microcosm (2 replicates each) onto total fungal media (Shokes 1978) and counting the number of colonies after 60 hours. Bacterial population density was measured by plating three dilutions (10^{-3}, 10^{-4}, and 10^{-5}) of each microcosm (2 replicates each) onto nutrient agar and counting the number of colonies after 48 hours. The number of crustaceans was determined by counting the number of cladocerans, ostracods, and copepods in a preserved 18-ml sample from each microcosm.

PHASE II

The aquatic systems in Phase II were flowthrough systems and ran for 286 days, from April 1979 to January 1980.

Nutrient Flowthrough

Nutrient solution was added in a discontinuous flow: one liter of solution was dripped in at a rate of one liter/2 hr every two days, resulting in a turnover time of twelve days. The solution was poured into a one-liter overhead beaker for gravity feed through tygon tubing, with flows regulated by a screw clamp. Output from the system was

defined as the solution overflowing from the opposite end of the tank through another tubing into covered collection beakers. Diel variations in nutrient concentrations were not measured but output samples were always collected about three hours after dawn for consistency. Polyethylene baffles were installed over the output ports after it was noticed in preliminary experiments that large and highly variable amounts of surface growth washed out of the systems with the output. The baffles probably resulted in greater biomass accumulation than would otherwise have occurred, and may have lengthened the time required for the microcosms to achieve steady state conditions.

Sample Collection

Sampling was initially done every six days, with the series of dissolved oxygen readings taken before each sampling. The sampling schedule was cut back to every eight days when trends in the data indicated that such an intensive sampling regime was unnecessary in order to see system response.

Prior to sampling, all microcosms were topped up to 6 l with deionized water to correct for evaporative and sample withdrawal losses. After suspended material had settled, samples of standing water and biota were collected by scraping a 1-cm wide strip of water surface, side and bottom material (2% of total surface area), and drawing it with suction into a 125-ml Erlenmeyer flask. Flasks were then topped up to 75 ml with water from the water column and stored on ice until analyzed. This procedure was necessary because of considerable quantities of attached growth which occurred in the Phase II microcosms. Samples of input and

output solutions were collected in 20-ml polypropylene scintillation vials, acidified with one drop of concentrated HCl, and refrigerated until analyzed.

Sample Analyses

Standing stock samples were divided into three 15-ml subsamples. The first 15 ml were filtered through a prewashed and preweighed 0.45 μm membrane filter, which was then dried at 60°C to a constant weight and used to determine dry weight biomass.

The second 15-ml subsample was filtered through a glass fiber filter for pigment analysis. The filter was ground by hand in 10 ml of 90% acetone, mixed on a vortex mixer, and extracted overnight in a cold room. After centrifugation at 2000 rpm for 20 minutes, the absorbance of the extract was read on a spectrophotometer at 663 and 750 nm before and after acidification (Strickland and Parsons 1968).

The third 15-ml subsample was preserved with Lugol's solution and stored for microscopic examination. Microscopic counts were made in Sedgwick-Rafter counting cells on an inverted microscope according to standard methods (American Public Health Association 1976). Crustaceans were counted on the biomass filters with a dissecting microscope.

Input and output solutions were analyzed for NH_3-N and NO_3-N on a Technicon AutoAnalyzer according to standard methodologies (American Public Health Association 1976). Samples for total phosphorus (TP) and total nitrogen (TN) were digested with an alkaline potassium persulfate solution according to D'Elia et al. (1977) with minor modifications: 4-ml samples were used due to sample size restriction, and no further

dilutions or additions were made after digestion. These samples were analyzed according to standard Cd reduction methods for NO_3-N and the ascorbic acid method for orthophosphate-phosphorus (PO_4-P). Results are reported in mg NO_3-N/1 and mg PO_4-P/1.

Cation analyses were run on a Jarrell-Ash Plasma Emission Spectrograph (Model No. 750). Standard dilutions of the elements of interest were run on the instrument to determine the lower detection limits and account for the matrix effect in the nutrient medium (Appendix B).

Cadmium analyses were conducted on a Perkin-Elmer Model 306 atomic absorption spectrophotometer equipped with a graphite furnace. Analyses were run according to procedures recommended in the instrument manual.

SECTION 3

RESULTS

PHASE I

Biomass

Biomass (filterable particulate matter) accumulation over the experimental period showed a significant increase in response to nutrient enrichment ($p = 0.0001$). Values averaged over the entire experiment indicated that only nutrient level 4 was significantly different from the others, increasing sharply over level 3 (Fig. 5b). Successional patterns of biomass accumulation reflect this effect. By day 60, biomass began to increase rapidly at high nutrient levels (Fig. 7), but less rapidly at the lower levels (Fig. 6). All appeared to approach a roughly defined upper limit by the end of the experiment (day 119).

Cadmium, introduced as a single dose at the beginning of the experiment, appeared to cause a slight increase in biomass accumulation (Fig. 5a), but the effect was not significant. There was no nutrient-cadmium interaction effect on biomass.

Chlorophyll a and Phaeo-pigments

The chlorophyll a response to nutrient enrichment was similar to that of biomass; a significant ($p = 0.0001$) increase occurred only at nutrient level 4 (Fig. 8). In the highly enriched systems,

chlorophyll a reached maximum values between days 60 and 90, and then decreased to lower stable values by the end of the experiment (Fig. 10). In the nutrient poor systems the pattern was similar but less distinct (Fig. 9).

Cadmium at 100 ppb resulted in a significant ($p = 0.05$) increase in chlorophyll a over systems with no cadmium (Fig. 8). One and 10 ppb Cd had no effect. A significant ($p = 0.01$) nutrient-cadmium interaction effect was indicated by the analysis of variance.

Phaeo-pigment concentrations showed a significant increase due to nutrient enrichment, but no cadmium or nutrient-cadmium interaction effect. Phaeo-pigments were present in low concentrations for most of the experiment but increased toward the end of the experiment in most of the systems (Figs. 11 and 12).

Community Metabolism

Mean net daytime production was significantly influenced by nutrient enrichment ($p = 0.001$). At nutrient level 4, net production was significantly elevated over the other nutrient levels (Fig. 13a). Cadmium had no significant effect on net daytime production (Fig. 14a). A significant ($p = 0.0001$) nutrient-cadmium interaction effect occurred for net daytime production.

Nighttime respiration showed a significant ($p = 0.001$) increase in response to nutrient enrichment; again, this effect was significant only at nutrient level 4 (Fig. 13b). Cadmium treatments resulted in a significant ($p = 0.05$) increase in nighttime respiration (Fig. 14b). The interaction effect of nutrients and cadmium also was highly significant

($p = 0.0001$).

Temporal patterns of net daytime production and nighttime respiration are shown for representative microcosms in Figures 15 and 16. Both reached early peak values around day 30, remained high at nutrient level 4, and gradually declined at lower nutrient levels.

The P/R ratio showed no response to nutrient enrichment due to the nearly identical responses of both production and respiration (Fig. 13c). Cadmium caused a significant ($p = 0.05$) decrease in P/R due to the significant increase in respiration (Fig. 14c). No interaction effect of nutrients and cadmium was observed for P/R.

Population Densities

Fungal, bacterial and crustacean population abundances all showed positive correlations ($p = 0.01$) with nutrient enrichment (Figs. 17, 18 and 19). Cadmium also significantly influenced population densities. Fungal abundance showed a positive correlation ($p = 0.05$) with cadmium (Fig. 17), while bacterial abundance revealed no cadmium effect (Fig. 18). Crustacean abundance abundance was negatively correlated ($p = 0.05$) with cadmium (Fig. 19); grand means of crustacean density at 10 and 100 ppb Cd were significantly lower than means at 0 and 1 ppb Cd.

PHASE II

Biomass

Time averaged biomass (filterable particulate matter) was significantly higher ($p = 0.0001$) in non-nutrient-limited (N:P = 10) micro-

cosms than in phosphorus-limited (N:P = 100) systems. Neither pulsed nor continuous cadmium inputs significantly influenced biomass accumulation, nor was there a significant nutrient-cadmium interaction. Temporal patterns of biomass accumulation are shown in Figures 20 and 21 for zero-cadmium controls under both nutrient regimes. The figures indicate relatively little accumulation in the N:P = 100 systems (Fig. 20), but steady accumulation up to about day 200 in the N:P = 10 systems (Fig. 21).

Chlorophyll a and Phaeo-pigments

Plant pigment concentrations were significantly greater ($p = 0.0001$) in the N:P = 10 systems than in the N:P = 100 systems and neither pigment showed a detectable response to cadmium, based on values averaged over the entire experiment. Chlorophyll a concentrations increased steadily up to about day 60 in the N:P = 100 systems (Fig. 22) and then declined to a relatively stable value by about day 130; phaeo-pigments followed a similar but less distinct pattern (Fig. 24). In the N:P = 10 microcosms, chlorophyll a values steadily increased to a stable value around day 150 (Fig. 23), while phaeo-pigment concentrations (Fig. 25) increased dramatically (but with high variance) around day 150, declining by the end of the experiment (day 286).

Community Metabolisms

Due to the strong interaction effect between nutrients and cadmium, the two treatments showed no significant main effects on net daytime production or nighttime respiration, according to our analysis of

variance. Zero-cadmium controls of both N:P = 10 and N:P = 100 treatments reached peak values around day 90 and then declined and oscillated within a reasonably well-defined operating range for the remainder of the experiment (Figs. 26a and 30a). Cadmium treatments did cause significant deviation, depending on nutrient levels and mode of cadmium input.

In the N:P = 10 systems, continuous 10 ppb Cd input had no significant effect on net daytime production (Fig. 31a). Pulses of Cd between days 28-100 caused a delay in peak net production to about day 150 (Fig. 32a). These pulses also lessened the immediate net production response to the Cd pulse on day 190, as compared to systems not receiving early Cd pulses (Fig. 33a). However, after a delay of about 30 days variance in net production increased markedly in the early and late Cd-pulsed systems (Fig. 32a). Microcosms receiving Cd only at day 190 (Fig. 33a) showed a significant decrease in net daytime production followed by a prompt (about 25 days) return to the former operating range.

In the N:P = 100 systems, continuous 10 ppb Cd input resulted in a dramatic increase in net production around day 110 in two of the four replicates. This is reflected by the extremely high variance in Figure 27. Since the responsive microcosms were in the same experimental block, the increased net production may be a result of some block effect which has not yet been identified. Cadmium pulses between day 28 and 100 resulted in a highly significant increase in net production around day 130 (Fig. 28a). The newly defined operating range was maintained until the day 190 Cd pulse which resulted in a decrease in net production followed by a prompt (about 25 days) rebound to the

former level. Phosphorus-limited systems receiving the Cd pulse only at day 190 (Fig. 29a) showed a time-delayed increase in net production followed by a gradual (about 50 days) return to the former operating range.

Patterns of nighttime respiration in response to both nutrient and cadmium treatments were practically identical to those described above for net daytime production (Figs. 26b-33b). Differences in magnitude were reflected in the production/respiration ratio (P/R). In the N:P = 100 systems P/R was significantly higher ($p = 0.0002$) than in the N:P = 10 systems and remained greater than 1.0 more of the time (Figs. 26c-33c). P/R showed no direct cadmium or nutrient-cadmium interaction effects.

Population Densities

Taxonomic data from Phase II were not analyzed statistically, but graphical examination of the data revealed interesting trends. Crustaceans (ostracods and copepods) were generally abundant in N:P = 10 microcosms (Figs. 34-37), but appeared in the N:P = 100 systems only in the two highly productive replicates receiving continuous 10 ppb Cd inputs (Fig. 38). In all cases crustacean populations did not become established until around day 130 or later.

Effects of cadmium are shown for N:P = 10 systems in Figures 35-37. Continuous 10 ppb Cd inputs resulted in a delay in initiation of population growth, wide oscillations in both ostracod and copepod numbers, and in lower total numbers of individuals (Fig. 35). Cadmium pulses between days 28 and 100 occurred before populations became established but

nevertheless caused a delay and oscillations in population growth (Fig. 36). The cadmium pulse at day 190 had marked effects on crustacean populations. In the previously pulsed systems (Fig. 36) copepod populations were destroyed just as they began to grow, while ostracod numbers oscillated and then finally began to grow by day 286. In microcosms not subject to earlier pulses of cadmium (Fig. 37), the pulse on day 190 brought about extinction of both populations after a few oscillations in numbers.

Other heterotrophic organisms were enumerated and their population numbers indicated responses to phosphorus limitation. Relative abundances of rotifers, nematodes, and Paramecium sp. all were distinctly greater in N:P = 10 than in N:P = 100 systems. Nematode and Paramecium sp. numbers showed no response to cadmium treatments, but decreases in rotifer numbers suggest responses to cadmium pulses, especially in the N:P = 100 systems (Figs. 39 and 40).

Autotroph population numbers showed no response to cadmium, but showed distinct differences in relative abundance as a result of phosphorus limitation. In general, following an early bloom of Chlamydomonas sp., N:P = 10 systems were dominated by thick surface, side wall and bottom mats of Ulothrix sp. followed in order of decreasing abundance by Chlorella sp., Chlamydomonas sp., Lepocinclis sp. and Ankistrodesmus sp. The N:P = 100 systems, also following an early bloom of Chlamydomonas sp., were dominated by Chlorococcum sp. followed by Chlorella sp., Chlamydomonas sp., Ankistrodesmus sp., Lepocinclis sp. and Ulothrix sp.; all occurred predominantly on the bottom and, to a lesser extent, on the sides of the containers. Blue-green algae were rarely observed in any

of the microcosms, probably because of the abundance of available nitrogen (Schindler 1977).

Chemical Element Dynamics

Concentrations of chemical elements and compounds were measured in inflowing and outflowing solutions of Phase II microcosms. For each chemical species, ratios of output/input concentrations were calculated and plotted against time. Values less than 1.0 indicate accumulation of the chemical within the system, while values greater than 1.0 indicate net loss from the system. Of the chemicals studied, boron, calcium, copper, magnesium, sodium, and zinc had values not significantly different from 1.0 ($p = 0.05$) throughout the experimental period. Total phosphorus (TP), total nitrogen (TN), NH_3-N, NO_3-N, manganese, iron and cadmium all fell significantly below 1.0 ($p = 0.05$) at some time during the experiment.

Nitrogen, especially NO_3-N, displayed the most interesting behavior in response to nutrient and cadmium treatments. In the N:P = 100 control microcosms (Fig. 41) there was little significant retention of nitrogen in any form, as compared with N:P = 10 controls (Fig. 45). Continuous 10 ppb Cd inputs had no significant effect on nitrogen retention in the N:P = 10 systems (Fig. 46), but resulted in significant uptake in the two highly productive replicates of the N:P = 100 systems (Fig. 42), again causing a considerable increase in variance. This increased variance is most apparent for NO_3-N and, to a lesser extent, for TN but is virtually undetectable for NH_3-N which differed little

from the controls.

Cadmium pulses between day 28 and 100 had little effect on nitrogen retention in the N:P = 10 microcosms (Fig. 47), but resulted in significant retention of NO_3-N after day 100 in the N:P = 100 systems (Fig. 43c). The cadmium pulse on day 190 resulted in a significant but transient increase in NO_3-N output in the latter systems (Fig. 43c) and an increase in variance in the former (Fig. 47c). Microcosms not receiving early cadmium pulses responded to the day 190 pulse with a significant increase in NO_3-N output in the N:P = 10 systems (Fig. 48c) and a significant decrease in NH_3-N output in the phosphorus limited systems (Fig. 44b). The apparent NO_3-N response in the latter (Fig. 44c) was not significantly different from the controls (Fig. 41c).

An analysis of variance of nitrogen outputs averaged over the entire experiment indicated a highly significant nutrient-cadmium interaction effect for TN ($p = 0.0001$), NH_3-N ($p = 0.005$), and NO_3-N ($p = 0.0001$). As a result, no significant main effects of cadmium were detected by the analysis. Averaging the data over time obliterated the temporal dynamics which indicated significant short term cadmium effects (Figs. 41-48).

The output/input ratio for total phosphorus (TP) was less responsive to nutrient and cadmium treatments than were the nitrogen ratios. In addition, TP showed much higher variability, especially in the N:P = 100 systems, since output concentrations were often near detection limits. Control microcosms with inputs of both N:P = 100 and N:P = 10 (Figs. 49a and 53a) showed initially rapid uptake of TP followed by a gradual approach to output/input not significantly

different from 1.0 around day 110. Phosphorus limited systems (Fig. 49a) then displayed roughly defined oscillations below and just equal to 1.0 for the remainder of the experiment. The ratio remained below 1.0 for most of the experimental period in the N:P = 10 systems (Fig. 53a). Retention of TP showed no detectable response to cadmium treatments in the N:P = 100 systems (Figs. 50a, 51a, and 52a). N:P = 10 systems displayed general trends in response to cadmium but few were clearly significant. Continuous 10 ppb Cd inputs resulted in greater overall TP retention (Fig. 54a) than was shown by the controls (Fig. 53a). Early cadmium pulses (Fig. 55a) appeared to cause an increase in TP output, while the pulse at day 190 resulted in a slight decrease in output in these, and in the systems not subjected to early cadmium pulses (Fig. 56a). In general, cadmium may have resulted in slightly greater TP retention but the effect was not significant at $p = 0.05$, according to an analysis of variance. Also, no nutrient-cadmium interaction effect was indicated.

Somewhat surprisingly, output/input ratios for manganese showed significant responses to cadmium treatments. Control microcosms under both nutrient regimes showed no accumulation of Mn (Figs. 49b and 53b). Continuous 10 ppb Cd inputs in the N:P = 100 systems (Fig. 50b) resulted in an increase in variance among replicates, beginning around day 100 (again, apparently due to some block effect). Continuous cadmium inputs had no measurable effect on Mn retention in the non-limited systems (Fig. 54b). Cadmium pulses between days 28 and 100 resulted in increased variance and significant Mn retention under both nutrient regimes (Figs. 51b and 55b). In the N:P = 10 systems the effect was

transient, followed by a brief net system loss of Mn around day 170 and then a slight gain, in response to the cadmium pulse on day 190. In the N:P = 100 systems (Fig. 51b) Mn continued to accumulate until the day 190 cadmium pulse which resulted in a gradual (about 40 days) increase in the output/input ratio to 1.0. N:P = 100 microcosms pulsed with cadmium only at day 190 showed no response with respect to Mn retention (Fig. 52b). Corresponding N:P = 10 systems (Fig. 56b) showed a considerable increase in variance but no significant gain or loss of Mn.

No detectable nutrient effect on iron output/input behavior was indicated (Figs. 49c-56c) but there was an apparently significant response to the cadmium pulse on day 100 in the N:P = 10 systems (Fig. 55c): After an initial period of accumulation similar to the control microcosms (Fig. 53c), the cadmium-pulsed systems continued to retain Fe until about day 150, followed by a brief period of net system loss. The cadmium pulse on day 190 (Fig. 55c) seems to have caused an increase in variance but little deviation from output/input = 1.0. Iron retention showed no measurable response to cadmium treatment in the N:P = 100 systems.

Output/input ratios were calculated for cadmium in the microcosms receiving continuous 10 ppb Cd inputs. Significant cadmium retention occurred in both the N:P = 100 and N:P = 10 systems (Figs. 57a and 57b), reaching greater total accumulation in the latter. Both displayed an inverse bell-shaped retention curve, approaching output/input = 1.0 toward the end of the experiment (day 286), but accumulation continued in the N:P = 10 systems (Fig. 57a). Cadmium output/input ratios were not

calculated for systems receiving cadmium pulses, but in each case cadmium concentrations in the output followed an exponential decay curve over time, related to the system turnover time of 12 days.

SECTION 4

DISCUSSION

PHASE I

Nutrient Effects

One objective of Phase I was an empirical evaluation of the "subsidy-stress" hypothesis (Odum et al. 1979). That hypothesis predicts that a gradient of increasing levels of a "usable" system input (e.g., nutrient enrichment) will result in a bell-shaped curve of system response defined in terms of energy flow (community metabolism). Thus, high levels of enrichment should act as a stress, depressing system performance. The nutrient gradient employed in Phase I (0.10/0.01, 0.5/0.05, 1.0/.1 and 10/1 ppm N/P) ranged from oligotrophic to hyper-eutrophic (Wetzel 1975). As shown in Fig. 13a and b, only the highest nutrient level caused a significant increase in net production and community respiration, at best only approaching the left shoulder of a subsidy stress curve. The P/R ratio showed no significant nutrient effect because of the simultaneous increase in net production and community respiration. Therefore, these results are inconclusive but suggest that the highest level may have approached a level of maximum performance. Extremely hyper-eutrophic conditions (more so than in this experiment) have been shown to depress production and respiration in microcosms. For example, Butler (1964) found that 88.0/35.0 ppm NO_3/PO_4 resulted in lower net production and respiration values (0.61 and 0.56 g $CO_2/m^2/12$ hr, respectively) than did NO_3/PO_4 = 44.0/18.0 ppm (P_D = 1.22 and R_N = 1.25 g $CO_2/m^2/12$ hr). Likewise, Wilhm and Long (1969) showed a slight depression in microcosm metabolism (P_D = 1.09 and R_N = 1.11 g $CO_2/m^2/12$ hr)

at NO_3/PO_4 = 120/20 ppm as compared to NO_3/PO_4 = 12/2 ppm (P_D = 1.12 and R_N = 1.13 g CO_2/m^2/12 hr). As in the present experiment, P/R showed no notable response to nutrient enrichment in these studies.

Most of the other variables measured in Phase I showed positive correlations with nutrient enrichment, none suggesting a stress response at the highest nutrient level. Concentrations of chlorophyll a, phaeo-pigments, and biomass, and the abundance of fungi, bacteria and crustaceans all increased with increasing nutrient concentrations.

Cadmium Effects

Odum et al. (1979) also predicted that toxic or lethal system inputs will have no subsidizing effect; such inputs are hypothesized to depress system performance at all levels of input, although it is known that low concentrations of some toxins have a stimulating effect on organisms. The cadmium gradient in Phase I covered three orders of magnitude (0, 1, 10 and 100 ppb), with the highest level well above accepted standards for aquatic ecosystems. Net daytime production showed no detectable response to cadmium, while nighttime respiration showed a significant increase ($p = 0.05$). This translates into a decrease in P/R in response to cadmium (Fig. 14a) and indicates an increase in energy flow through heterotrophic system components. Over prolonged periods this would result in destruction of the system. Thus, using P/R as a measure of ecosystem performance, our results support the subsidy-stress hypothesis with respect to toxic substance (cadmium) inputs. Furthermore, in Phase II, cadmium pulses often resulted in a considerable increase in variance among replicates (e.g., Figs. 32, 47,

55 and 56), also in accordance with the hypothesis.

The significant increase in chlorophyll a with increasing cadmium concentration (Fig. 8a) can most likely be attributed to the decrease in crustacean grazers. Cadmium at 100 ppb virtually eliminated the crustaceans (Fig. 19), and resulted in the highest chlorophyll a concentrations. The toxic effect of cadmium on crustaceans has been noted previously by Marshall and Mellinger (1980) and Eiseler et al. (1972). One explanation for the increase in chlorophyll a concentration is that reduced grazing allowed algal cells to remain in the water column longer, thereby increasing the standing crop of chlorophyll. The fact that chlorophyll and net daytime production were not positively correlated indicates that, while cadmium may not be as lethal to the algae as it is to the animals, it does reduce the rate of photosynthesis per unit of chlorophyll. The assimilation ratio (net daytime production/chlorophyll a) at 10 and 100 ppb Cd was roughly half the value at 0 and 1 ppb Cd. As uneaten algae cells died, they contributed to the detrital food chain resulting in relatively large numbers of decomposers (especially fungi) and an increase in community respiration.

Interaction of Cadmium and Nutrients

Significant interaction effects between cadmium and nutrient enrichment were exhibited for net daytime production, nighttime respiration, and chlorophyll a. The effect resulted in an increase in each variable. No interaction was indicated for phaeo-pigments, biomass and population densities.

A major interactive effect appeared to result from a synergistic

augmentation of cadmium and nutrient effects at the highest extreme of each treatment. Cadmium had a greater stress effect on the herbivore trophic level than on the autotrophic or saprotrophic levels. Accordingly, the main effect of cadmium on the ecosystem as a whole was an alteration in trophic structure. A decrease in primary consumers or grazing animals apparently resulted in an increase in the standing crop of producers (algae) and decomposers (fungi), and this was reflected in increased community respiration. In effect, the system responded to cadmium perturbation by switching from a grazing to a detritus food chain. The persistence of crustaceans in the highest nutrient-highest cadmium levels suggests that nutrient enrichment may reduce the toxic effects of cadmium.

Stress and Ecosystem Performance

Interpretation of the above results emphasizes the importance of the definition of "stress" with respect to ecosystems. Barrett et al. (1976) and Leffler (1977) consider ecosystem stress to be any externally induced response which deviates from the system's normal pattern of behavior. Odum et al. (1979) define "stress" as any negative deviation, and "subsidy" as any positive deviation from the normal operating range of system performance. System performance is defined in terms of energy flow through the system (e.g., productivity), and the effect of a perturbation is interpreted as a reduction (subsidy) or increase (stress) in "maintenance cost or ... overall [system] function." Rather than productivity or respiration alone, the relationship between the two (i.e., P/R) is probably the best measure of energetic maintenance cost to the

ecosystem, and therefore, an indicator of subsidy or stress.

In terms of P/R, nutrients had no effect on system performance at the levels of enrichment used in Phase I, or those used by Butler (1964) and Wilhm and Long (1969). Much higher levels are apparently necessary to evaluate the subsidy-stress hypothesis with respect to nutrients. Cadmium, on the other hand, caused a significant decrease in P/R, as predicted by the hypothesis. A similar effect was noted by Giddings and Eddlemon (1978) for arsenic perturbations in aquatic microcosms; P/R was negatively related to As concentration. Both studies suggest the existence of toxicity thresholds for Cd and As, respectively, since the lowest concentrations studied (1.0 ppb Cd and 66 ppb As) had no detectable effect on P/R.

PHASE II

Two distinct perspectives underlie biogeochemical studies of ecosystems. The first focuses on the influence of ecosystem dynamics on patterns of chemical element behavior, particularly input-output behavior as a function of ecological succession and perturbation response. This is the context of several recent studies of large scale ecosystems (e.g., Rykiel 1977, Woodmansee 1978, Borman and Likens 1979). The second perspective focuses on the behavior of ecosystems in response to chemical element perturbations, such as increased nutrient loading or inputs of toxic substances. This view is the basis for studies of eutrophication and environmental toxicology. Both perspectives are essential for an understanding of the interactions between ecosystems and their input and output environments. The following discussion

considers results from Phase II from both perspectives.

Element Dynamics as a Function of Ecosystem Behavior

Vitousek (1977) proposed a family of curves representing temporal patterns of ecosystem output/input for essential (limiting and non-limiting) and non-essential elements (Fig. 2). These curves are projected as the inverse of net ecosystem production, (or biomass increment in the development or succession of the ecosystem). The magnitude of deflection is viewed as being a function of the degree to which an element is limiting. Any disturbance severe enough to reduce net production is proposed to result in a corresponding reduction in element retention, since there will be a reduction in rate of incorporating elements into biomass, again depending on the degree of element limitation. Our results generally confirm these trends.

Outputs of boron, calcium, copper, magnesium, sodium and zinc, all essential but in excess of biotic demand, remained equal to inputs throughout the experiment. Output curves for nitrate-nitrogen (Figs. 41c-48c), also essential but more nearly limiting, were practically mirror images of the corresponding net daytime production curves (Figs. 26a-33a), with the exception of the initial 60-day lag in NO_3-N uptake in N:P = 10 systems (Figs. 45c-48c). Thus, nitrate was retained by the system during periods of high productivity. Ammonia-nitrogen displayed rapid uptake within these microcosms during the same period, suggesting preferential utilization of NH_3-N by the early bloom of Chlamydomonas sp., followed by additional utilization of NO_3-N by the later bloom of Ulothrix sp. Since NO_3-N output responded significantly to cadmium treatments in

the absence of any NH_3-N response, cadmium may have selectively inhibited NO_3-N metabolism (autotrophic and heterotrophic). In N:P = 100 systems (Figs. 41b-44b), NH_3-N was accumulated in all cases, while NO_3-N showed significant retention only after a bloom of Chlorococcum sp. which followed the cadmium pulses between days 28 and 100 (Fig. 43c). The cadmium pulse on day 190 resulted in a significant increase in NO_3-N output. These results again suggest 1) preferential NH_3-N utilization but with NO_3-N supporting population blooms, and 2) cadmium inhibition of NO_3-N uptake.

Outputs of manganese and to a lesser extent, iron (Figs. 49b and c to 56b and c) were roughly inverse to net production (Figs. 26a-33a), especially in response to cadmium pulses. These patterns suggest that both elements were present in excess of biotic demand much of the time but approached limiting concentrations during population blooms.

Total phosphorus (in the form of PO_4-P in the inputs) showed rapid initial uptake in all microcosms (Figs. 49a-56a), preceding peak metabolic activity by about 60 days. In the N:P = 100 control systems (Fig. 49a), TP gradually increased in concentration in the output solutions to nearly equal input concentration (0.06 ppm) by about day 100. Since very little nitrogen was accumulated during this period (Fig. 41) phosphorus may have been sequestered through luxury consumption (by autotrophic and heterotrophic organisms) and utilized later during peak activity, thus reducing the uptake of new phosphorus inputs. After day 110 TP outputs again fell below input levels, but in the absence of any change in net daytime production (Fig. 26a). This may have resulted from an exhaustion of the phosphorus accumulated earlier. Interestingly, the large changes in net daytime production which followed cadmium pulses (Fig.

28a and 29a) caused only small deviations from the TP output patterns just described. This suggests that the phosphorus accumulated early in succession was sufficient to sustain a large amount of metabolic activity. In addition, it indicates that phosphorus was strongly retained within the systems even after major disturbances. The exact mechanism of this retention has not been identified, but may be the result of efficient recycling between heterotrophic and autotrophic organisms which often occur in intimate contact in particulate aggregates in microcosms (Kurihara 1978).

Retention patterns for all of the elements discussed above generally support Vitousek's (1977) proposal (Fig. 2) with two possible exceptions. First, maximum uptake of all essential elements studied did not coincide with maximum metabolic activity, as discussed above for phosphorus. Luxury consumption may have been responsible for the early occurrence of maximum phosphorus retention, and might be expected to occur for other essential, limiting elements as well. Second, disturbances (i.e., cadmium pulses) which caused significant changes in metabolic activity, were not reflected most strongly in the retention patterns of the element most limiting in system inputs (i.e., phosphorus). Outputs of NO_3-N, present in abundance relative to phosphorus, showed the strongest disturbance response, possibly as a result of selective cadmium effects on nitrogen metabolism. Since Vitousek's (1977) ideas were developed for terrestrial watershed ecosystems subject to variable nutrient inputs and other environmental conditions, and to rather drastic "destructive events" (i.e., clearcutting or fire), our evaluations may not be entirely valid. Also, it should be noted that our estimates

of ecosystem productivity are based on calculations of net daytime production of oxygen. Net ecosystem production (the difference between net daytime production and nighttime respiration, or the slope of the biomass accumulation curves) is currently being studied for a more complete evaluation of the hypothesis.

Henderson (1975) proposed the existence of a finite capacity for ecosystem accumulation of toxic substances. He suggested a temporal output/input curve somewhere between non-essential and essential, limiting elements in Vitousek's (1977) scheme (Fig. 2). Our data provide a preliminary evaluation of this idea for cadmium. Figure 57 shows cadmium retention patterns for microcosms receiving continuous 10 ppb Cd inputs under both phosphorus-limiting and non-limiting conditions. The curves indeed support Henderson's hypothesis and suggest further that overall cadmium accumulation is a function of productivity. In the less productive systems (Fig. 57), cadmium outputs approached input levels by the end of the experiment (286 days), while the more productive systems continued to accumulate cadmium. Since inorganic sediments were not present in the microcosms, cadmium must have been retained or stored in the biomass but it is not possible to tell from these data whether the mechanism was active biochemical uptake by living cells or sorption onto detrital materials. Both processes have been shown to occur for cadmium (Khalid et al. 1977, Sarsfield and Mancy 1977).

Ecosystem Behavior as a Function of Element Dynamics

The observations discussed above reflect the influence of ecological processes on the dynamics of essential elements. In general,

outputs of essential elements in shortest supply relative to demand (N, P, Mn, Fe) responded most strongly to successional and disturbance-induced changes in ecosystem behavior. Ecosystem behavior, in turn, was largely a function of alterations in the chemical nature of system inputs. The effects of these alterations (phosphorus limitation and cadmium inputs) are discussed below.

A further aspect of the problem of toxic substance accumulation in ecosystems is the ultimate effect of the toxicants on ecological processes. In Phases I and II of this work, we have indicated that cadmium seems to most strongly affect grazing herbivores, thus altering trophic structure and changing overall ecosystem behavior. These effects resulted from relatively large concentrations of cadmium (100 ppb Cd in Phase I and 750 ppb Cd in Phase II). However, small concentrations accumulating over longer time periods might be expected to have similar effects, particularly if some threshold toxic concentration is achieved. Such an effect may have occurred in two of the four replicate N:P = 100. An abrupt and highly significant increase in net production (Fig. 27a), community respiration (Fig. 27b), and NO_3-N uptake (Fig. 42c) occurred around day 100 in these systems after a total input of approximately 500 µg of cadmium By day 100 very little of the inflowing cadmium had accumulated within the systems (Fig. 57a); in fact this point marks the beginning of significant cadmium accumulation. If a threshold response did occur it resulted from relatively low concentrations of cadmium. For reasons which are not clear, the other two replicates failed to display this behavior and we thus are unable to make an evaluation. Further research will be required to clarify the existence and quan-

titative nature of toxicant accumulation thresholds. The N:P = 10 systems (Fig. 58) accumulated considerably more cadmium than the N:P = 100, but showed no detectable response, suggesting that cadmium was immobilized within the systems.

Schindler (1977) suggested that phosphorus is the single most important essential element directing the behavior of aquatic ecosystems, since it is more often scarce, relative to biotic demand, than other elements. This idea is substantiated by the success with which biotic activity can be predicted from phosphorus loading models (e.g., Dillon and Rigler 1974). In the Phase II experiment, phosphorus limitation significantly influenced all of the variables measured, causing reductions in biomass, plant pigments, community metabolic activity and nutrient retention, and alterations in community structure. Of perhaps greater interest is the fact that these manifestations also influenced system responses to cadmium perturbations (i.e., significant nutrient-cadmium interaction effects). In general, N:P = 100 microcosms were more sensitive (in terms of net daytime production, nighttime respiration and nutrient accumulation) to cadmium treatments than the N:P = 10 systems. This observation agrees with Pomeroy's (1975) hypothesis that ecosystem stability is a function of the availability of essential elements. With respect to toxic substance perturbations, this could be due to immobilization of toxicants in dead organic matter, which is usually abundant in eutrophic systems, or to the dominance of generally euryaceous organisms under nutrient rich conditions. Both mechanisms are likely to contribute to ecosystem stability in any given situation.

The response of an ecosystem to any perturbation will be influenced

by the developmental history of the system (Leffler 1978). Thus, systems frequently exposed to a particular type of disturbance may develop a degree of resistance to that disturbance through selection for resistant organisms. Some ecosystems have actually become dependent on environmental perturbations for maintenance of structural and functional integrity (pulse-stability sensu Odum 1969). Examples include fire maintained forests and tidal-pulse maintained salt marshes. We have attempted to determine if developmental history (in terms of cadmium exposure) might influence the resistance of an ecosystem to toxic substance perturbations.

In the N:P = 100 systems, early cadmium pulses resulted in significant increases in net daytime production (Fig. 28a), nighttime respiration (Fig. 28b), and uptake of NO_3-N (Fig. 43c) and Mn (Fig. 51b). Thus, by day 190 these systems were significantly different from those not receiving the early cadmium pulse. The cadmium pulse on day 190 produced different responses in the two types, but the differences were not as expected. The previously pulsed microcosms showed an immediate but transient decrease in metabolic activity (Fig. 32), and an increase in output of NO_3-N (Fig. 43a), and Mn, (Fig. 51b), while the previously unpulsed systems responded with a gradual, but long-lived increase in metabolic activity (Fig. 29) and NH_3-N uptake (Figs. 44b). Interestingly, the latter response was qualitatively similar to the initial cadmium response of the early-pulsed systems, both showing an increase in net daytime production and nighttime respiration. In Phase I, this effect was attributed to the release of primary producers from grazing pressure due to the decline in macroinvertebrate herbivores (crustaceans). In

the present case, macroinvertebrate grazers were never abundant, but microinvertebrates (primarily rotifers) may have served the same function. In fact, total rotifer numbers declined considerably following early cadmium pulses (Fig. 39) and the single, day-190 pulse (Fig. 40). Since the algal community in these systems consisted primarily of small unicellular forms (e.g., Chlorococcum sp., Chlorella sp. and Chlamydomonas sp.) potentially available to rotifers, the altered trophic structure explanation of system-level cadmium response seems plausible. Marshall and Mellinger (1980) report the same effect in toxicity studies in a Canadian shield lake. However, altered trophic structure alone does not account for the observed decrease in metabolic activity and increase in nutrient output following the cadmium pulse on day 190 in the previously exposed systems (Figs. 28 and 43). Rotifer numbers showed no response (Fig. 39) suggesting selection for cadmium resistant strains after the earlier pulses. Cadmium appears to have directly inhibited metabolic activity of primary producers, and perhaps heterotrophs as well, but with no detectable change in community structure. It is possible that when cadmium was first added, removal of grazers was the dominant factor. Later, after grazers had developed cadmium resistance, photosynthetic inhibition may have been more important (Jeff Giddings, personal communication). It is not clear from these data why phosphorus limited systems were more sensitive to cadmium than non-limited systems.

In the N:P = 10 systems (Fig. 32a) early pulses of cadmium resulted in a delay, but no significant increase, in peak metabolic activity over controls (Fig. 30a). The cadmium pulse on day 190 caused a slight, but not significant decrease in net daytime production and nighttime respira-

tion followed by a large increase in variance among the replicates approximately 20 days later (Fig. 32a). In the previously unpulsed systems the day-190 cadmium pulse resulted in a significant but transient decrease in community metabolism (Fig. 33) and increase in NO_3-N output (Fig. 48c). It is suggested that the large pulse of cadmium directly affected primary production as well as heterotrophic activity, thus depressing overall system metabolism.

In general, then, early cadmium pulses appeared to increase system resistance to later pulses in the N:P = 10 systems, and decrease resistance but increase resilience (sensu Waide et al. 1975) to later pulses in the N:P = 100 systems. The fact that ostracod numbers (Figs. 36 and 37) eventually rebounded from, and rotifer numbers (Figs. 39 and 40) were apparently unaffected by the day-190 cadmium pulse only after previous exposure to cadmium, supports the idea of increased stability due to selection for cadmium tolerant organisms.

SECTION 5

COMPARISON OF STATIC AND FLOWTHROUGH MICROCOSMS

Nutrient Treatments

Data from the Phases I and II experiments are summarized in Table I to provide a gross comparison between selected attributes of static and flowthrough microcosms not subjected to cadmium treatment. Phase I preceded Phase II and was run by different personnel, but both experiments were conducted in the same growth chamber under similar environmental conditions. In addition, all microcosms were established in identical containers, in the same basic medium (quantitatively modified for nutrient manipulations) and inoculated from the same laboratory stock microcosms. In Phase II the containers were equipped with input and output tubing to allow for flowthrough of the nutrient solution. For comparision, data in Table 1 are from control microcosms (i.e., no cadmium treatment) at nutrient levels two (N:P=0.5/0.05) and four (N:P=10.0/1.0) in Phase I, and phosphorus-limited (N:P=6.2/0.06) and non-limited (N:P=0.2/0.02) systems in Phase II. Values for biomass, chlorophyll a, phaeo-pigments, net daytime production and nighttime respiration were averaged over the last 1/3 of each experimental period so that approximately steady state conditions could be compared. For the static systems this represents days 77-119 and for the flowthrough systems, days 198-286. All other variables were calculated from these data, as indicated. Many of the values showed considerable variability as reflected in large standard deviations. Because of this and differences in experimental design, statistical comparisons were not made. However, these data provide the closest possible comparison,

Table 1. Comparison of nutrient effects on static and flowthrough microcosms.

	Static Microcosms[1]		Flowthrough Microcosms[2]	
Variable	Low Nutrient[3] (0.5/0.05)	High Nutrient[3] (10/1)	Low Phosphorous[3] (6.2/0.06)	High Phosphorous[3] (6.2/0.62)
Biomass	48(66)	235(129)	40(18)	867(327)
Chlorophyll a (Chl)	0.03(0.03)	0.81(0.70)	0.13(0.06)	2.97(1.17)
Phaeo-pigments (Pha)	0.10(0.12)	0.60(1.53)	0.09(0.04)	2.23(2.61)
Net Daytime Production (P_D)	0.92(0.76)	1.71(0.77)	0.65(0.28)	2.60(0.37)
Nighttime Respiration (R_N)	0.66(0.38)	1.57(0.58)	0.57(0.36)	2.42(0.45)
P_D/R_N	1.39	1.09	1.14	1.07
Gross Production ($P_G=P_D+R_N$)	1.58	3.28	1.22	5.02
Net Community Production ($P_N=P_D-R_N$)	0.26	0.14	0.08	0.18
P_G/B	0.03	0.01	0.03	0.006
P_D/Chl	30.67	2.11	5.00	0.88
Chl/B	0.0006	0.003	0.003	0.003
Chl/Pha	0.30	1.35	1.44	1.33

[1] All values averaged over days 77-119

[2] All values averaged over days 198-286

[3] mg N/mg P in nutrient medium.

Note: Biomass, chlorophyll a and phaeo-pigments in mg/l; net daytime production and nighttime respiration in mg O_2/l/12 hrs.; standard deviation in parentheses.

based on levels of phosphorus enrichment.

In general, the low phosphorus systems of both types behaved similarly with respect to community metabolism (P_D and R_N) and biomass accumulation. This is surprising since by day 286 the flowthrough systems had accumulated roughly 3 mg P, compared to 0.3 mg P which is the total amount which could have been taken up in the static systems. This suggests that the static systems operated at much higher efficiency (ie., on 10 times less phosphorus) than the flowthrough systems. Higher efficiency in the static systems is also indicated by higher values for net community production and for P_D/Chl (the assimilation ratio) which suggests greater oxygen production per unit chlorophyll. These observations imply relatively greater recycling of phosphorus in the static than flowthrough micocosms. The flowthrough systems appeared to have higher chlorophyll a concentrations and consequently, higher value for chlorophyll a/biomass and chlorophyll a/phaeo-pigments.

In the high phosphorus systems, most of the variables showed higher values in the flowthrough than in the static systems. In this case, roughly 60 mg P had accumulated in the flowthrough microcosms compared to, at most, 6 mg P in the static systems. The higher assimilation ratio in the static microcosms again indicates greater efficiency in these systems.

It is interesting that a 10 to 20-fold increase in phosphorus resulted in only a two to four-fold increase in net daytime production and nighttime respiration in both static and flowthrough systems. It would appear that some other factor was limiting to metabolic activity at the high levels of enrichment, (perhaps some other nutrient, or light

penetration through thick algal mats) or that phosphorus was immobilized.

Finally, a notable difference between the static and flowthrough systems was in the timing of peak metabolic activity. Nutrient flow-through resulted in peak net daytime production and nighttime respiration around day 90 (Fig. 26 and 30), compared to around day 30 in the static system (Figs. 15 and 16). This represents a difference of about 60 days or roughly a three-fold expansion of time scales of activity. The magnitude of expansion might be a function of system turnover time, which in this case was 12 days.

To summarize, static microcosms appeared (1) to operate at higher efficiency in terms of assimilation ratios and metabolic activity per unit phosphorus, and (2) complete development over shorter time scales than flowthrough microcosms. Phosphorus enrichment in both system types increased net daytime production and nighttime respiration but not in a linear fashion; at high levels of enrichment some other factor appeared to be limiting to community metabolism. Phosphorus enrichment also lowered net production efficiency, in terms of assimilation ratios, in both static and flowthrough systems.

Cadmium Treatments

Table 2 presents a summary of cadmium effects on static versus flow-through microcosms. The format is similar to that of Table 1 with respect to nutrient treatments. Static systems represented are the 10 ppb Cd and 100 ppb Cd treatments at nutrient levels two (N:P=0.5/0.05) and four (N:P=10.0/1.0). Flowthrough systems are the continuous 10 ppb Cd input treatments under phosphorous-limited (N:P = 100) and non-limited

Table 2. Comparison of cadmium effects on static and flowthrough microcosms.

	Static Microcosms[1]				Flowthrough Microcosms[2]	
	Low Nutrient (0.5/0.05)[3]		High Nutrient (10.0/1.0)[3]		Low Phosphorgus (6.2/0.06)[3]	High Phosphorgus (6.2/0.62)[3]
Variable	10ppbCd	100ppbCd	10ppbCd	100ppbCd	10ppbCd	10ppbCd
Cadmium Accumulated	60	600	60	600	300	600
Biomass (B)	67(41)	72(45)	246(156)	246(105)	89(49)	835(369)
Chlorophyll-a (Chl)	0.15(0.11)	0.15(0.14)	0.80(0.81)	1.61(1.25)	0.29(0.29)	2.63(1.67)
Phaeopigments (pha)	0.04(0.06)	0.05(0.12)	0.14(0.26)	0.43(1.09)	0.16(0.15)	3.92(3.80)
Net Daytime Production (P_D)	1.10(0.72)	0.82(0.46)	1.69(0.72)	1.79(0.75)	2.10(1.02)	2.52(0.70)
Nighttime Respiration (R_N)	0.82(0.32)	0.69(0.25)	1.58(0.59)	1.65(0.58)	1.94(0.98)	2.29(0.57)
P_D/R_N	1.34	1.19	1.07	1.08	1.08	1.10
Gross Production ($P_G=P_D+R_N$)	1.92	1.51	3.27	3.44	4.04	4.81
Net Community Production ($P_N=P_D-R_N$)	0.28	0.13	0.11	0.14	0.16	.23
P_G/B	0.03	0.02	0.01	0.01	0.05	0.006
P_D/Chl	7.33	5.47	2.11	1.11	7.24	0.96
Chl/B	0.002	0.002	0.003	0.65	0.003	0.003
Chl/Pha	3.72	3.00	5.71	3.74	1.81	0.67

[1] All values averaged over days 77-119.
[2] All values averaged over day 198-286.
[3] mgN/mgP in nutrient medium.

Note: Cadmium accumulation in µg Cd/6l microcosm; biomass, chlorophyll a and phaeo-pigments in mg/l; net daytime production and nighttime respiration in mg O_2/l/12 hrs.; standard deviations in parentheses.

(N:P = 10) conditions. By the end of the experiment the N:P = 100 microcosms had accumulated roughly 300 μg Cd, while the N:P = 10 microcosms had accumulated approximately 600 μg Cd. This compares with 60 μg Cd and 600 μg Cd, the maxiumum which could have been taken up in the 10 ppb Cd and 100 ppb Cd treated static microcosms, respectively. Values shown in Table 2 are averages over days 77-119 in the static systems, and days 198-286 in the flowthrough systems (as in Table 1).

A comparison of data in Tables 1 and 2 reveals several general trends. In the static microcosms the most notable cadmium response is reflected in chlorophyll a concentrations and secondary variables which include chlorophyll a (P_D/Chl,Chl/B and Chl/Pha). This observation is supported by data presented earlier (Fig.8). Chlorophyll a in the high nutrient static systems showed the greatest response to 100 ppb Cd, while the low nutrient static system responses to 10 ppb Cd and 100 ppb Cd were indistinguishable for all variables. This reemphasizes the interactive effects of high nutrient-high cadmium concentrations discussed in Section 4. In contrast, only the low phosphorus flowthrough microcosms showed a noticeable cadmium response and this was in terms of net daytime production, nighttime respiration and the related secondary variables. The high phosphorus flowthrough systems showed no detectable response.

From these observations, we are unable to draw any firm conclusions with respect to relative sensitivities of static and flowthrough microcosms. It would appear (although tenuously) that low nutrient static systems showed detectable responses to relatively less accumulated cadmium than either low or high phosphorus systems. However, it is

possible that the low phosphorus flowthrough systems responded to considerably less accumulated cadmium than indicated in Table 2 (see Section 4). Unfortunately, a block effect in our experiment precludes evaluation. To more precisely address this problem, future experiments should include exactly comparable levels of nutrient enrichment, equivalent pulsed toxicant inputs into static and flowthrough system (early and late in succession), and several low level continuous toxicant inputs into flowthrough systems.

Relative Sensitivity of Variables

Table 3 is a general, qualitative summary of responses to cadmium of all variables measured in the static and flowthrough microcosms. This comparison includes the effects of cadmium pulses in the flowthrough systems. The purpose of Table 3 is to provide a gross evaluation of the relative sensitivities of the variables. The presence of a response ("+" indicates an increase in value, "-" a decrease in value, and "0" no response) is based on statistical analyses presented earlier in this report, or on obvious response patterns (e.g., crustacean abundance in flowthrough microcosms).

A comparison of variables in Table 3 suggests that community metabolism (especially respiration) and population densities (especially grazers) provide the best overall measures of cadmium effects. This agrees with the conclusion of Odum et al. (1979) that ecosystem stress evaluations should focus on variables at the ecosystem and population levels of organization (energy flow and key population densities, respectively). The P/R ratio decreased in response to cadmium in the

Table 3. Qualitative comparison of microcosm responses to cadmium.

	Static Microcosms		Flowthrough Microcosms	
	Low Nutrient	High Nutrient	Low Phosphorus	High Phosphorus
Biomass	0	0	0	0
Chlorophyll a	0	+	+	0
Phaeopigments	0	0	0	0
Net Daytime Production	0	0	+-	-
Nighttime Respiration	+	+	+-	-
P/R	-	-	0	0
Population densities				
Algae	+	+	+	0
Grazers	-	-	-	-
Bacteria	0	0	N.M.	N.M.
Fungi	+	+	N.M.	N.M.
Nutrient Output				
TN	N.M.	N.M.	-+	0
NH_3-N	N.M.	N.M.	-	0
NO_3-N	N.M.	N.M.	-+	+
TP^3	N.M.	N.M.	0	0
Mn	N.M.	N.M.	-+	-
Fe	N.M.	N.M.	0	-

Note: + indicates increase in value; - indicates decrease in value; 0 indicates no response; N.M. indicates that a variable was not measured.

static microcosms due to an increase in community respiration. Giddings and Eddlemon (1978) also observed a decrease in P/R in static microcosms exposed to arsenic. In the present experiment, net production and community respiration in the flowthrough systems responded identically to cadmium, resulting in no measurable P/R response. We are unable to tell at present whether this difference is due to the actual nutrient flowthrough or to the pulsed nature of cadmium inputs in the flowthrough microcosms.

Biomass and plant pigment concentrations were generally the poorest indicators of cadmium effects. This is not surprising for biomass since, as a cumulative system property, it would not be expected to reflect short term system dynamics in response to chemical perturbations. Biomass accumulation rates might be more revealing. As measures of autotrophic mass and condition, plant pigments might be more sensitive to toxicants which selectively affect primary producers.

In the flowthrough microcosms, output/input ratios of nitrogen (especially NO_3-N) proved to be quite sensitive to cadmium pulses, responding as the inverse of net production. This may have been the result of a direct cadmium influence on nitrogen metabolism. Giesy et al. (1979) found no NO_3-N output response to cadmium continuously introduced into stream channel microcosms, possibly because of significantly lower cadmium (5 and 10 ppb) and NO_3-N concentrations (3.6-10.4 ppb), or other properties of the stream systems (e.g., biotic composition). The influence of toxic substances on nitrogen metabolism requires further research.

Finally, manganese and iron outputs in response to cadmium pulses

were suggestive of the pattern described above for NO_3-N, but the trends were not as clear. And, again, the mechanisms involved are not known. Nonetheless, these results emphasize the potential utility of essential element dynamics as an indication of ecosystem stress response. Phosphorus outputs showed no significant response to cadmium treatments at either level of enrichment, indicating that phosphorus is efficiently retained within the systems even after disturbances. Evans (1977) found similar results in flowthrough reef-flat microcosms exposed to copper perturbations.

SECTION 6

CONSIDERATIONS AND RECOMMENDATIONS FOR TOXICITY TESTING

Results of these experiments suggest some tentative answers to the questions raised in the Introduction:

1) Which ecosystem properties are most sensitive or best reflect ecosystem response to toxicant perturbations?

Of the ecological variables measured in this study, community metabolism (net daytime production and especially nighttime respiration) and densities of various taxonomic groups provided the most consistent indicators of cadmium effects. The ratio of net production to community respiration (P/R) has been suggested as a useful measure of toxicant stress in microcosms (Giddings and Eddlemon 1978), but proved responsive to cadmium only in the static systems in our study; in the flowthrough system P_D and R_N both responded similarly, resulting in no net change in P/R. Reasons for this difference are not clear, but it does seem clear that P_D and R_N expressed individually are important and easily measured variables in microcosm studies. Biomass and plant pigment concentrations were the least sensitive to cadmium of the variables measured in our study. Biomass accumulation rates and pigment ratios might prove to be more useful. In the flowthrough systems, output/input ratios of NO_3-N, Mn and Fe showed significant responses to cadmium treatment. This illustrates the potential utility of output/input ratios (especially nitrogen) for toxicity screening and suggests further that

some toxicants might selectively alter specific metabolic pathways. Estimates of rates of metabolism of certain essential elements (e.g., N, P, S) should be considered for use in microcosm screening tests. Thus, based on our results, the most useful ecological variables for evaluating toxicant effects in aquatic microcosms appear to be those that reflect: 1) overall community metabolism (P_D, R_N and P/R), 2) changes in community composition (relative abundances of key functional or trophic groups), and 3) dynamics of essential elements (output/input ratios and possibly activity of specific metabolic processes). Sampling frequency in this study was approximately once per week for most of the variables. The observed trends could have been detected from less frequent sampling over most of the experimental periods but with more intense sampling early in succession and immediately after perturbations.

2) What influence will other environmental variables (e.g., pH, nutrient enrichment, light intensity) have on ecological effects of a toxic substance?

Nutrient enrichment and phosphorus limitation significantly influenced the cadmium response of most of the variables measured in this study. In general, the poorly enriched microcosms were more sensitive to cadmium than their highly enriched counterparts. The importance of this finding for toxicity screening in microcosms is that standard testing conditions, such as levels of nutrients and other factors, are likely to influence test results. This unavoidable bias can be minimized or at least accounted for by conducting screening tests in matrix

or factorial experimental designs which include potentially interacting factors. In particular, if tests are run in microcosms of site specific derivation, then environmental factors important in a given geographic area (e.g., salinity, pH, temperature extremes) could be incorporated into the test, along with toxicant levels, for a more meaningful evaluation. Any number of factors could be included in such a scheme (including several toxicants), but experimental costs would increase with each factor. Judicious choice of potentially important factors would be required. An especially important environmental factor which this study did not consider was the effect of inorganic sediments (and the associated biotic community) on cadmium toxicity. Because soils and sediments are important biogeochemical factors in all ecosystems, they might be more appropriately included as a nominal experimental condition rather than a separate factor, unless the interactive ecological effects of toxicants and sediments are of interest. Since this study focused on biotic processes and was, therefore, ecologically incomplete, we would suggest a complimentary follow-up experiment of similar design, which incorporates sediments as an experimental condition applied equally over all treatments. This would add more realistic conditions and allow for inferences as to the influence of sediments on cadmium toxicity.

3) Will ecosystem response be a function of the timing or frequency of toxicant inputs with respect to stages of ecosystem development?

The mode of toxicant introduction into microcosms is an important consideration for toxicity testing. Since toxic substance inputs into

natural ecosystems occur over wide ranges of frequency and magnitude, one-time additions of a toxicant to microcosms might not provide a meaningful evaluation of ecological effects. In the present study, cadmium was added to the static microcosms only at the beginning of the experiment, precluding any consideration of toxicant input dynamics. We attempted to address this problem in flowthrough microcosms by applying cadmium in pulses at several stages in succession. Results showed that cadmium pulses early in succession significantly affected system response to later pulses, possibly due to selection for tolerant organisms. We are unable, with these data, to evaluate relative sensitivities of different successional stages. This could be easily done, however, in a factorial experiment using time of pulse as one factor and magnitude of pulse as another. We also compared flowthrough microcosm responses to continuous chronic versus acute pulsed cadmium exposure. Continuous 10 ppb Cd inputs may have caused a toxic threshold response, but results are inconclusive. Giesy et al. (1979) found no evidence for cadmium threshold responses in stream microcosms exposed to continuous 5 and 10 ppb Cd inputs.

4) What degree of realism (biotic and abiotic complexity) should be incorporated into microcosms for use in toxicity screening?

Generally, the microcosms used in this study (small volume [6 l] with naturally derived communities) were sensitive to moderately low concentrations of cadmium (100 ppb). The lowest concentrations, however, caused no response in the static systems (1 and 10 ppb Cd) and a

possible but inconclusive response in the flowthrough systems (10 ppb Cd). In contrast, others have found significant ecological responses to low levels of cadmium (5 and 10 ppb Cd; Giesy et al. 1979) and copper (10 ppb Cu; Evans 1977) in relatively large, ecologically complex, outdoor microcosms. This suggests a possible direct relationship between microcosm size (or complexity) and toxicant sensitivity, but the relationship is not clear. Conversely, a broad interpretation of the results of Van Voris et al. (1980) would suggest that the most sensitive systems (i.e., least resistant to perturbation) are relatively low in "functional complexity." Until some empirical means is found to evaluate functional complexity, however, this problem will be difficult to resolve. It is also possible that physical or chemical properties (e.g., pH or water hardness) of the various microcosms are related to their various sensitivities. In any event, our results suggest that small laboratory microcosms are potentially useful for estimating gross ecological effects of toxic substances, perhaps as an early phase in multiple-stage testing followed by later but more selective studies in more complex systems (subsamples from specific ecosystems; eg., Giddings and Eddlemon 1978).

We are unable to judge the relative sensitivities of static versus flowthrough microcosms used in this study. We suggest, however, that nutrient flowthrough provides a degree of realism lacking in static microcosms and allows for consideration of chemical input-output dynamics, which proved to be sensitive to cadmium perturbations. In addition, continuous low level input of toxicant provides a means for evaluating chronic toxicity. It should be noted that continuous

nutrient flowthrough appeared to result in a 60-day delay in peak metabolic activity compared to static conditions. This suggests that screening tests in flowthrough microcosms might require longer periods of observation if entire successional sequences are to be studied. However, responses to cadmium pulses were relatively rapid and observable over shorter time periods (approximately 30-60 days in most cases). The behavior of flowthrough microcosms has been suggested to be related to system turnover time (Leffler 1978) which, in the present experiment, was 12 days. Turnover times which provide maximum toxicant sensitivity will have to be determined for toxicity screening tests.

A Hierarchical Approach

As mentioned in the Introduction, testing standards have not yet been developed for evaluating ecological effects of toxic substances prior to their widespread release into the environment. We suggest that a potentially useful screening protocol for aquatic ecosystems might consist of a series of factorial experiments in aquatic microcosms of increasing complexity: (1) Relatively simple, static microcosms (with and without sediments), (2) flowthrough microcosms (with and without sediments), and (3) detailed but selective studies in more complex microcosm subsamples from specific ecosystems. Steps (1) and (2) are based partly on results from the present experiment; although sediments were not studied, they have been shown to influence the toxicity of a number of compounds (e.g., Hongve et al. 1980). In addition, separate consideration of natural sediments corresponds to previous conclusions that toxicant effects on pelagic and sediment communities should be

studied in separate screening experiments (Leffler 1980, personal communication). We include sediments in the protocol as a point for further research. Step (3) is based on results from Ausmus et al. (1980) which suggest that laboratory microcosms can be constructed which reasonably mimic specific natural ecosystems (ponds), and that such systems are most useful for later stages of screening of toxic substances.

The protocol is tentative in that details of analysis and interpretation have not been developed. A general outline is as follows (the steps are similar in rationale to those described for terrestrial microcosms in Gillett and Witt [1977], pp. 5-6):

1) Based on consideration of available information concerning a toxicant (chemical properties, species bioassay data, simulation model predictions, etc.), short-term factorial experiments are conducted in simple static microcosms to elucidate gross ecological effects. The factors to be included are indicated by available information, but may be simply toxicant levels versus the presence and absence of sediments. If other factors require evaluation, then sediments might be considered in separate but concurrent experiments. The experiments might be designed to test a statistical null hypothesis of no toxicant effect over some range of concentrations (e.g., several orders of magnitude). In such a case, a minimum set of response variables should include community metabolism (productivity and respiration), toxicant and selected nutrient concentrations (for evaluations of uptake/release of nitrogen and phosphorus, for example), and abundances of key taxonomic groups

(e.g., primary producers, grazers and microbial decomposers). Other variables might be appropriate, especially in cases where specific modes of toxicant activity are known or suspected (e.g., rates of nitrogen fixation for chemicals that inhibit nitrogenase activity).

If, as a result of these experiments, a chemical proves to have highly undesirable ecological effects, even at low concentrations, no further testing may be required. If moderate or no effects are detected, testing should be continued at the next level.

(2) Based on results from the static experiments, flowthrough microcosms are employed to evaluate chronic or threshold effects of low level, continuous toxicant inputs. In addition, the effects of toxicant input dynamics (inputs of various intensity, duration or frequency) can be studied if desired. As before, factors to be included depend on available information. Effects of sediments might be included as a factor or studied in separate experiments. In addition to response variables considered in step (1), output/input relationships for selected nutrients and for the toxicant should be measured.

Again, if dramatic ecological effects are discovered during these experiments, further testing may be unnecessary. Otherwise, tests are conducted at the next level.

(3) Results from steps (1) and (2), combined with existing information, should provide a reasonable estimation of gross ecological effects of a toxic substance. The purpose of the last step is to analyze some of the details of toxicant activity in microcosms derived from

specific ecosystems and to detect effects which might be site specific. Ecosystems of interest might be those expected to receive excessive exposure to a toxic substance. Details of experimentation with this type of aquatic microcosm are described in Ausmus et al. (1980). Appropriate analyses include toxicant transport and degradation (via radioisotope-labeled compounds), bioaccumulation ratios, nutrient concentrations in interstitial water, and community metabolic activity (productivity and respiration). Other variables might be of interest in specific situations. Information from such experiments should suggest mechanisms for ecological effects which may have been observed, but less well understood, in steps (1) and (2).

Any suspected toxicant which fails to show adverse effects in all three hierarchical steps might be expected to have little impact in natural aquatic ecosystems, at least over the concentration ranges studied. However, this statement cannot be confirmed from existing information. Further research is needed to validate experimentally derived results through studies in natural systems, and to assess the feasibility of a hierarchical approach to toxicity screening. The advantage of such an approach is that each step yields increasingly greater information about the effects of a toxicant, and more closely approximates natural ecosystems.

SECTION 7

CONCLUSIONS

1) Of the variables measured in this study, the most useful for evaluating the ecological effects of cadmium were: a) community metabolism (net daytime production and nighttime respiration), b) changes in community composition (relative abundances of trophic groups), and c) output/input ratios for NO_3-N, Mn and Fe. Biomass and plant pigment concentrations were the poorest indicators of cadmium effects. The response of specific metabolic activities (e.g., for N, P and S) to toxic substances requires further research and should be considered for incorporation into toxicity screening tests.

2) Nutrient enrichment and phosphorus limitation significantly influenced cadmium effects on most of the variables measured in this study. The use of a factorial experimental design provides a means of including potentially important interacting factors into microcosm screening tests. The effects of inorganic sediments on system response to cadmium should be investigated for comparison with results of this study.

3) Pulsed cadmium inputs early in succession significantly affected system responses to cadmium pulses later in succession (in flow-through microcosms) possibly as a result of selection for cadmium

tolerant organisms. Continuous 10 ppb Cd inputs may have resulted in a threshold response due to cadmium accumulation, but results are inconclusive.

4) A hierarchy of microcosm experiments, including 1) static microcosms (with and without sediments), 2) flowthrough microcosms (with and without sediments), and 3) microcosm subsamples from natural ecosystems, appears potentially useful for screening purposes. Each step provides increasingly greater information and more closely approximates natural ecosystems.

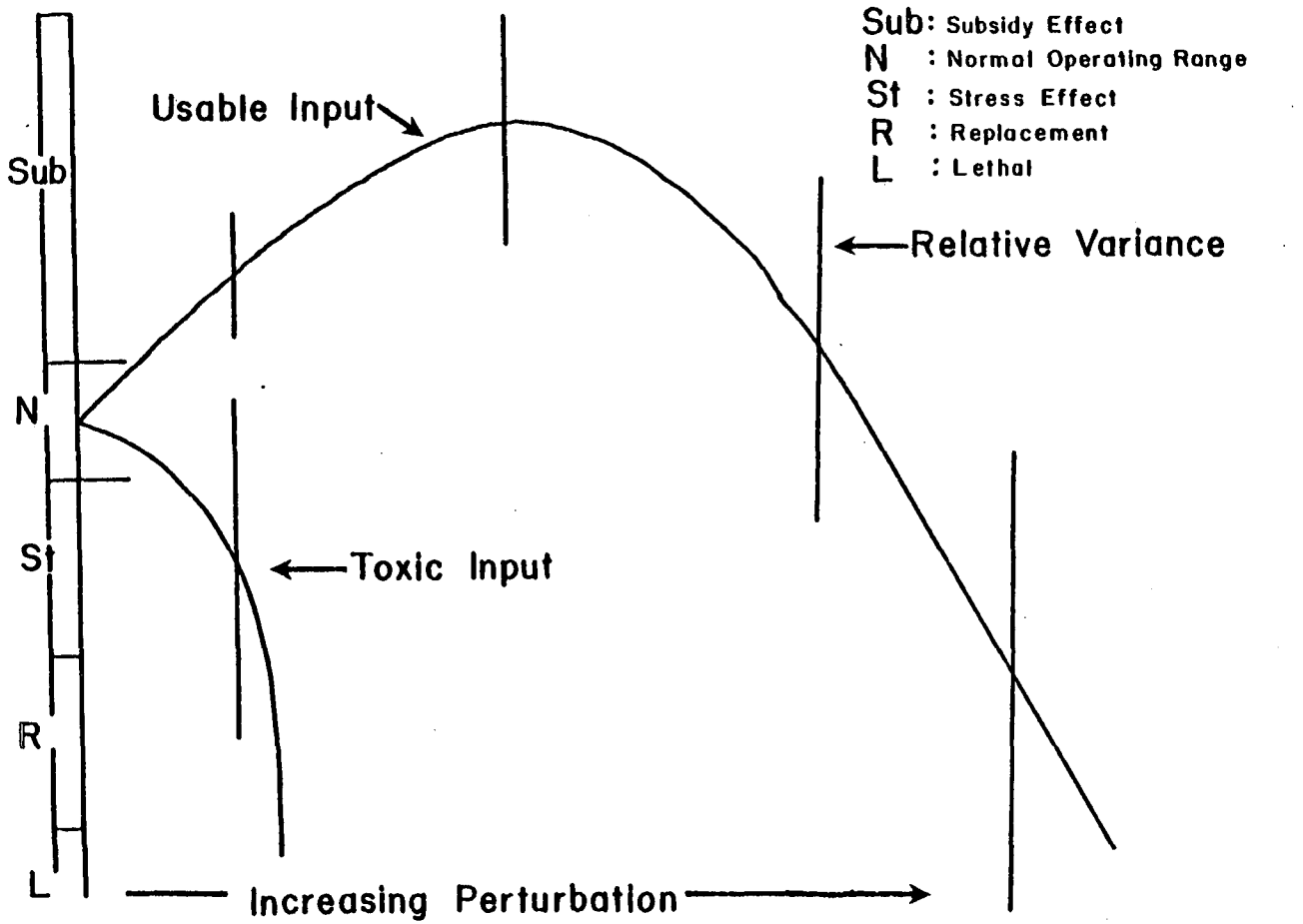

FIGURE 1. Hypothesized patterns of ecosystem response to usable and toxic inputs (redrawn from Odum et al. 1979).

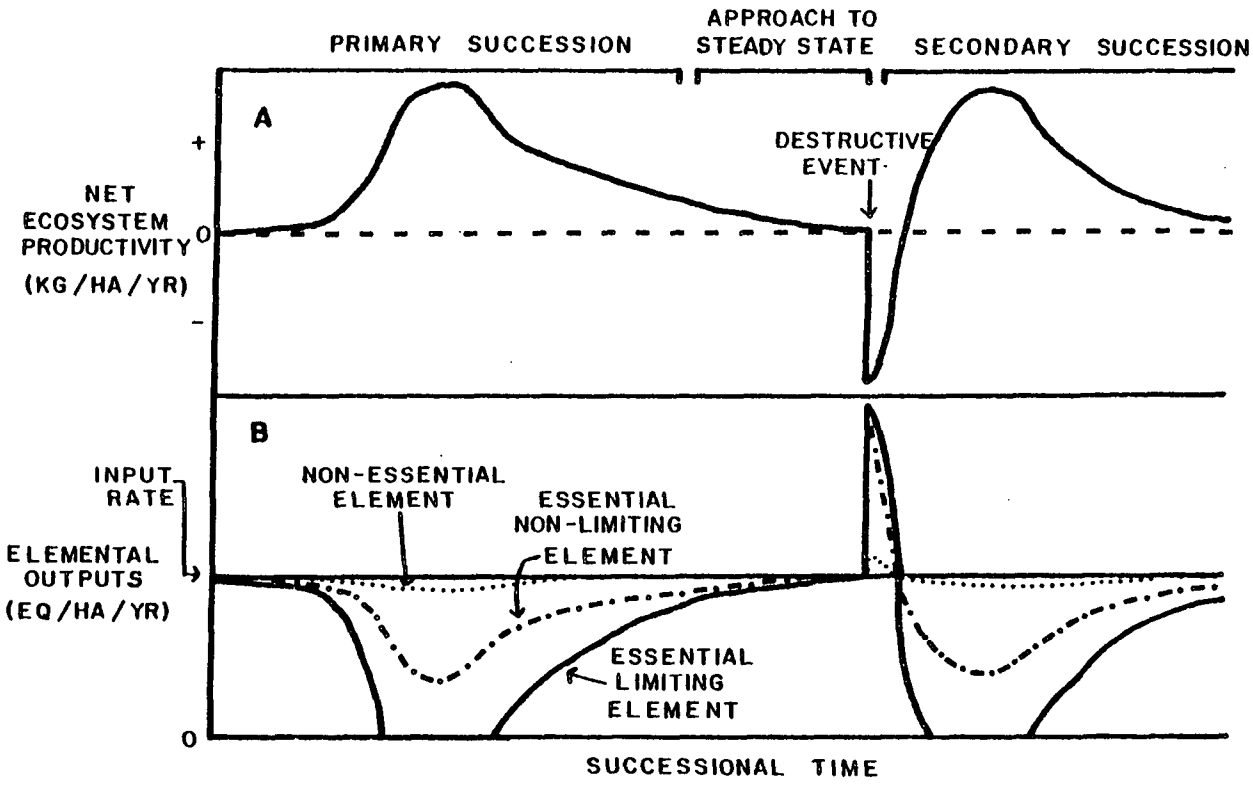

FIGURE 2. Hypothesized patterns of net ecosystem productivity (A) and element retention (B) through ecosystem succession (redrawn from Vitousek 1977).

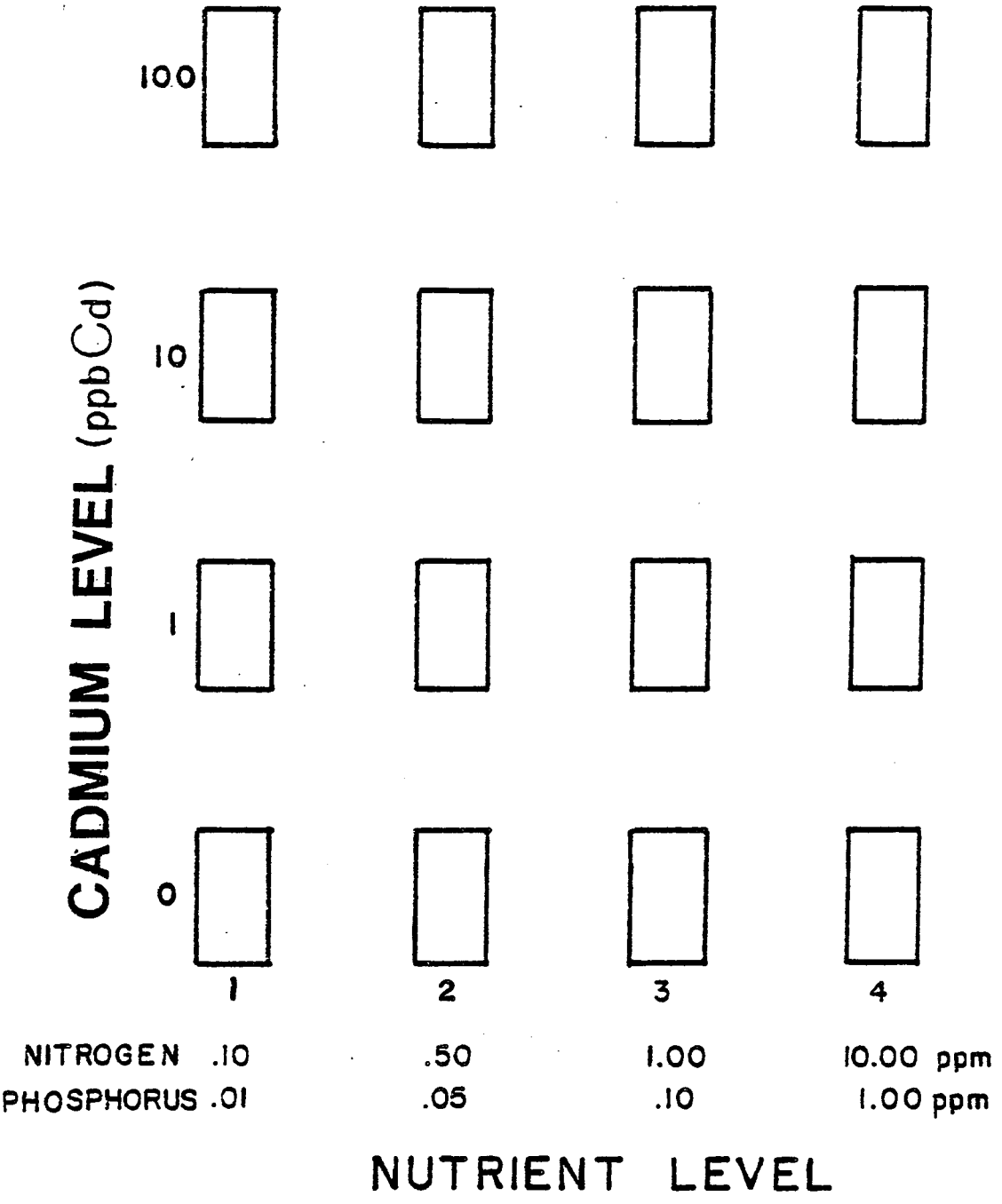

FIGURE 3. Experimental design for Phase I, with three replications of each treatment.

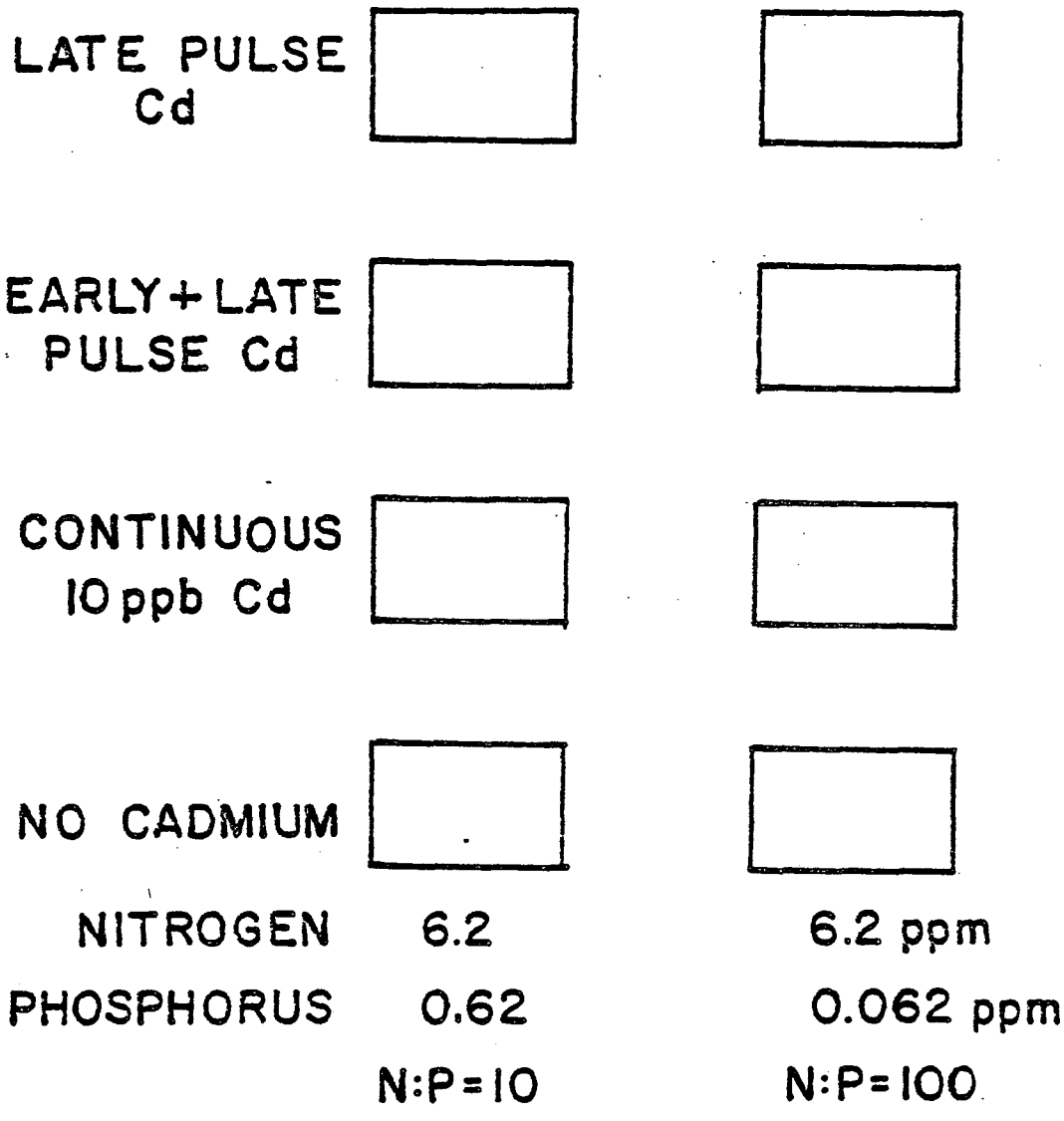

FIGURE 4. Experimental design of Phase II, with four replications of each treatment.

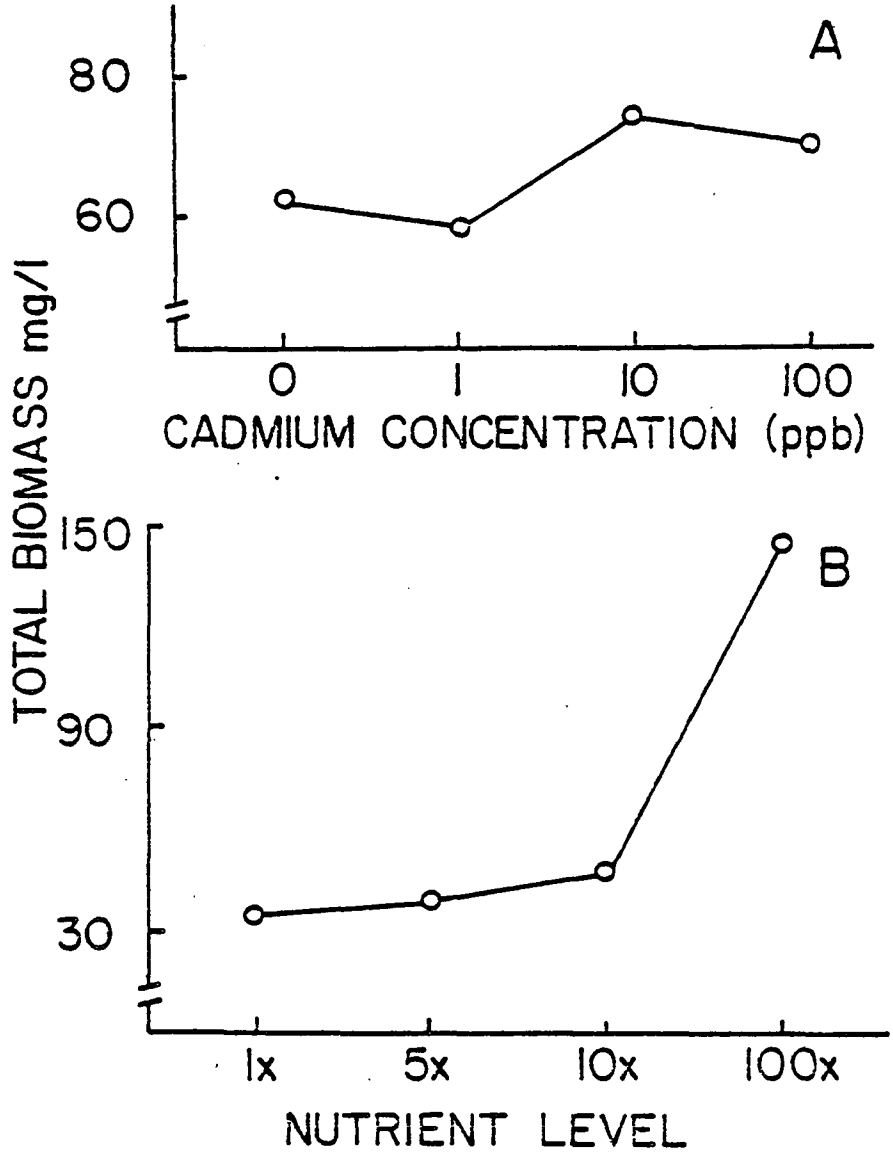

FIGURE 5. Influence of cadmium (A) and nutrient enrichment (B) on average biomass concentration in static microcosms. Each point represents the mean over the entire experiment.

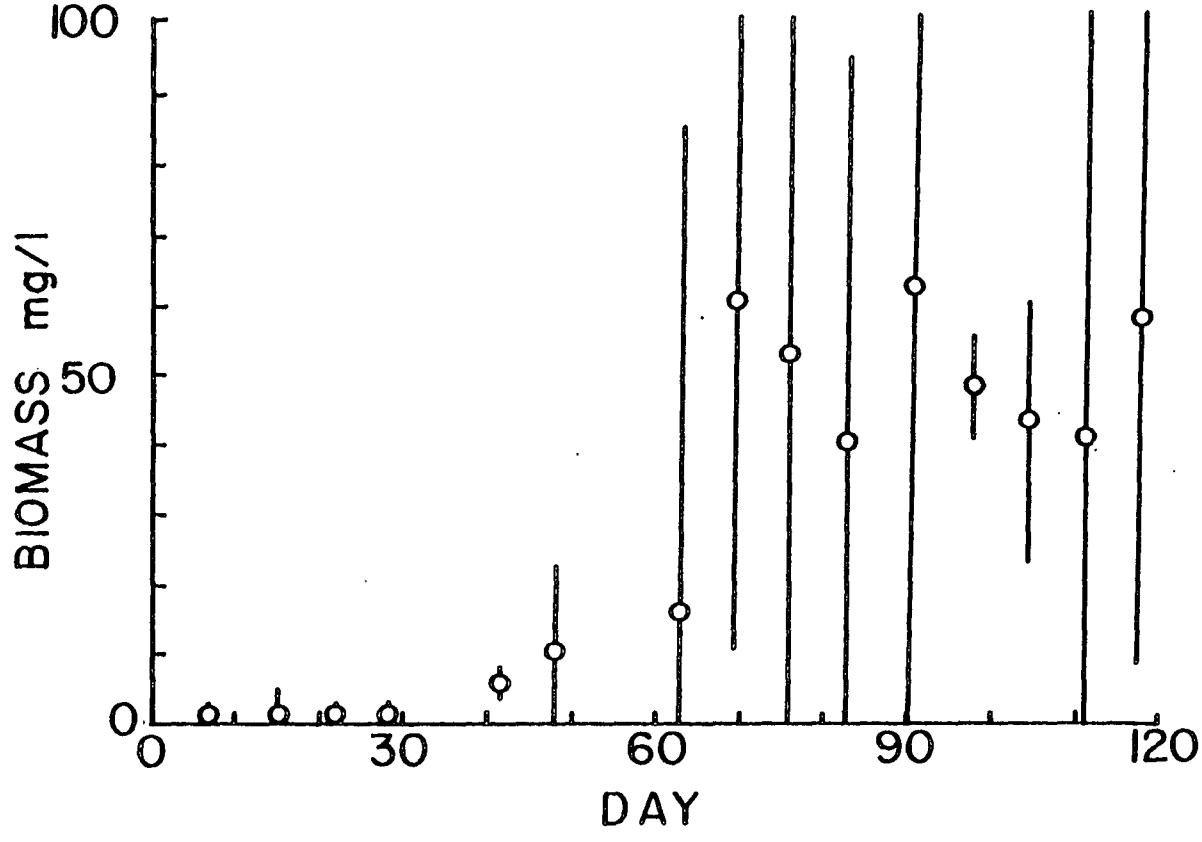

FIGURE 6. Biomass concentrations through time in lowest nutrient (Level 1) control static microcosms. Each point is the mean of three replicate systems with 95% confidence bars.

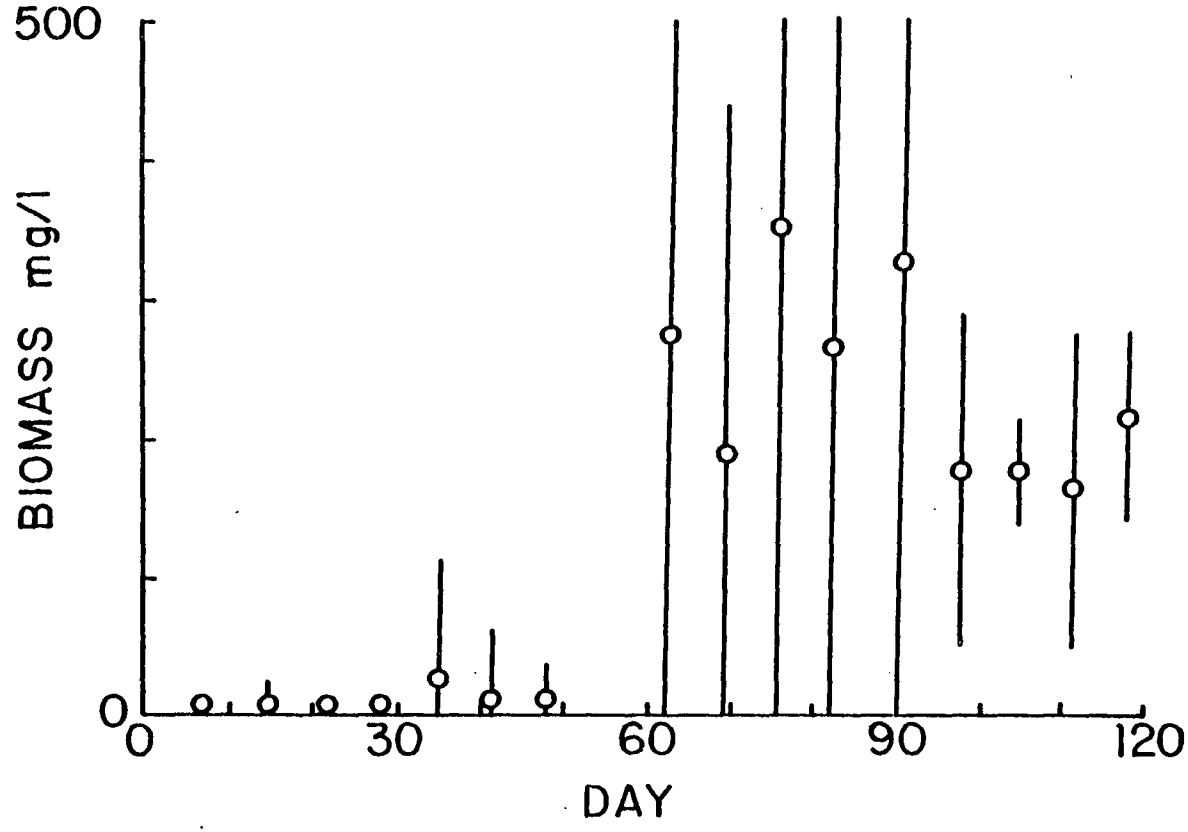

FIGURE 7. Biomass concentrations through time in highest nutrient (Level 4) control static microcosms. Each point is the mean of three replicate systems with 95% confidence bars.

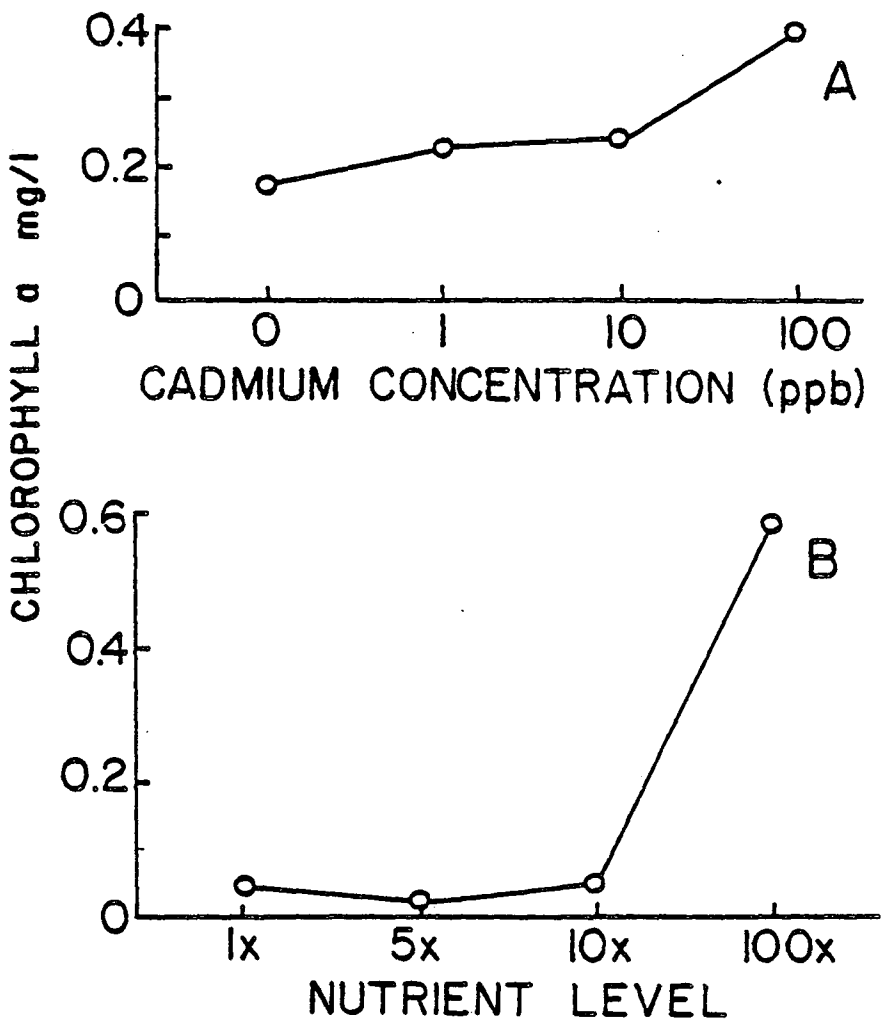

FIGURE 8. Influence of cadmium (A) and nutrient enrichment (B) on average chlorophyll concentrations in static microcosms. Each point represents mean over the entire experiment.

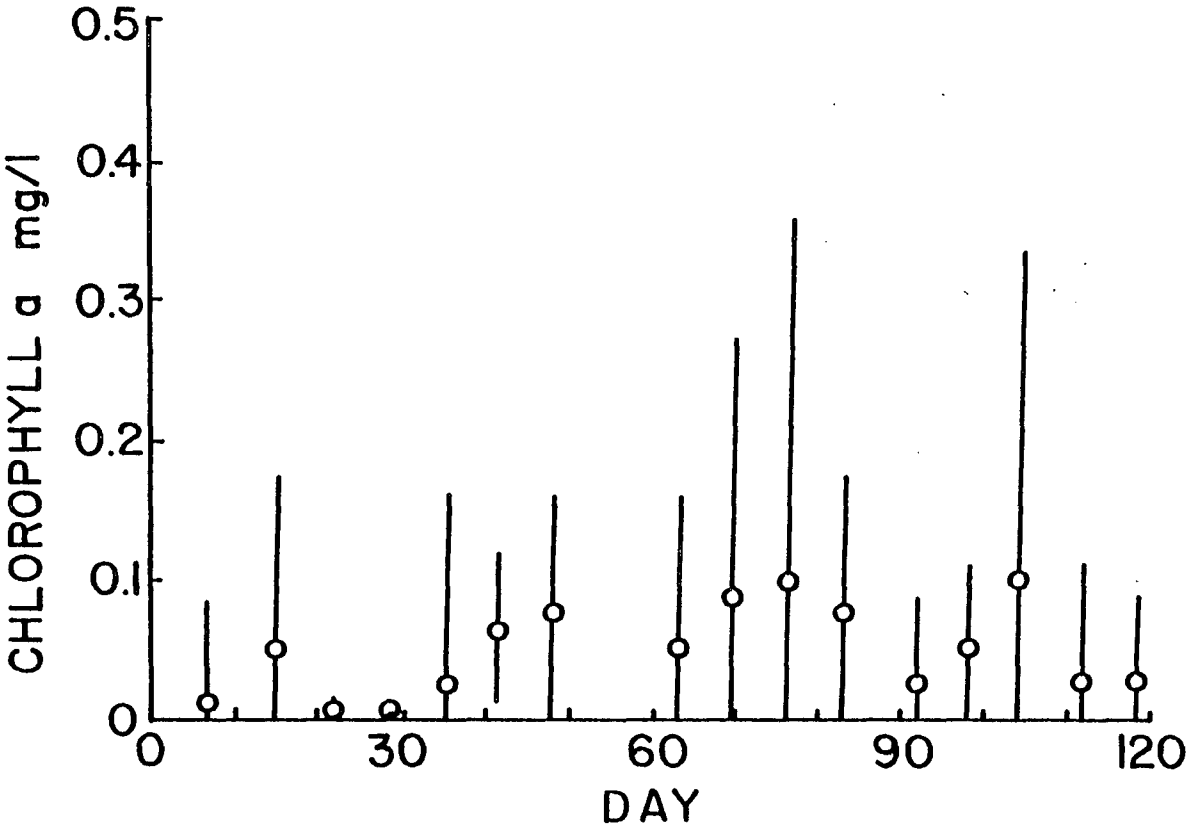

FIGURE 9. Chlorophyll a concentrations through time in lowest nutrient (Level 1) control static microcosms. Each point is the mean of three replicate systems with 95% confidence bars.

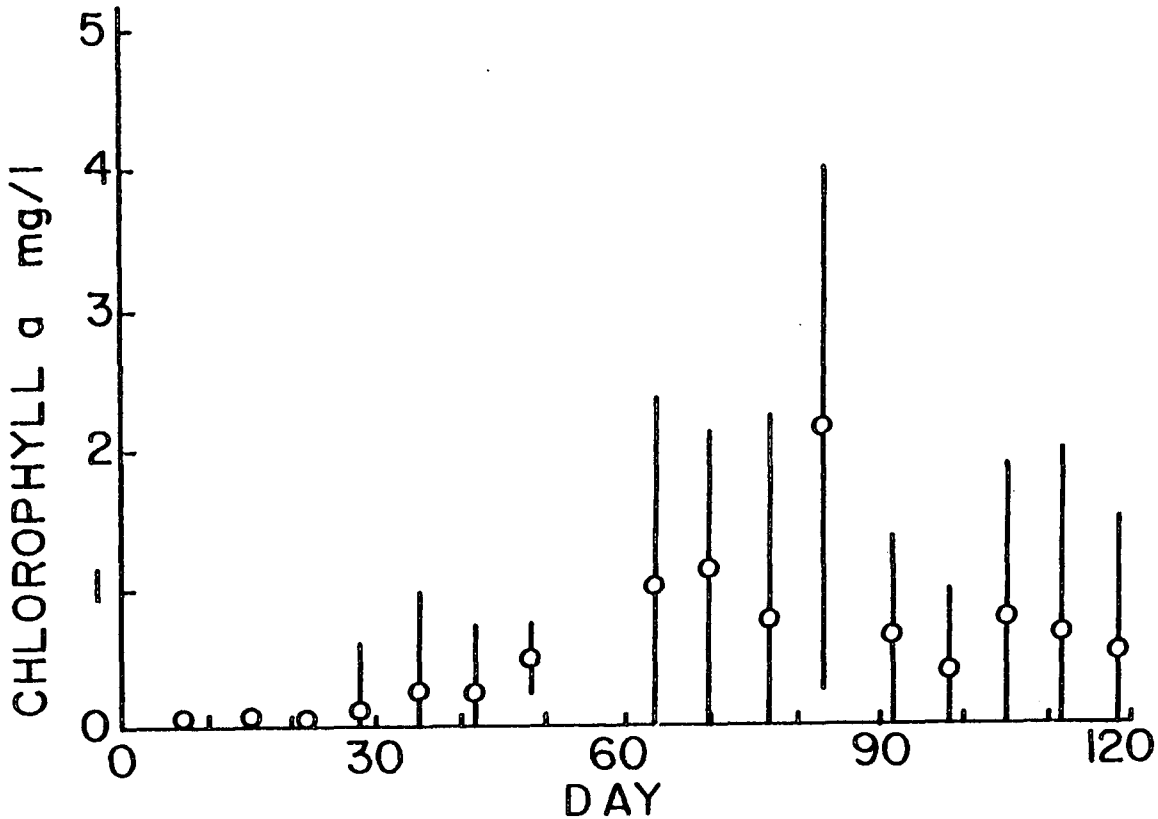

FIGURE 10. Chlorophyll a concentration through time in highest nutrient (Level 4) control static microcosms. Each point is the mean of three replicate systems with 95% confidence bars.

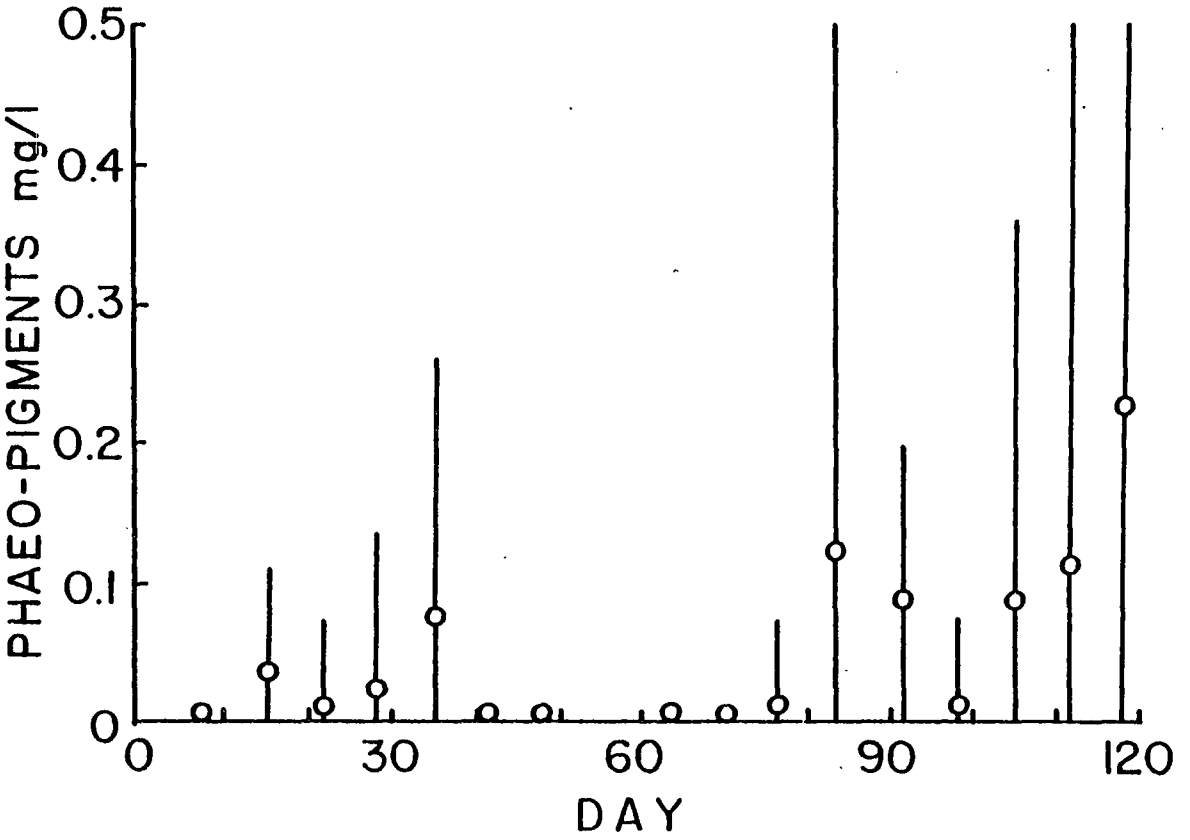

FIGURE 11. Phaeo-pigment concentrations through time in lowest nutrient (Level 1) control static microcosms. Each point is the mean of three replicate systems with 95% confidence bars.

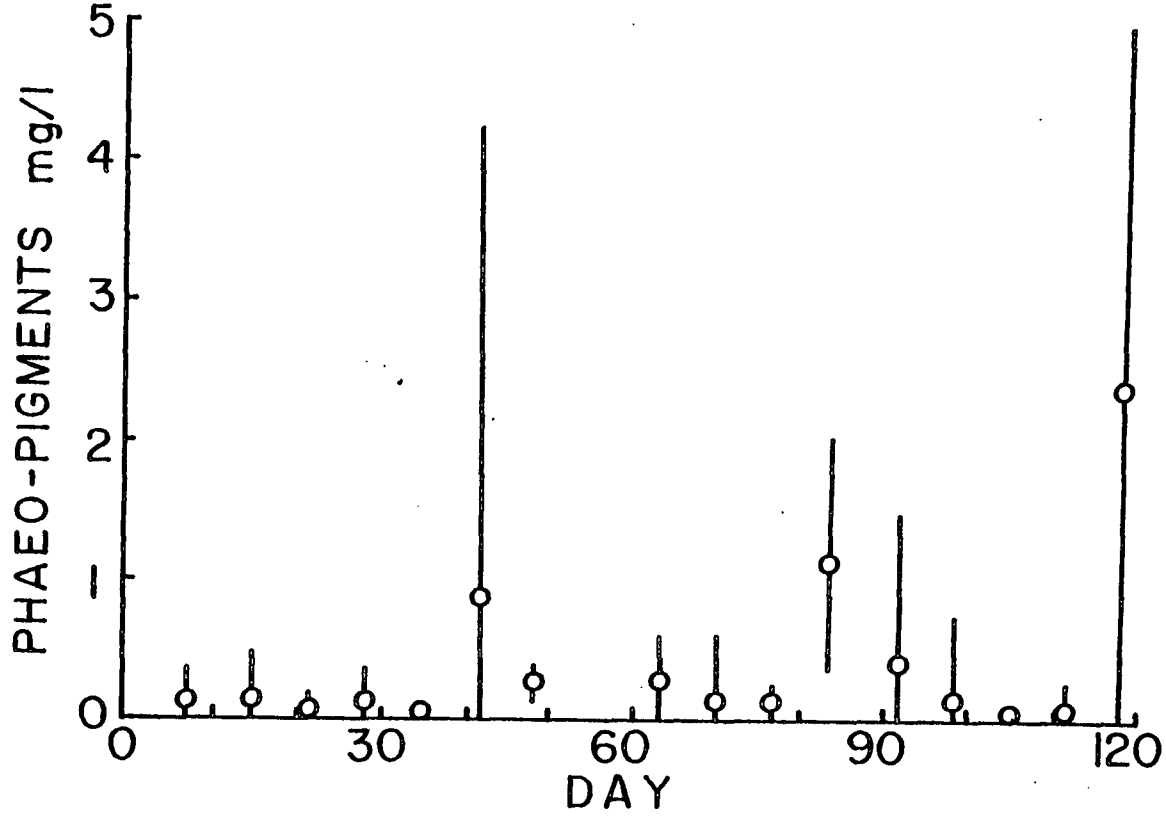

FIGURE 12. Phaeo-pigment concentrations through time in highest nutrient (Level 4) control static microcosms. Each point is the mean of three replicate systems with 95% confidence bars.

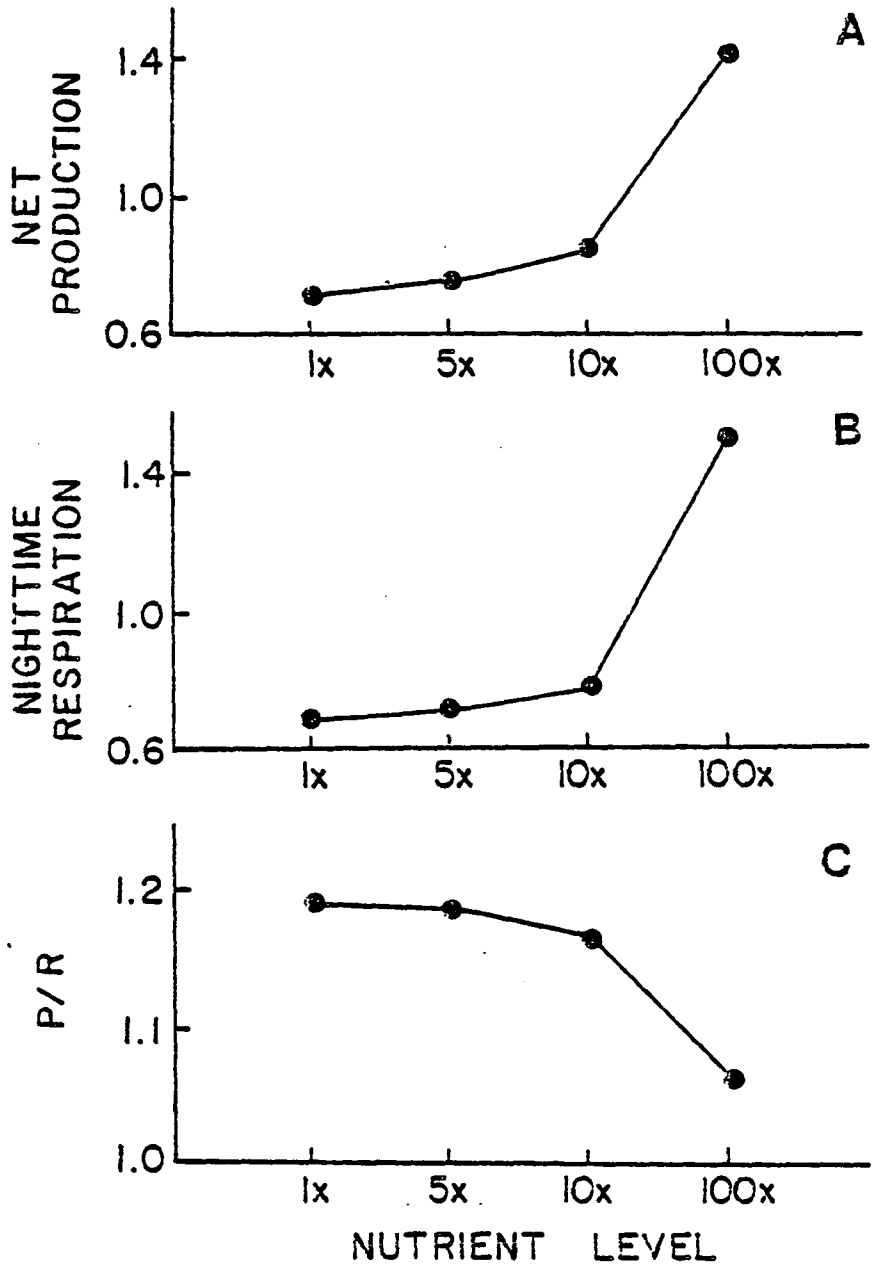

FIGURE 13. Net production and nighttime respiration, in mg O_2/l/hr, and P/R for the four nutrient levels in static microcosms. Each point represents the mean over the entire experiment.

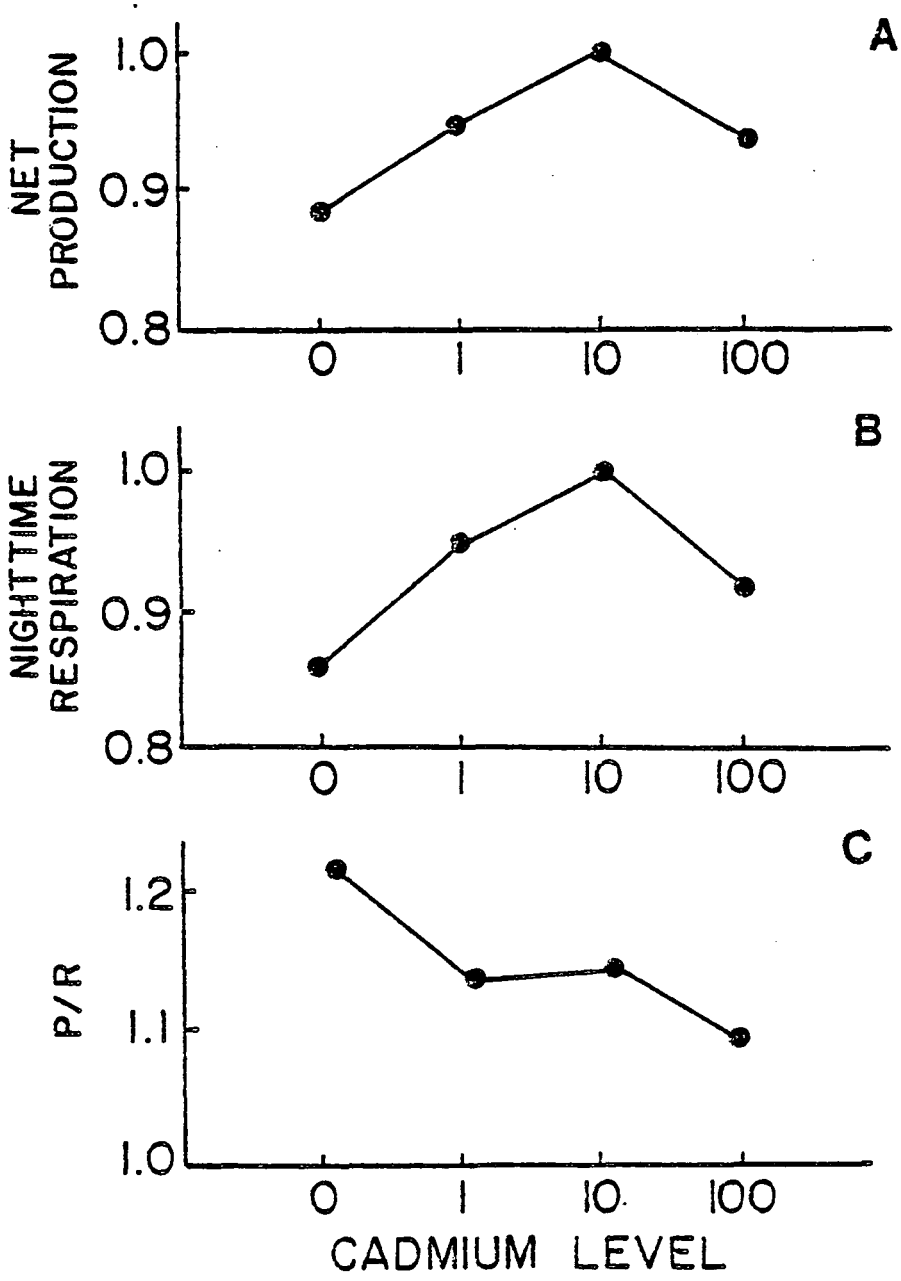

FIGURE 14. Net production and nighttime respiration, in mg O_2/l/12 hr, and P/R for the four levels of cadmium in static microcosms. Each point represents the mean over the entire experiment.

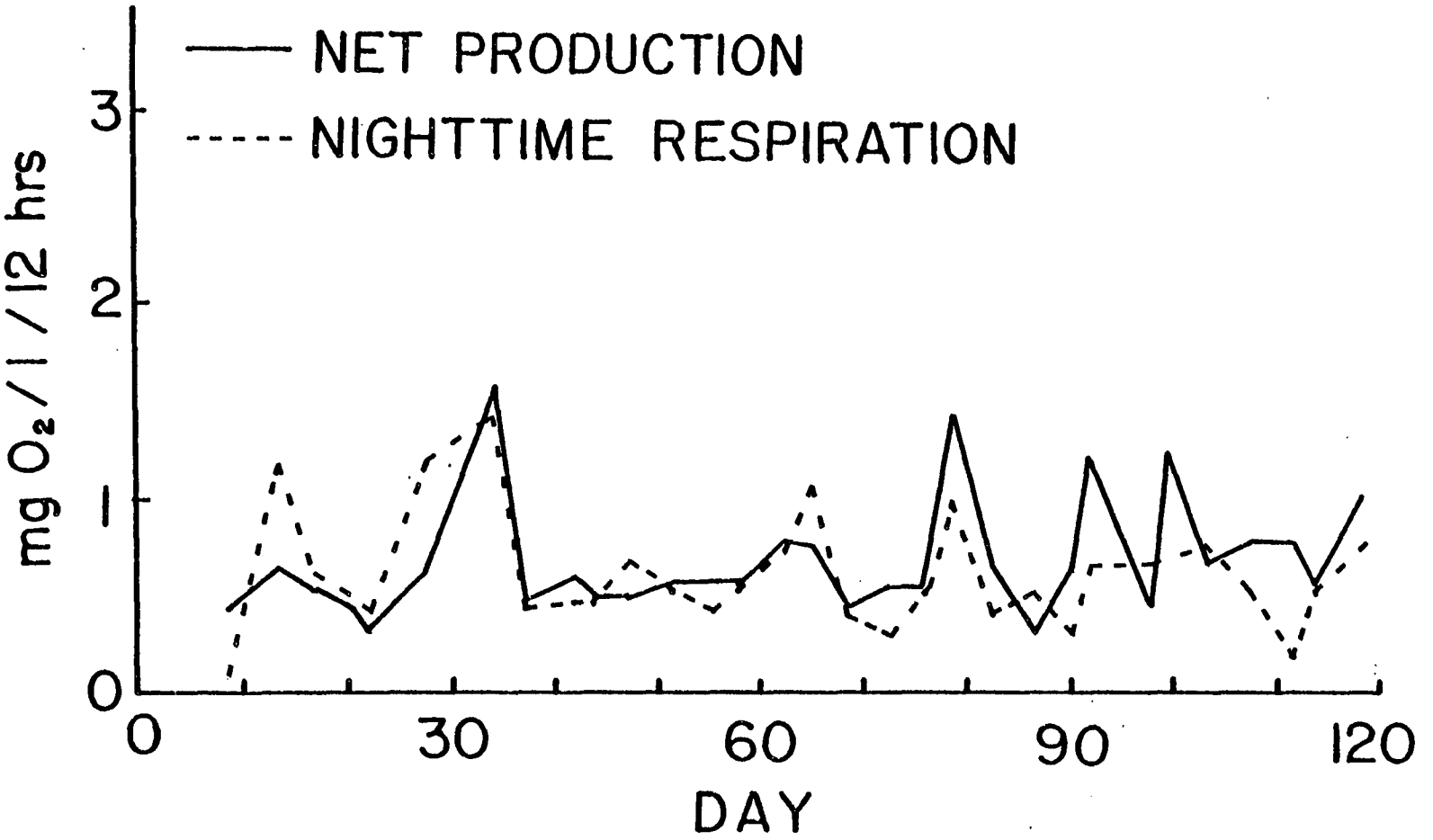

FIGURE 15. Community metabolic activity through time in lowest nutrient (Level 1) control static microcosms.

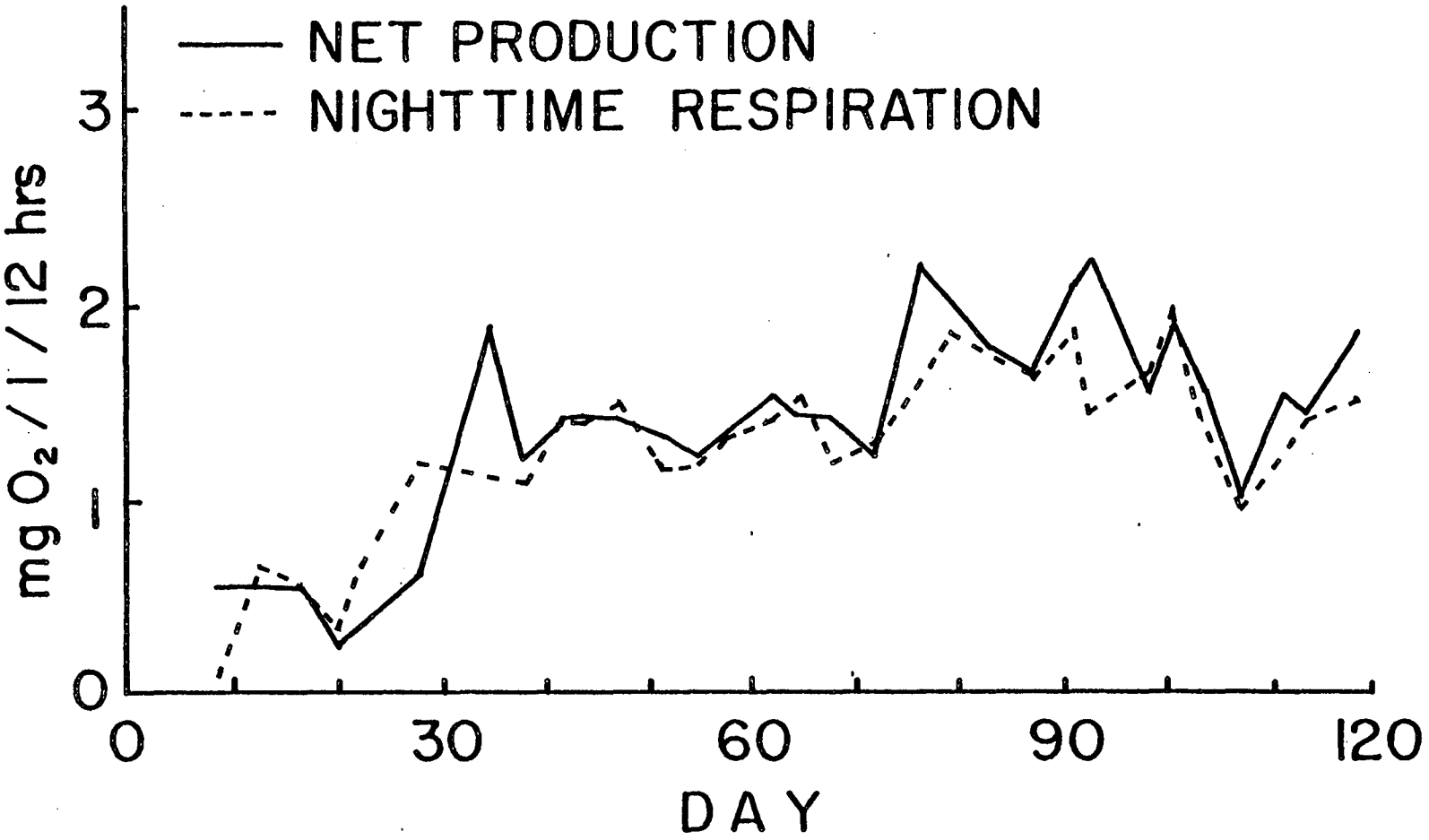

FIGURE 16. Community metabolic activity through time in highest nutrient (Level 4) control static microcosms.

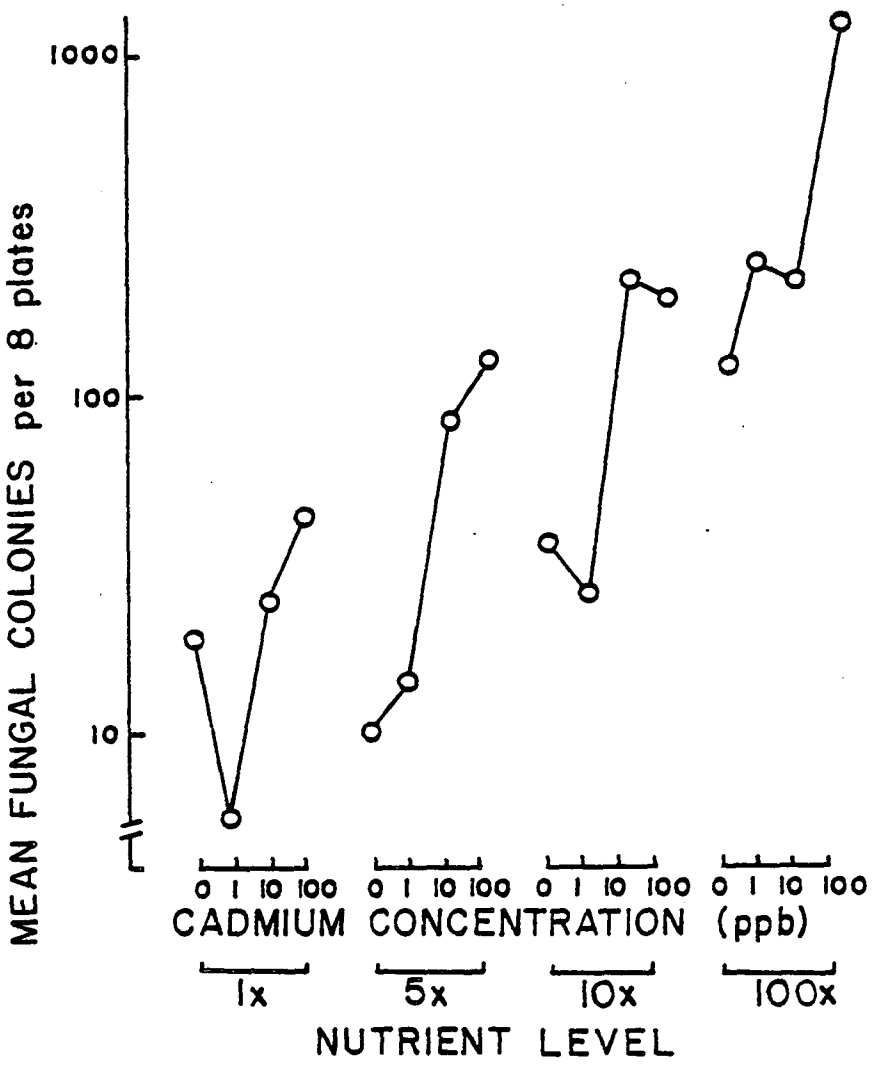

FIGURE 17. Influence of cadmium and nutrient enrichment on mean fungal colony abundance in static microcosms. Each point represents the mean over the entire experiment.

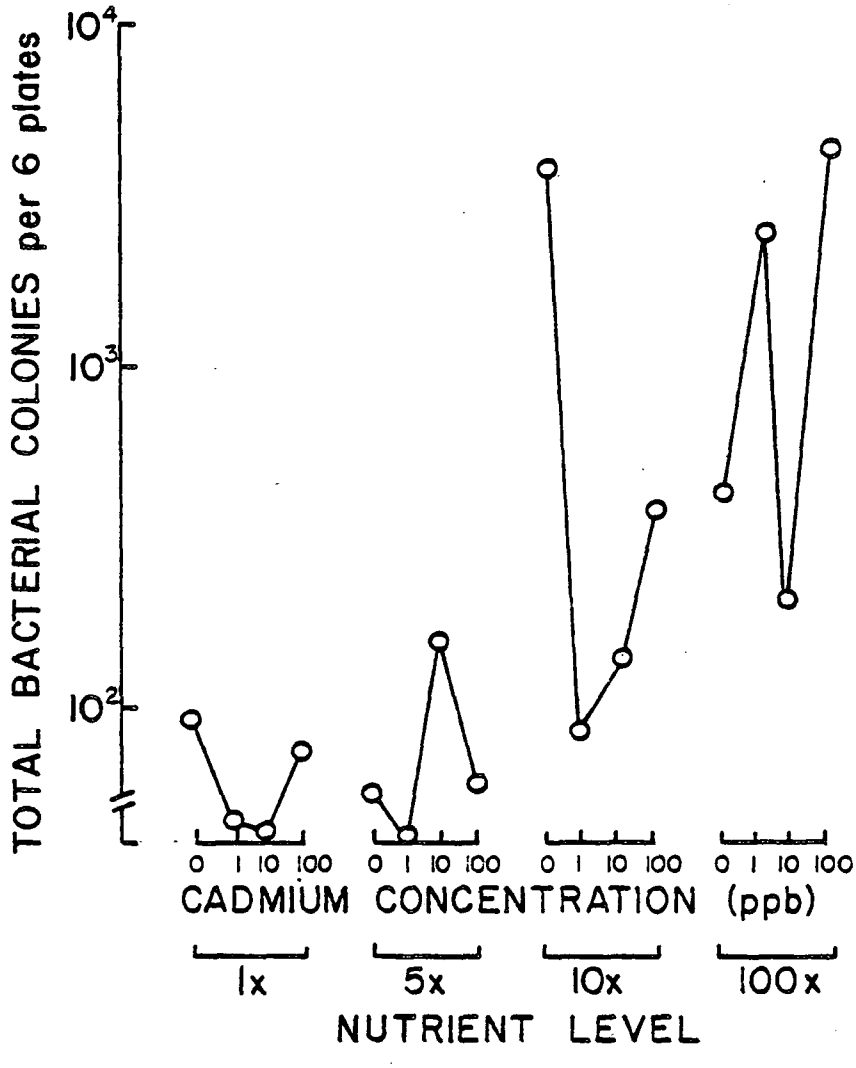

FIGURE 18. Influence of cadmium and nutrient enrichment on bacterial colony abundance in static microcosms. Each point represents the mean over the entire experiment.

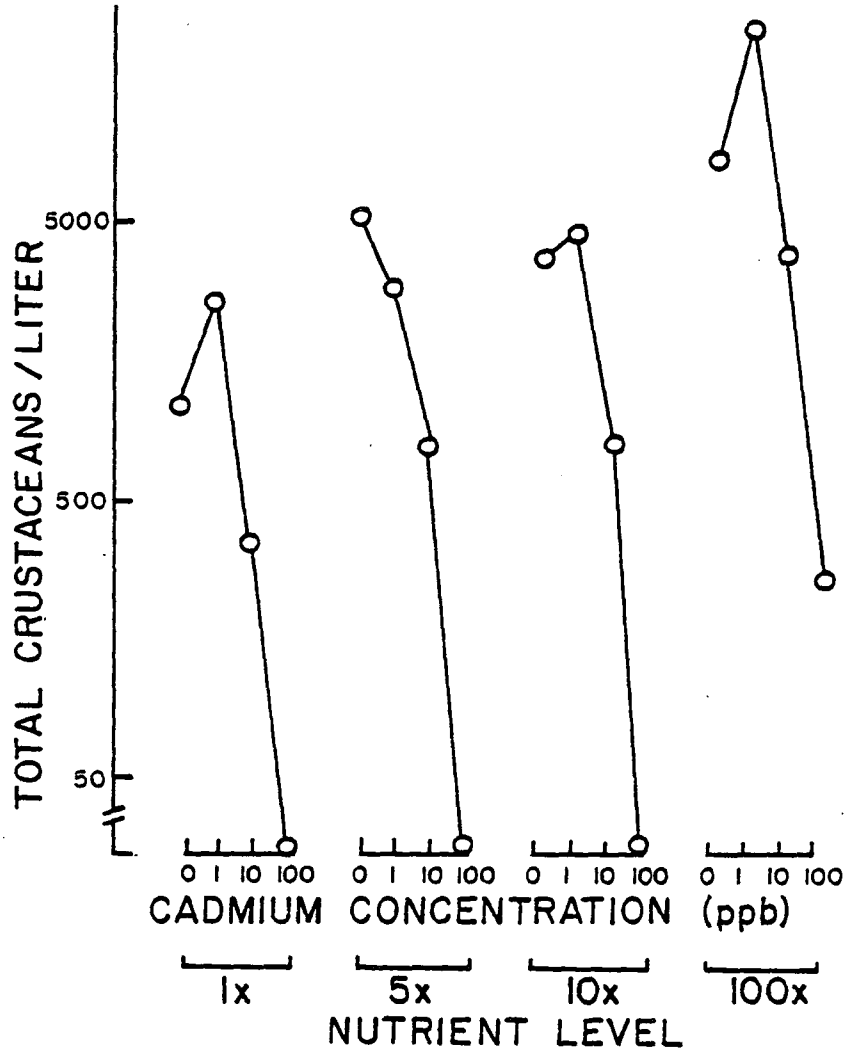

FIGURE 19. Influence of cadmium and nutrient enrichment on crustacean abundance in static microcosms. Each point represents the mean over the entire experiment.

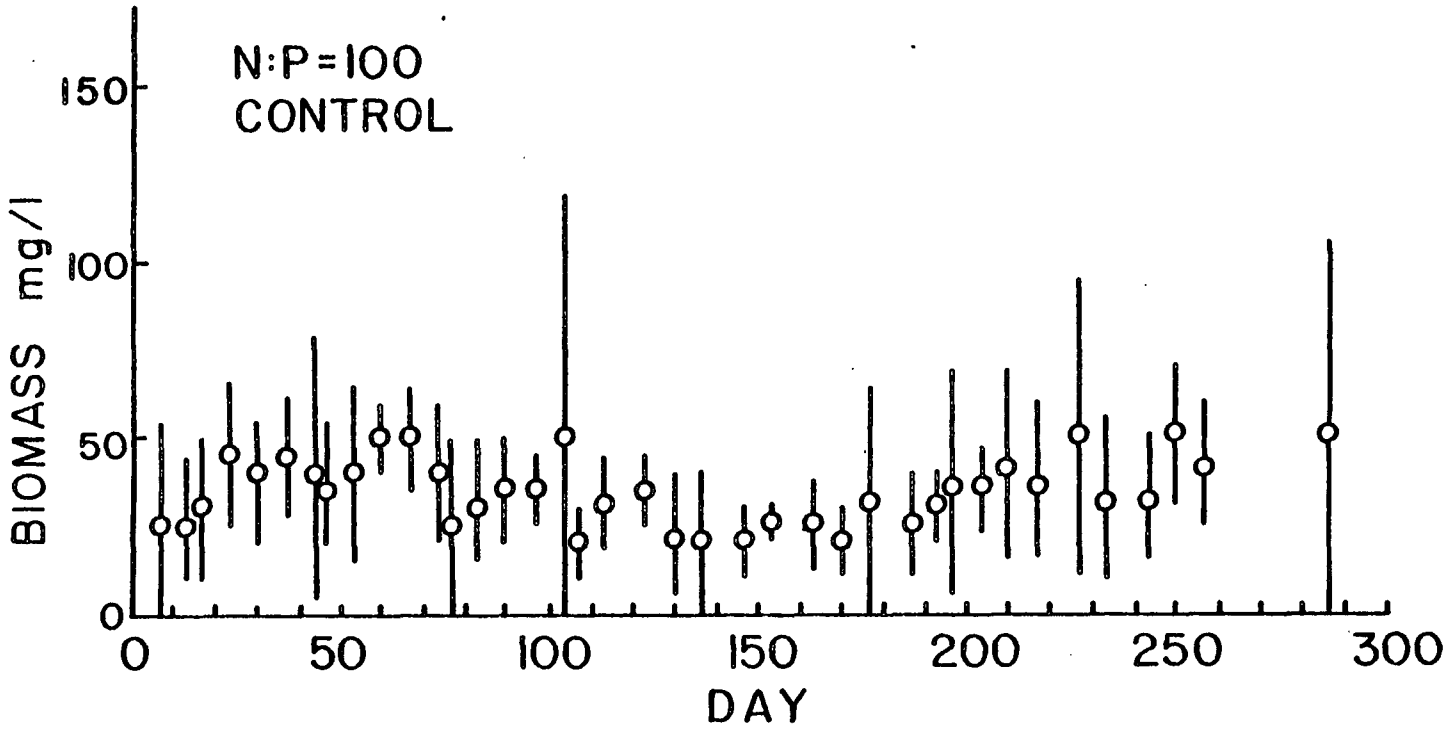

FIGURE 20. Biomass concentrations through time in phosphorus limited control flowthrough microcosms. Each point is the mean of four replicate systems with 95% confidence bars.

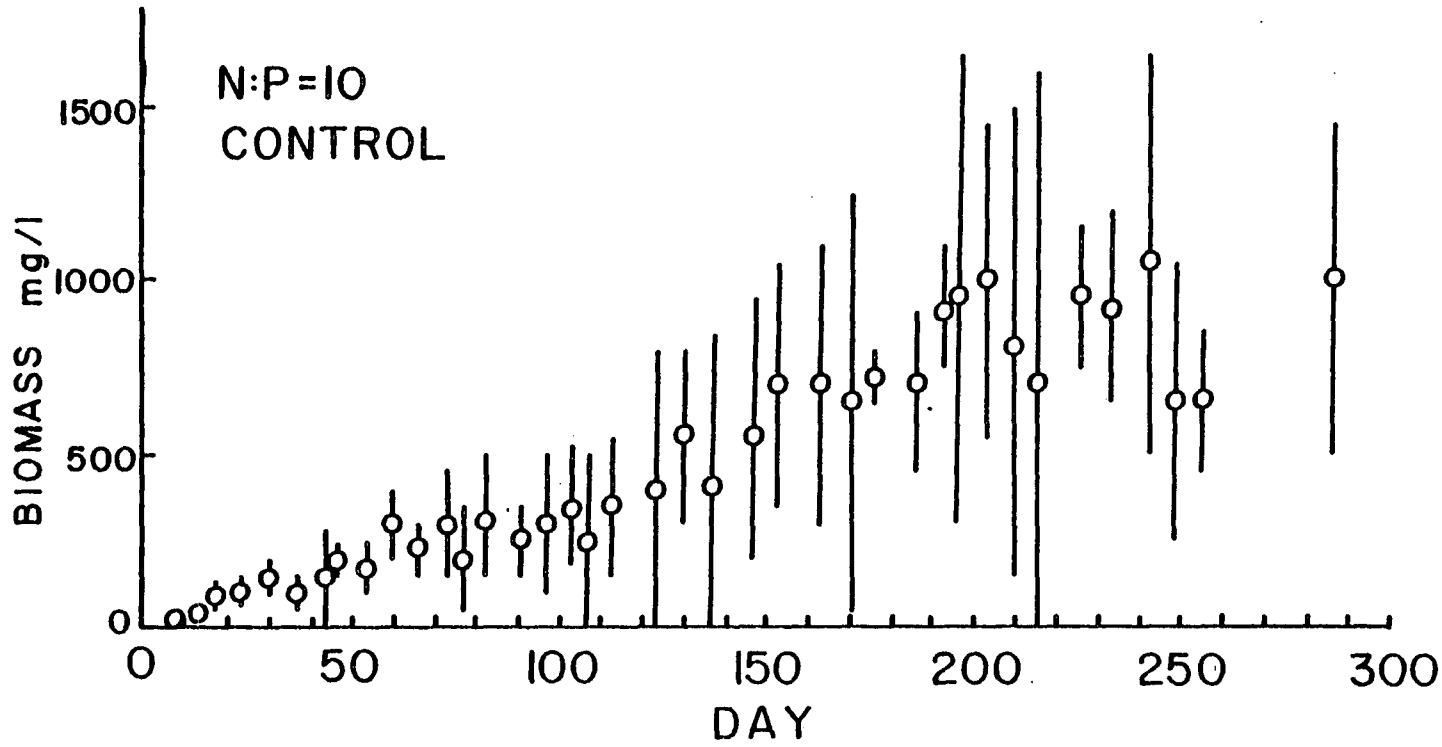

FIGURE 21. Biomass concentrations through time in non-phosphorus-limited control flowthrough microcosms. Each point is the mean of four replicate systems with 95% confidence bars.

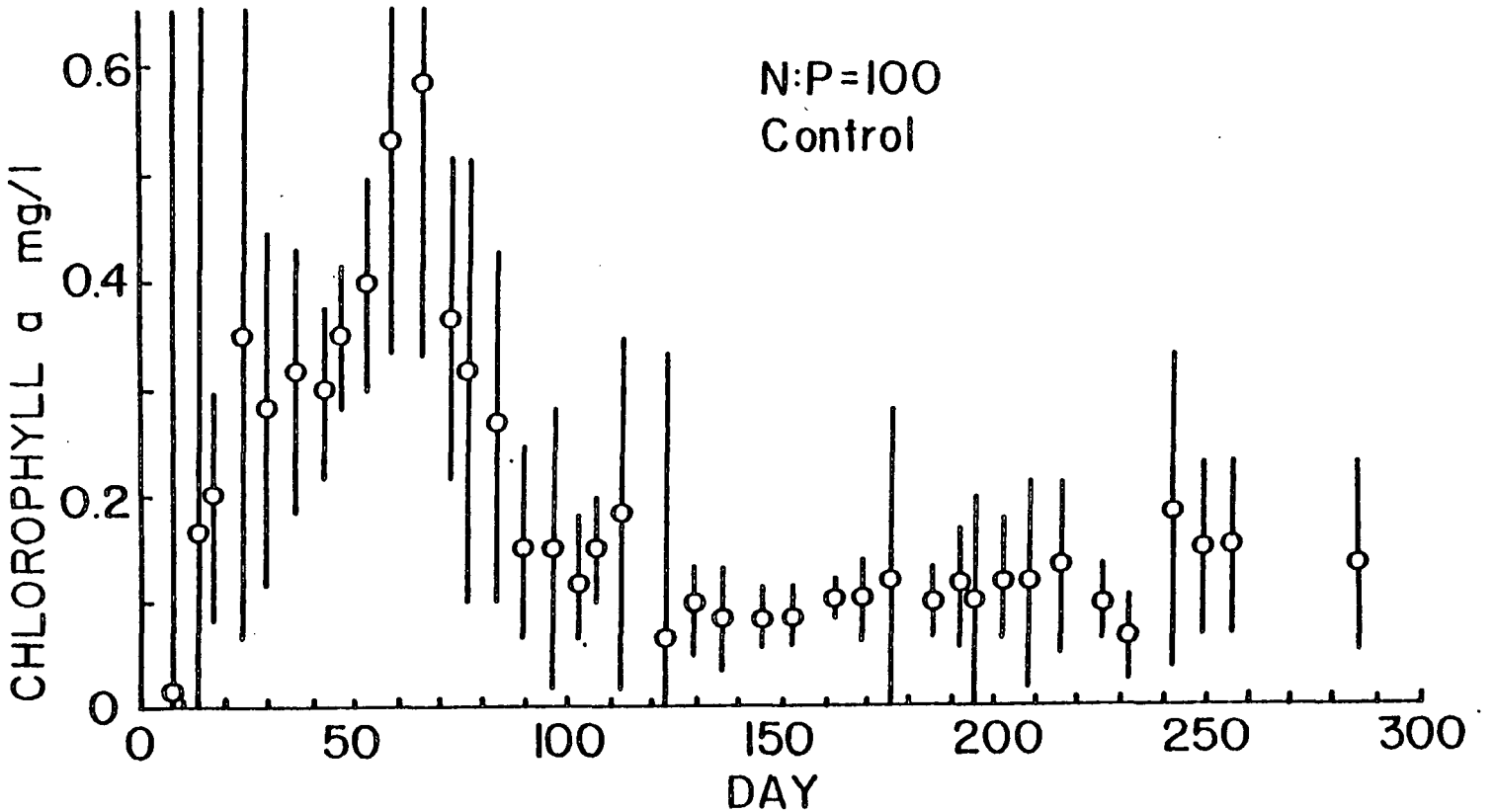

FIGURE 22. Chlorophyll a concentrations through time in N:P = 100 control flowthrough microcosms. Each point is the mean of four replicate systems with 95% confidence bars.

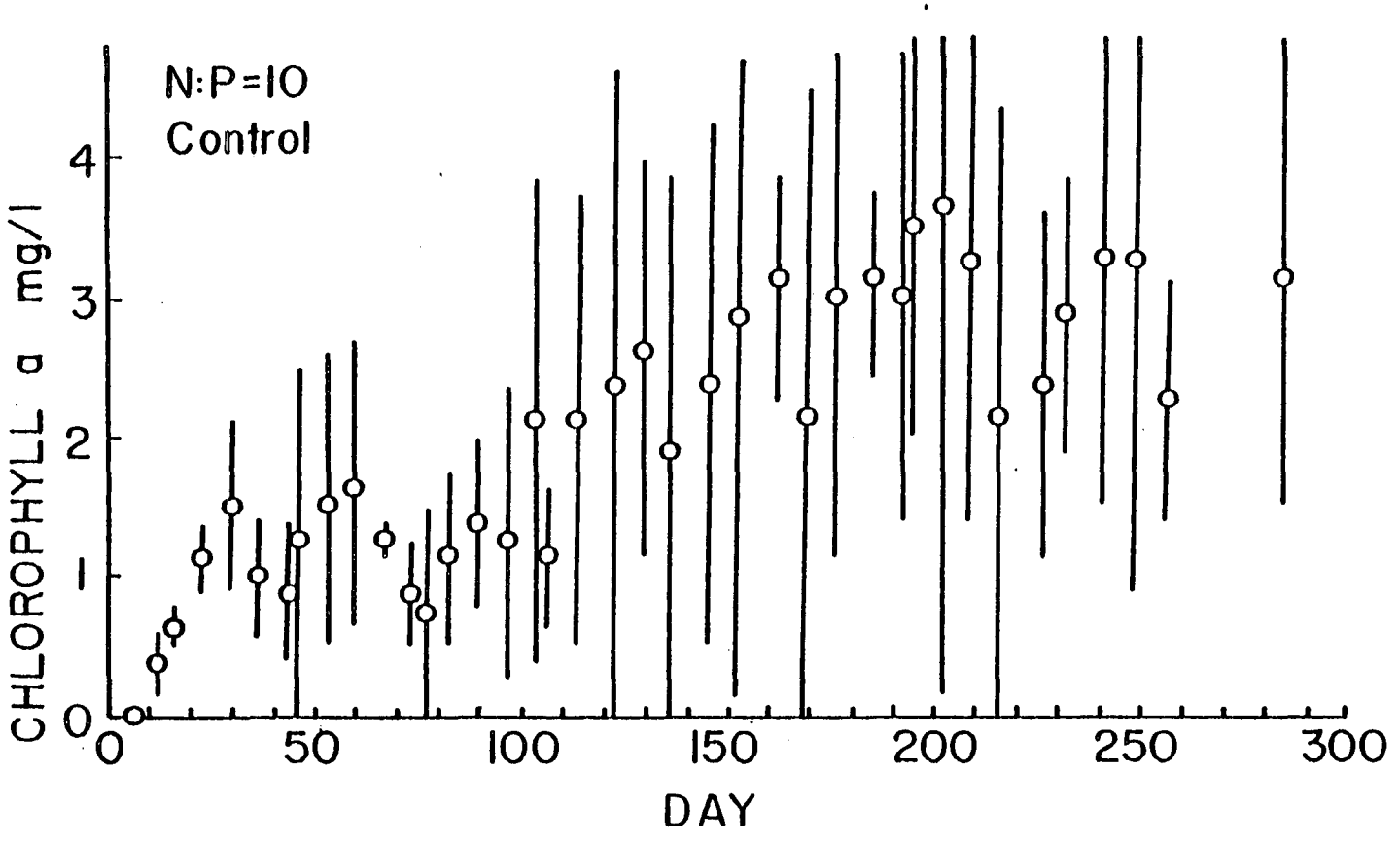

FIGURE 23. Chlorophyll a concentrations through time in N:P = 10 control flowthrough microcosms. Each point is the mean of four replicate systems with 95% confidence bars.

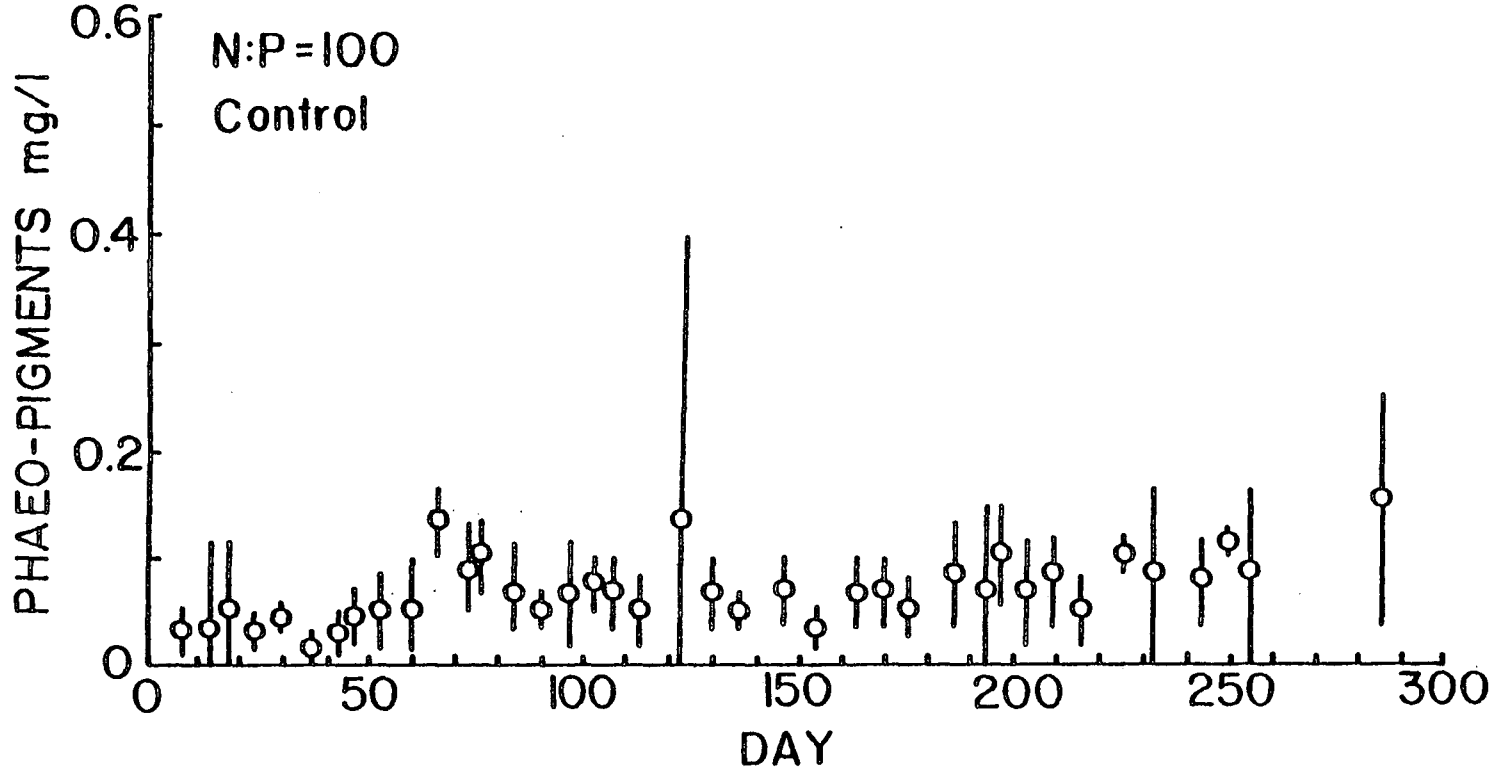

FIGURE 24. Phaeo-pigment concentrations through time in N:P = 100 control flowthrough microcosms. Each point is the mean of four replicate systems with 95% confidence bars.

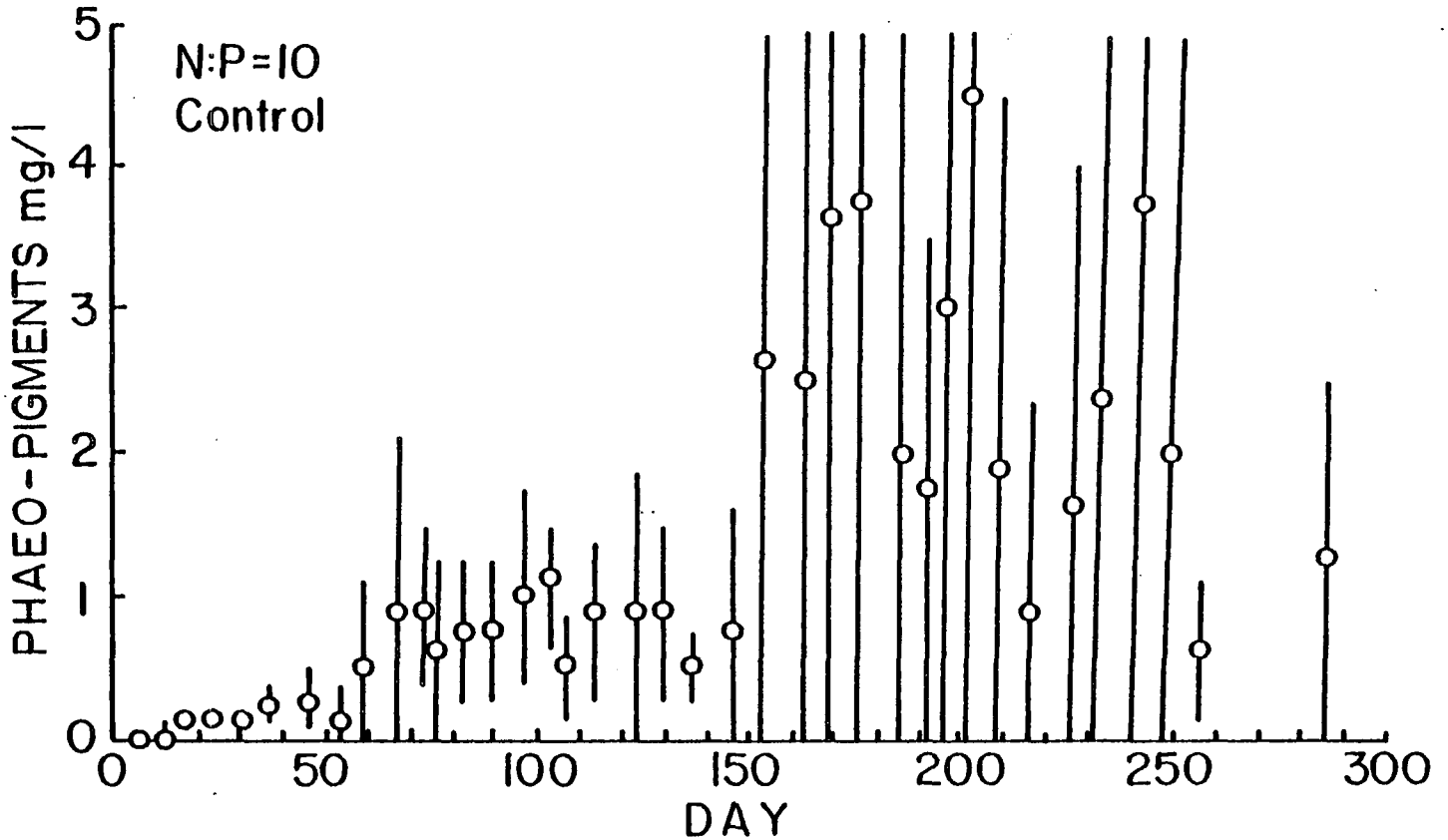

FIGURE 25. Phaeo-pigment concentrations through time in N:P = 10 control flowthrough microcosms. Each point is the mean of four replicate systems with 95% confidence bars.

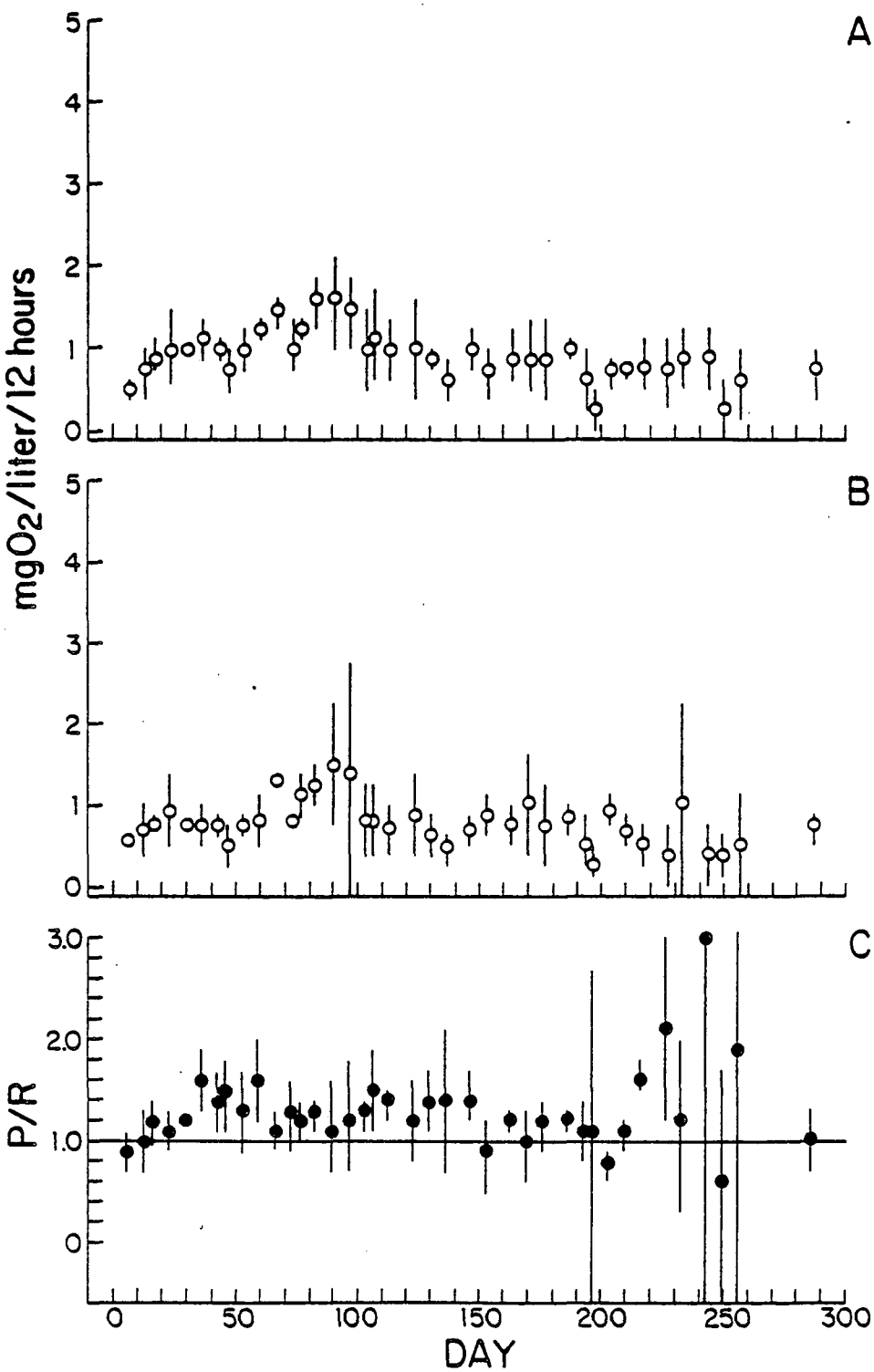

FIGURE 26. Net daytime production (A), nighttime respiration (B), and P/R (C) through time in flowthrough microcosms with input N:P = 100 and no cadmium. Each point is the mean of four replicate systems with 95% confidence bars.

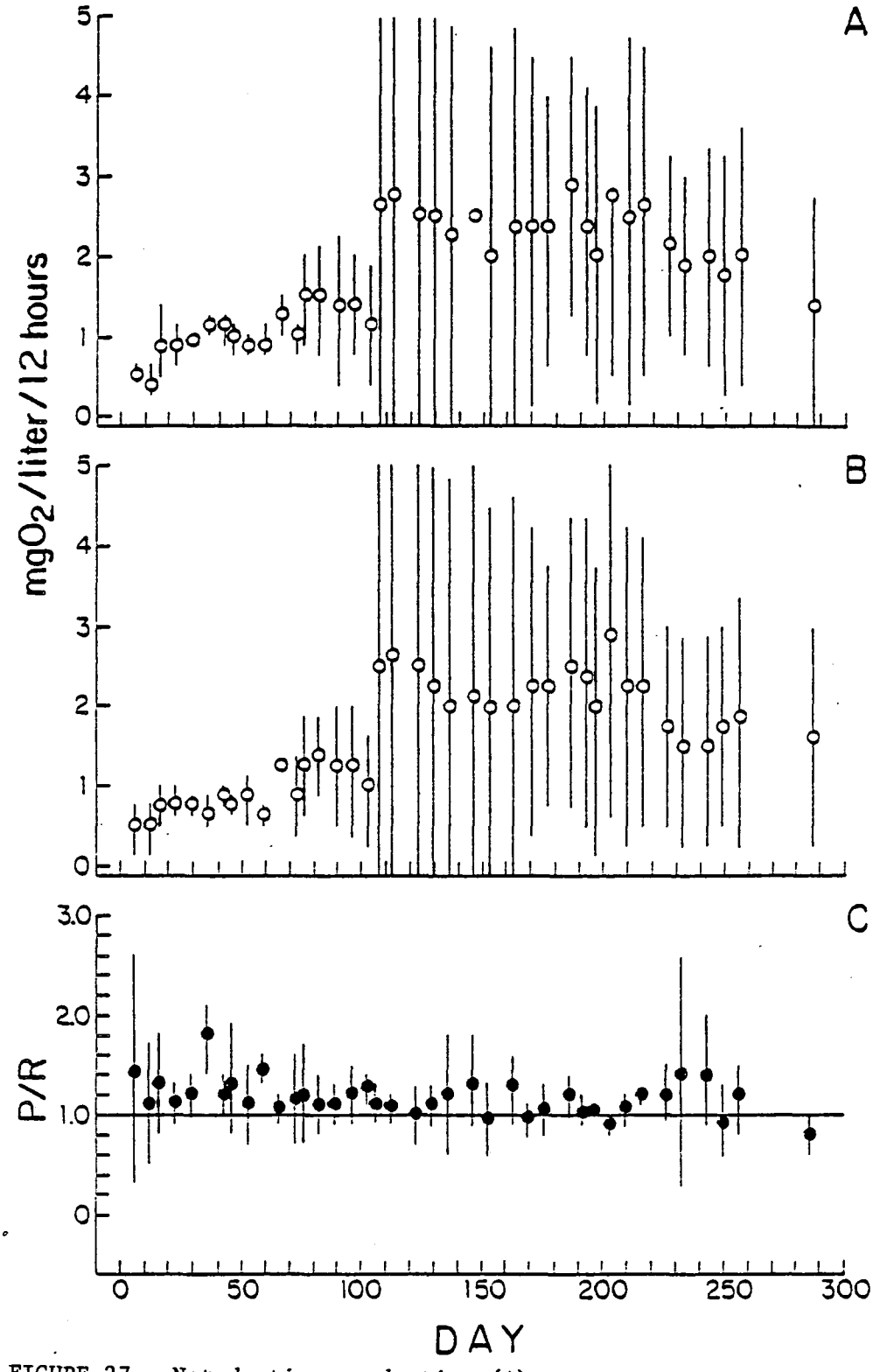

FIGURE 27. Net daytime production (A), nighttime respiration (B), and P/R (C) through time in flowthrough microcosms with input N:P = 100 and continuous 10 ppb Cd input. Each point is the mean of four replicate systems with 95% confidence bars.

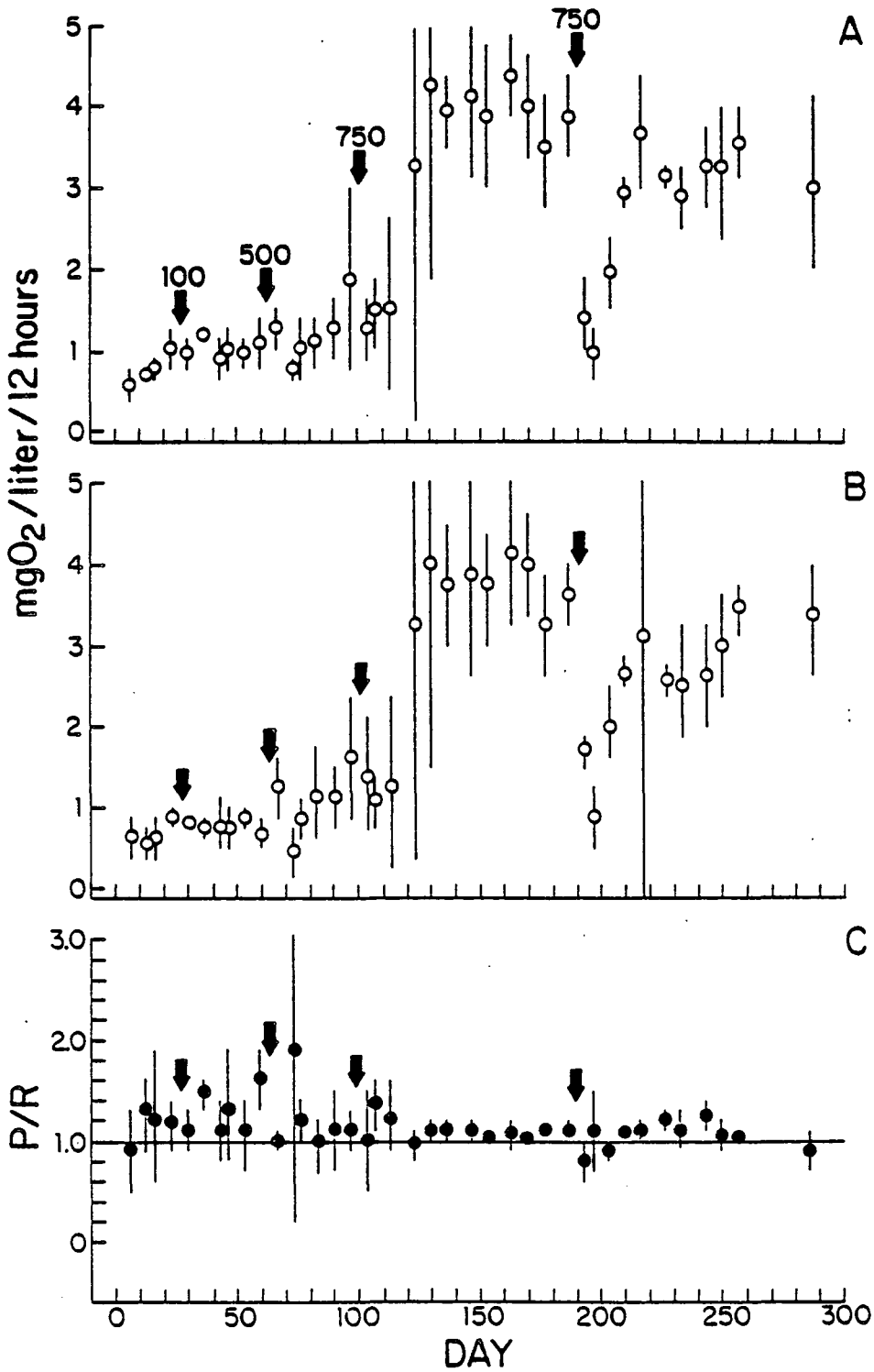

FIGURE 28. Net daytime production (A), nighttime respiration (B), and P/R (C) through time in flowthrough microcosms with input N:P = 100 and cadmium pulses as indicated in ppb Cd by arrows. Each point is the mean of four replicate systems with 95% confidence bars.

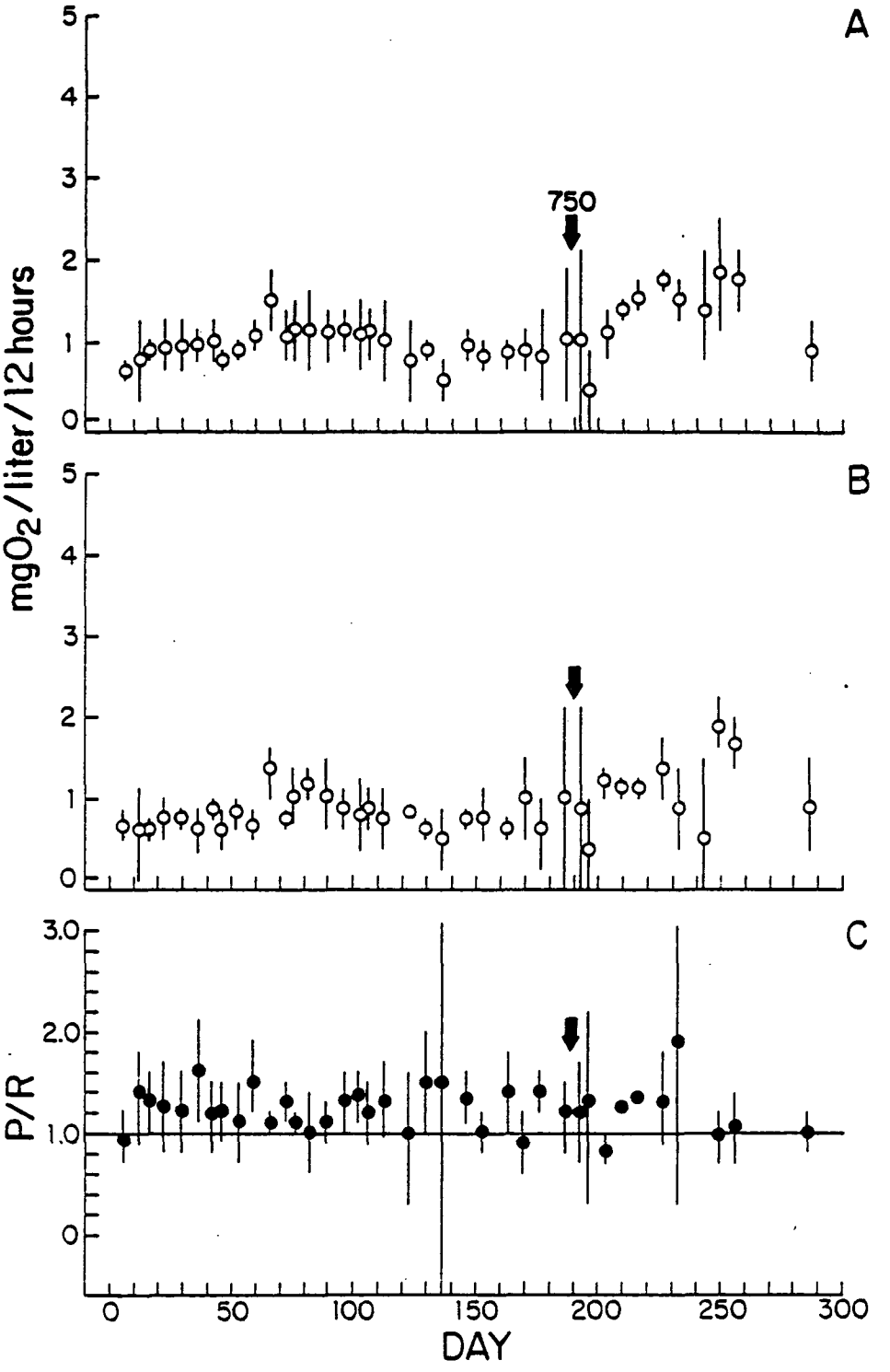

FIGURE 29. Net daytime production (A), nighttime respiration (B), and P/R (C) through time in flowthrough microcosms with input N:P = 100 and cadmium pulse as indicated in ppb Cd by arrow. Each point is the mean of four replicate systems with 95% confidence bars.

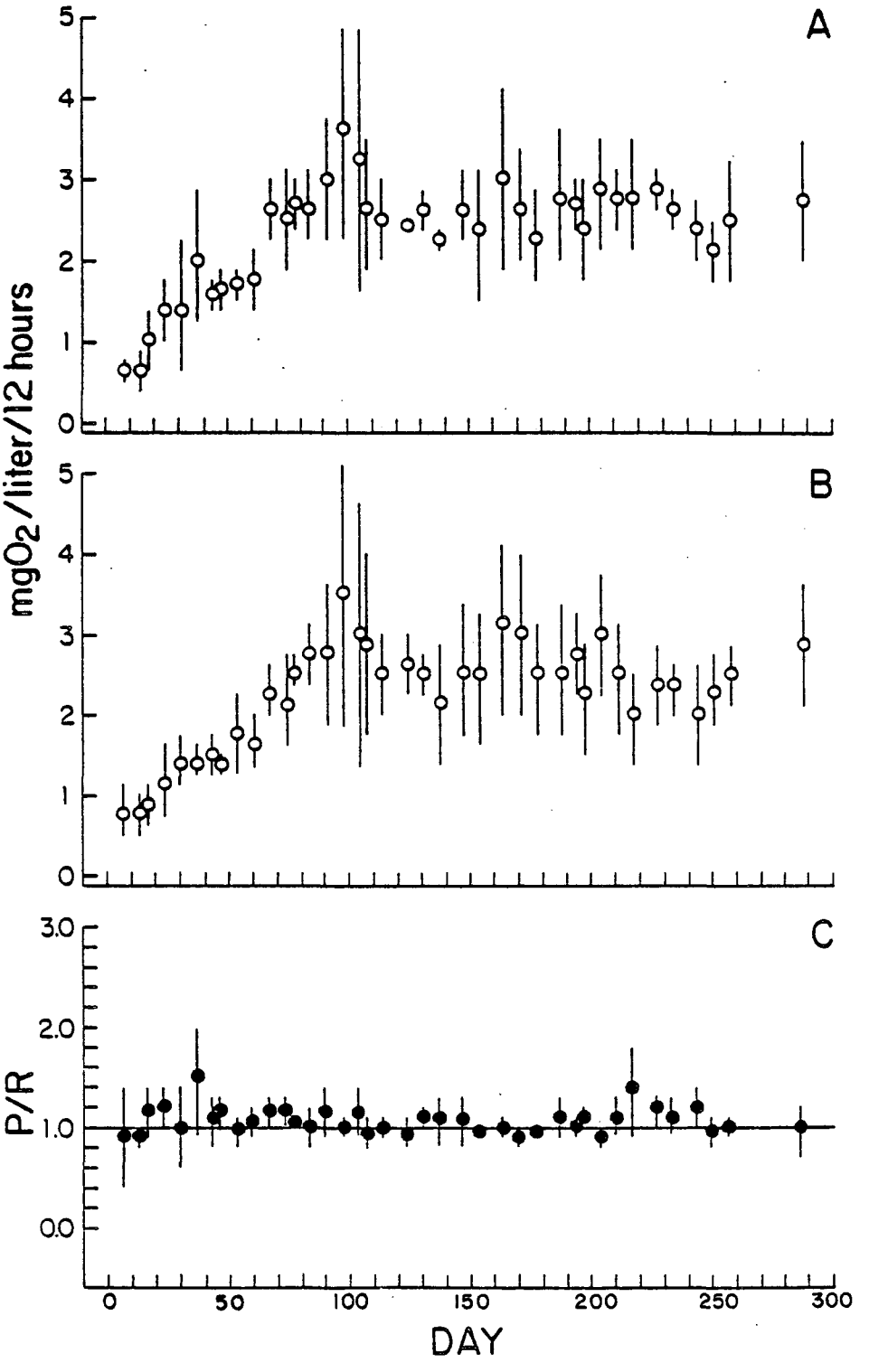

FIGURE 30. Net daytime production (A), nighttime respiration (B), and P/R (C) through time in flowthrough microcosms with input N:P = 10 and no cadmium. Each point is the mean of four replicate systems with 95% confidence bars.

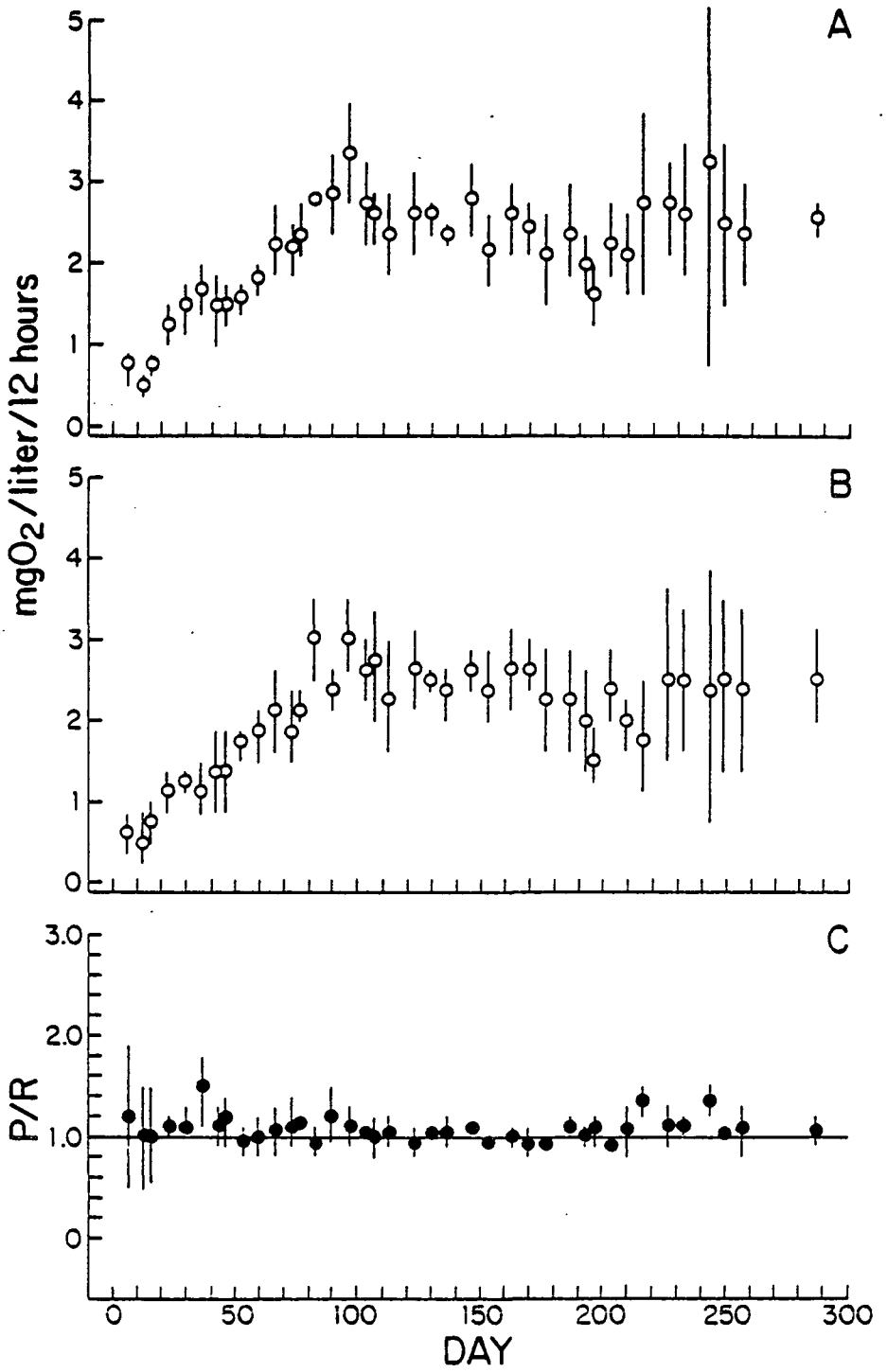

FIGURE 31. Net daytime production (A), nighttime respiration (B), and P/R (C) through time in flowthrough microcosms with input N:P = 10 and continuing 10 ppb Cd inputs. Each point is the mean of four replicate systems with 95% confidence bars.

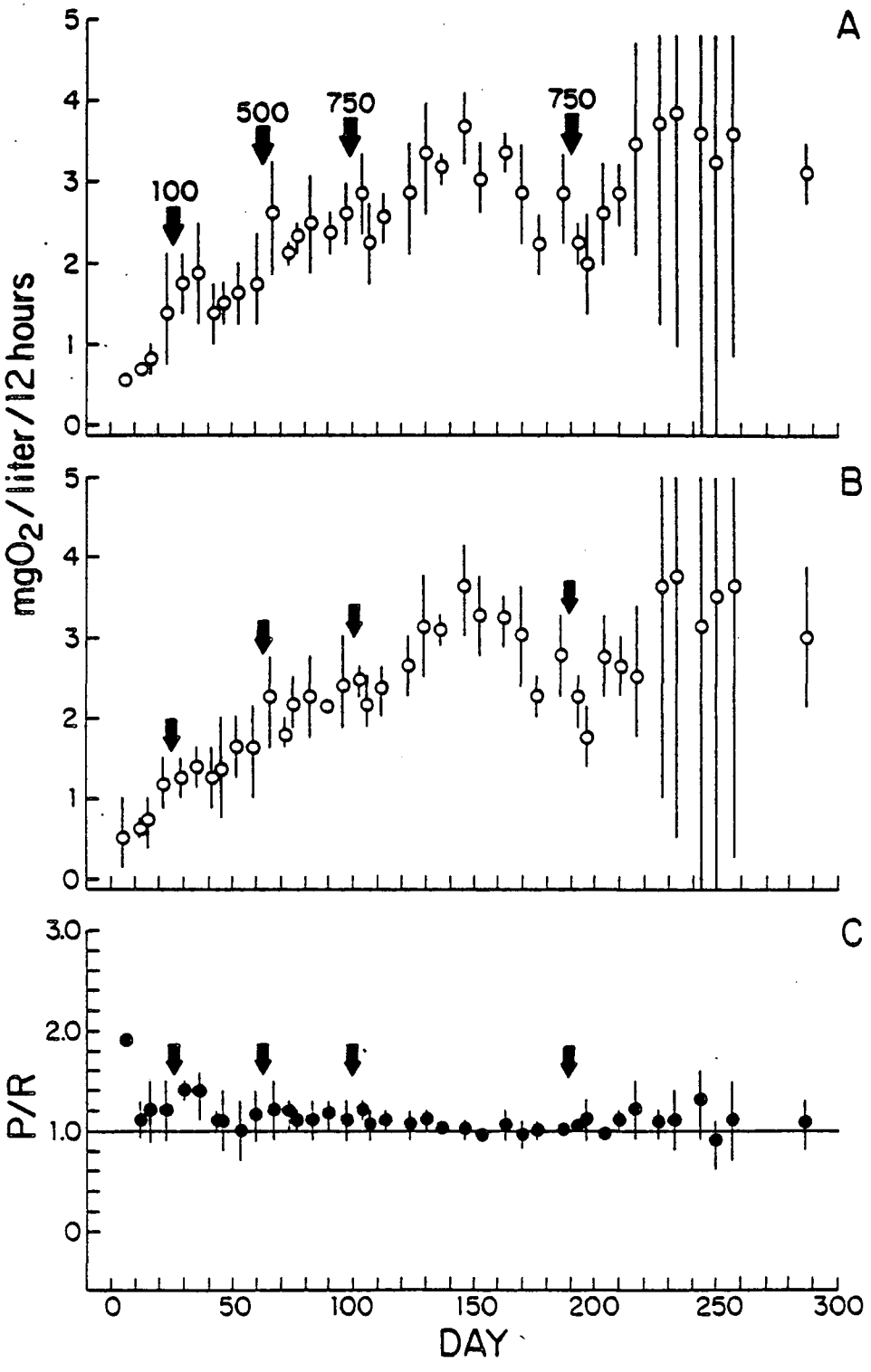

FIGURE 32. Net daytime production (A), nighttime respiration (B), and P/R (C) through time in flowthrough microcosms with input N:P - 10 and cadmium pulses as indicated in ppb Cd by arrows. Each point is the mean of four replicate systems with 95% confidence bars.

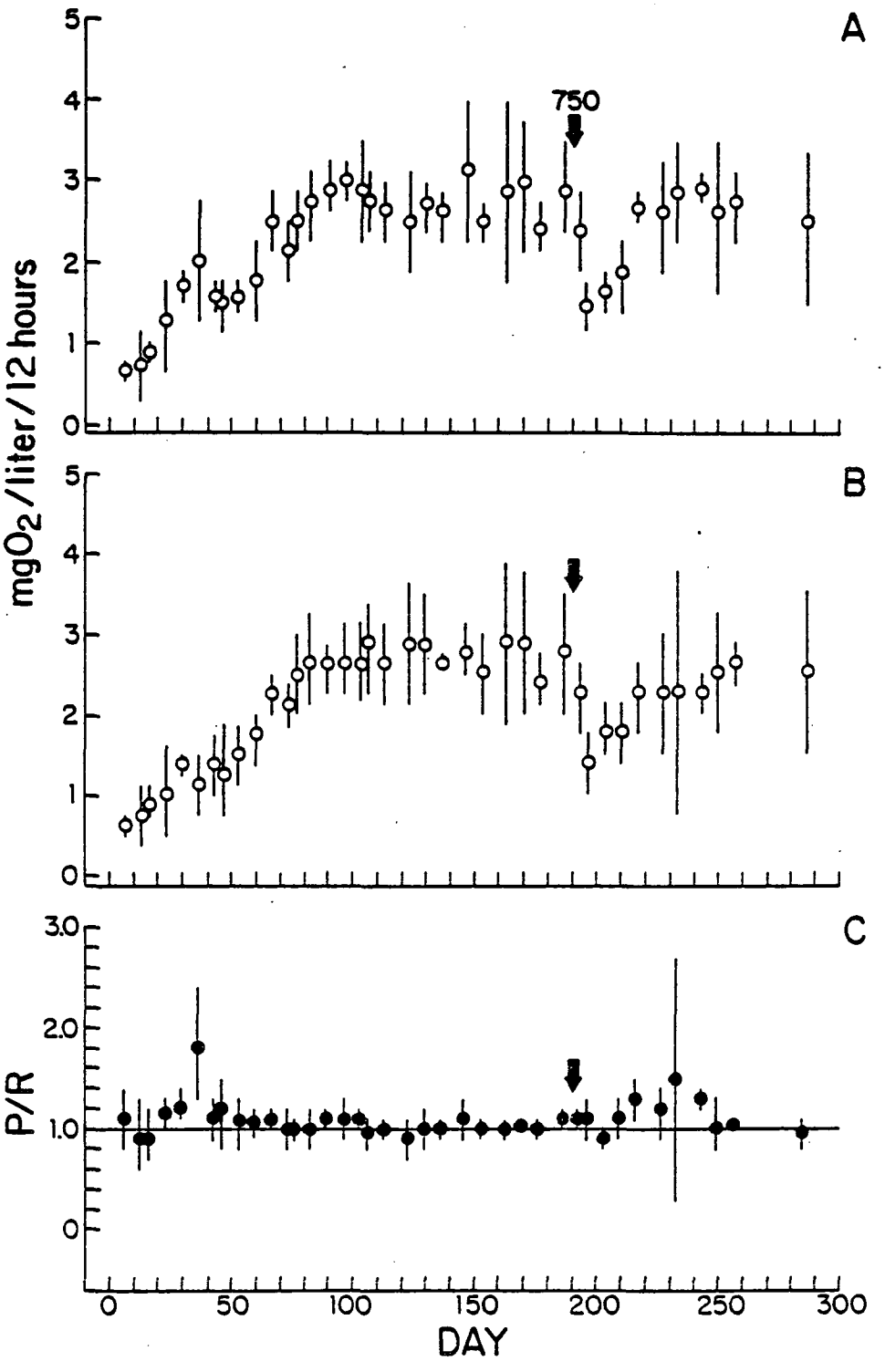

FIGURE 33. Net daytime production (A), nighttime respiration (B), and P/R (C) through time in flowthrough microcosms with input N:P = 10 and cadmium pulse as indicated in ppb Cd by arrow. Each point is the mean of four replicate systems with 95% confidence bars.

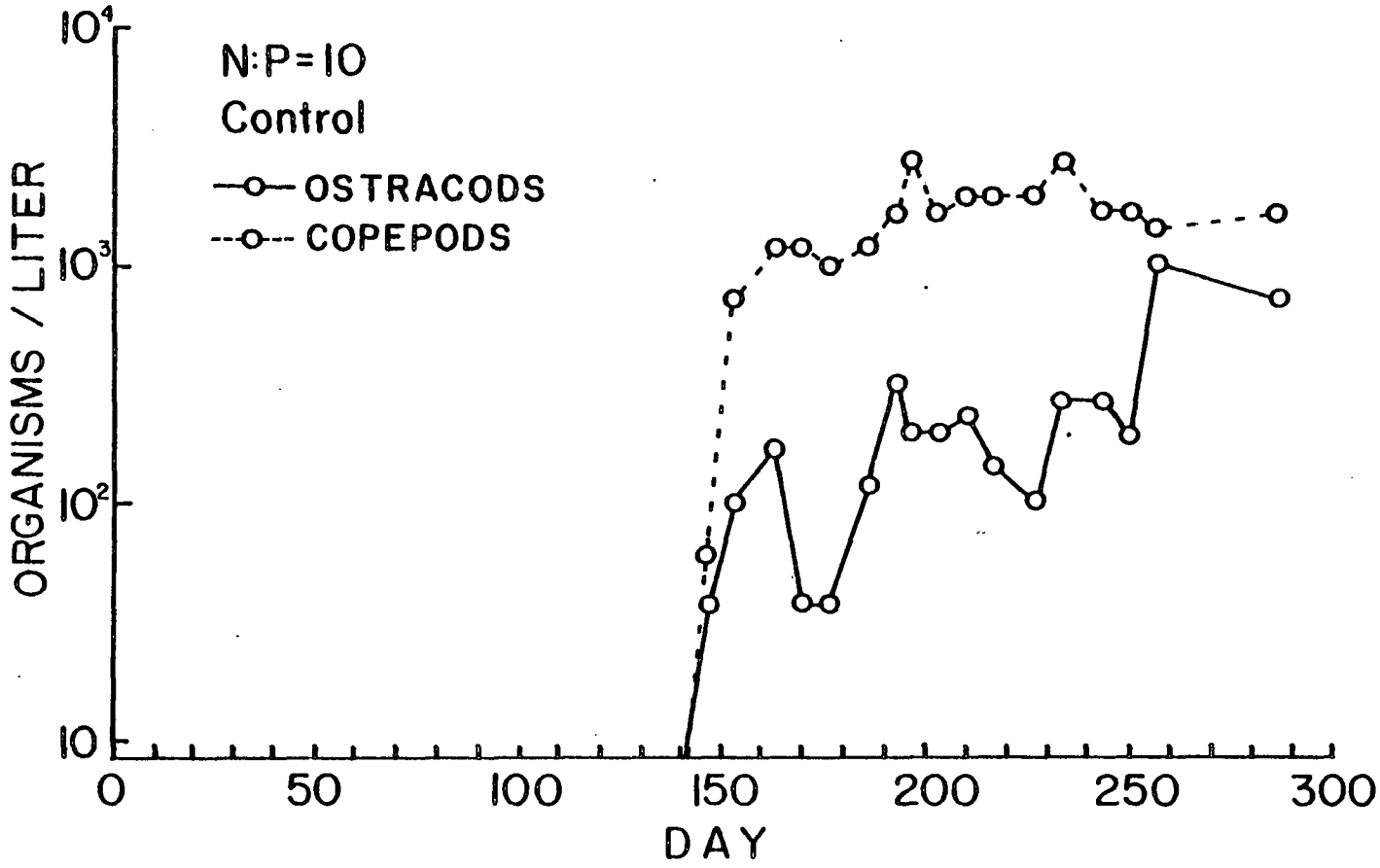

FIGURE 34. Crustacean abundance through time in flowthrough microcosms with input N:P = 10 and no cadmium. Each point is the mean of four replicate systems.

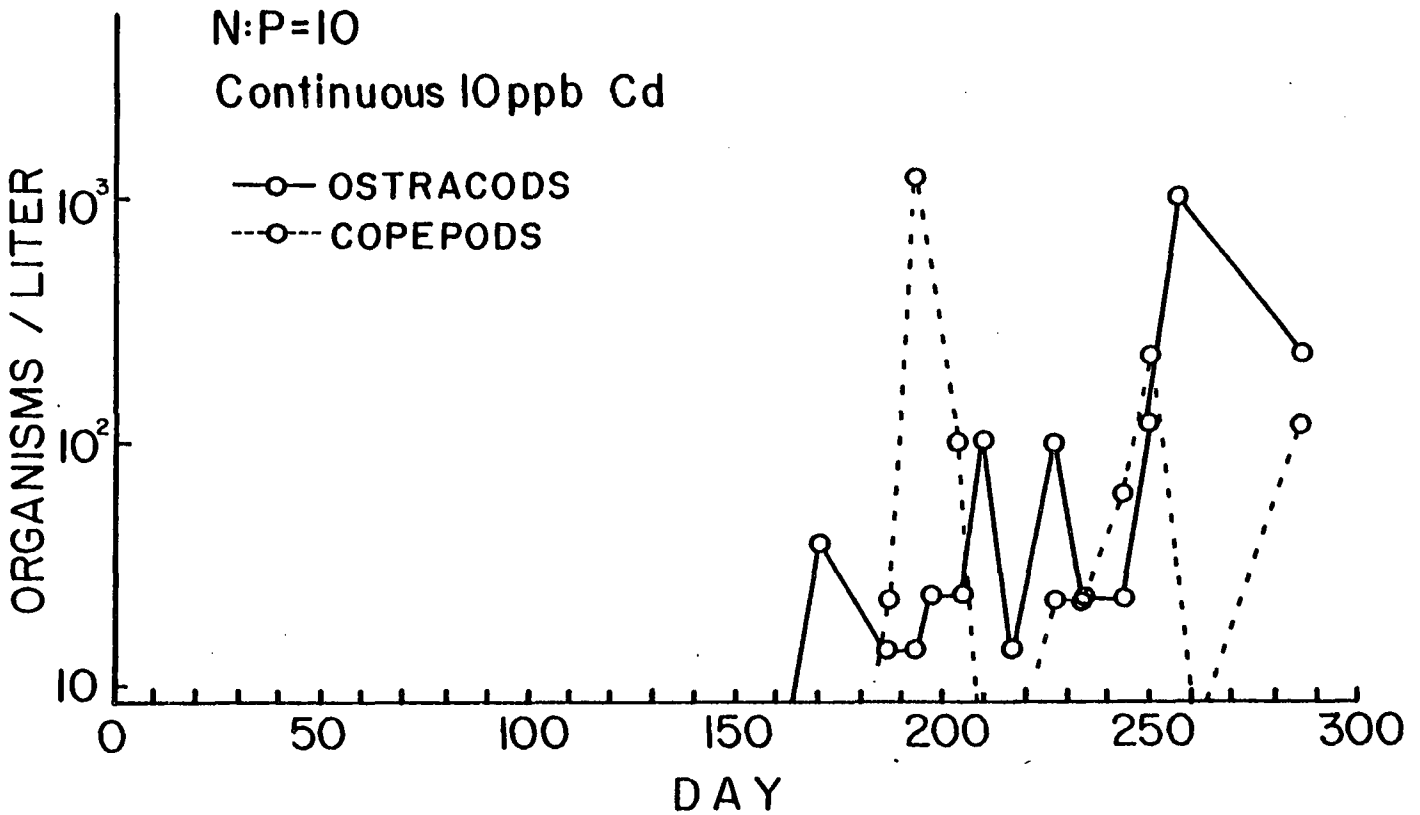

FIGURE 35. Crustacean abundance through time in flowthrough microcosms with input N:P = 10 and continuous 10 ppb Cd inputs. Each point is the mean of four replicate systems.

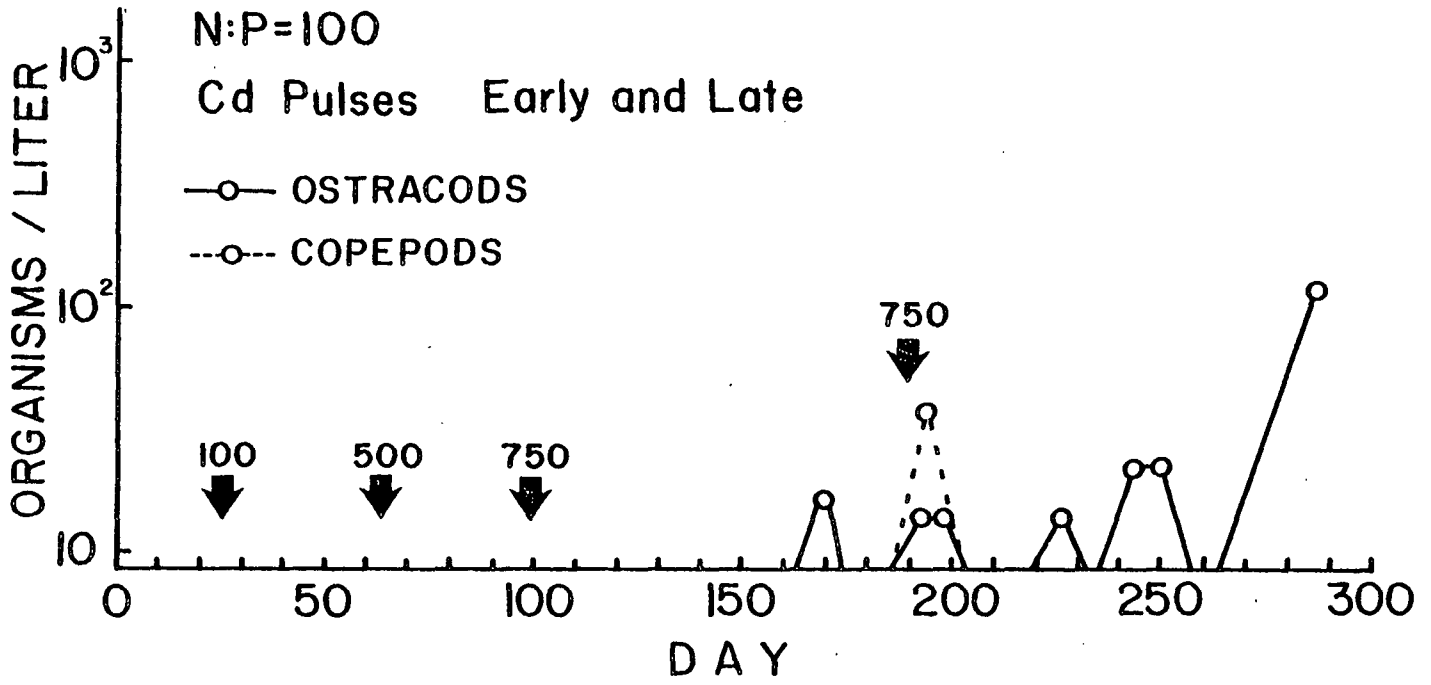

FIGURE 36. Crustacean abundance through time time in flowthrough microcosms with input N:P = 10, and cadmium pulses as indicated in ppb Cd by arrows. Each point is the mean of four replicate systems.

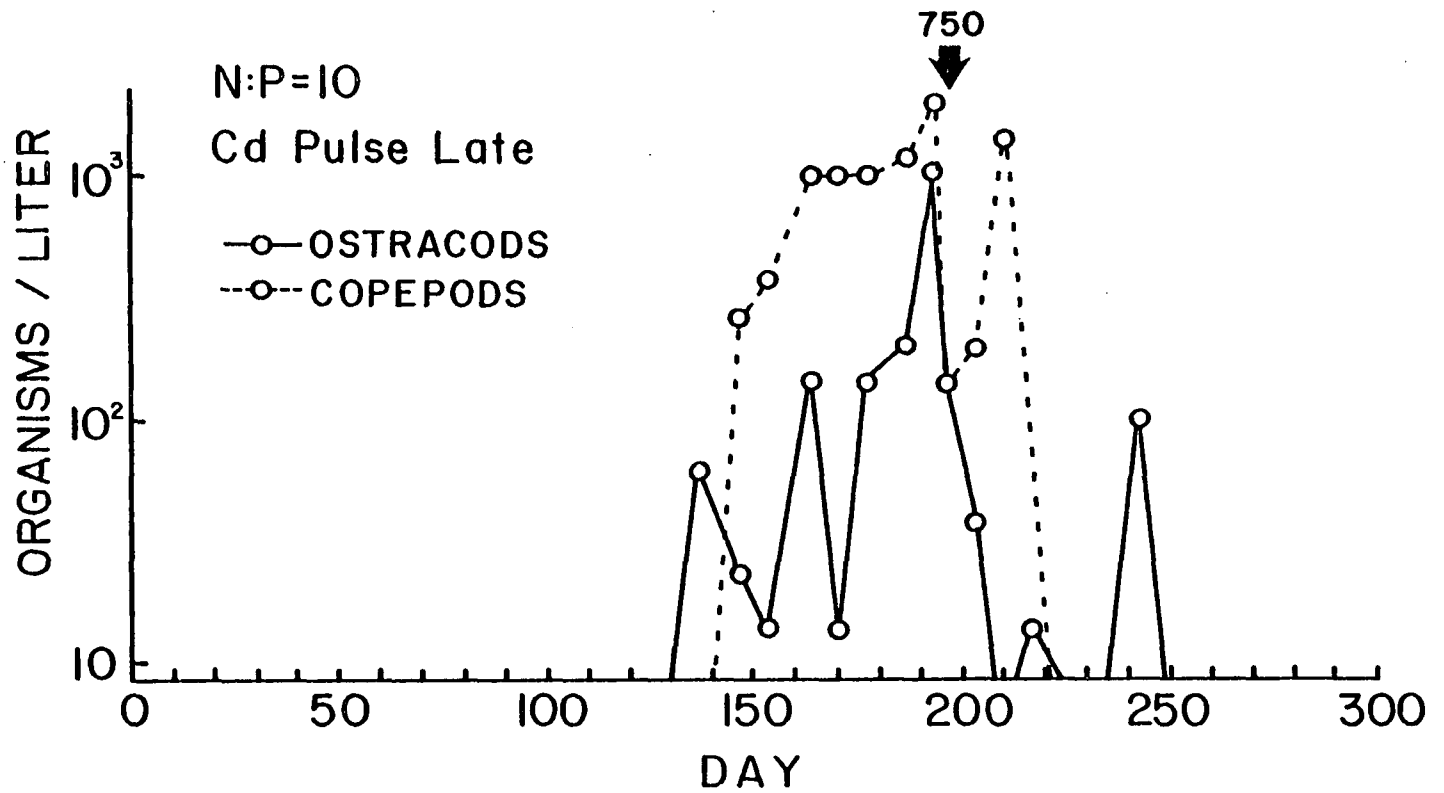

FIGURE 37. Crustacean abundance through time in flowthrough microcosms with input N:P = 10 and cadmium pulse as indicated in ppb Cd by arrows. EAch point is the mean of four replicate systems.

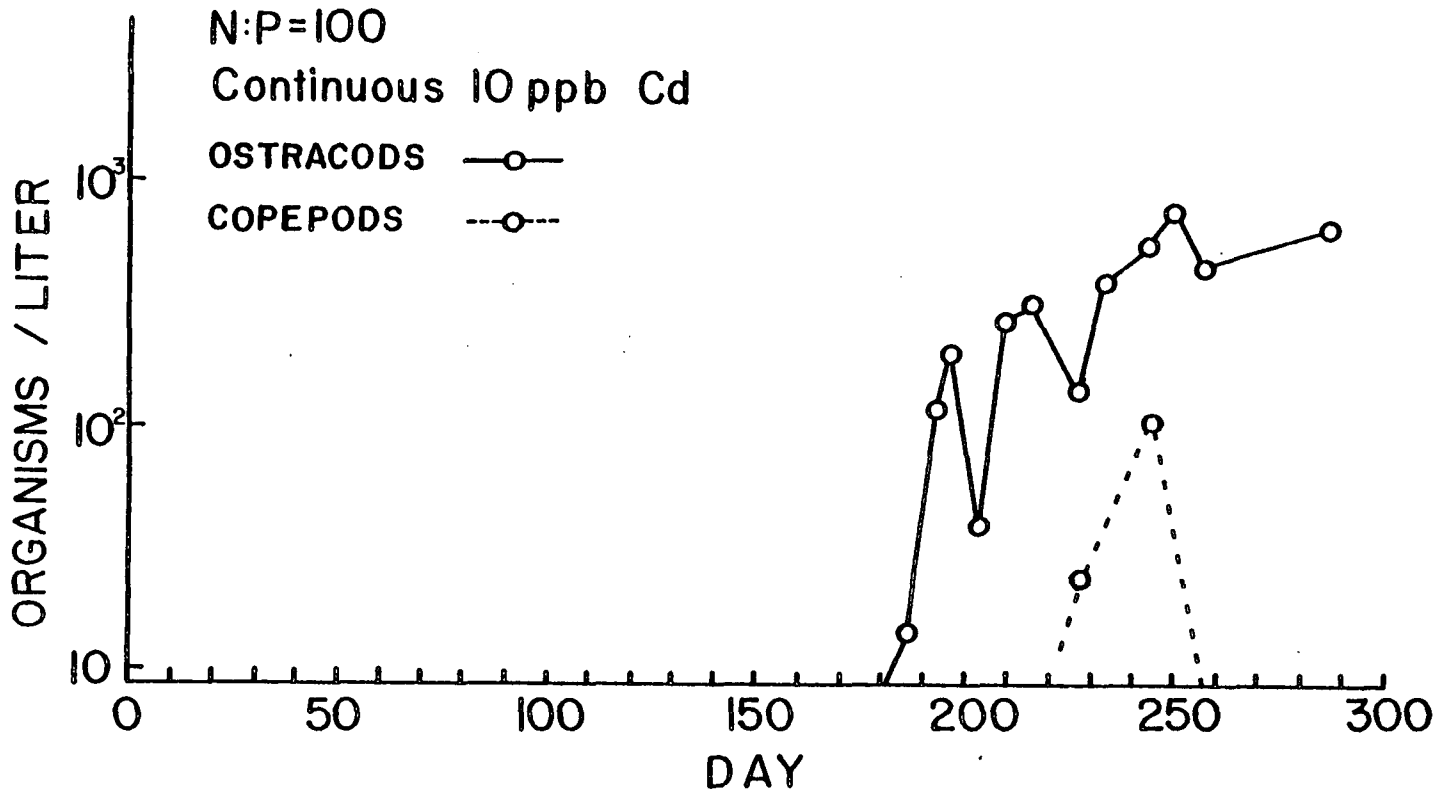

FIGURE 38. Crustacean abundance through time in flowthrough microcosms with input N:P = 100 and continuous 10 ppb Cd inputs. Each point is the mean of four replicate systems.

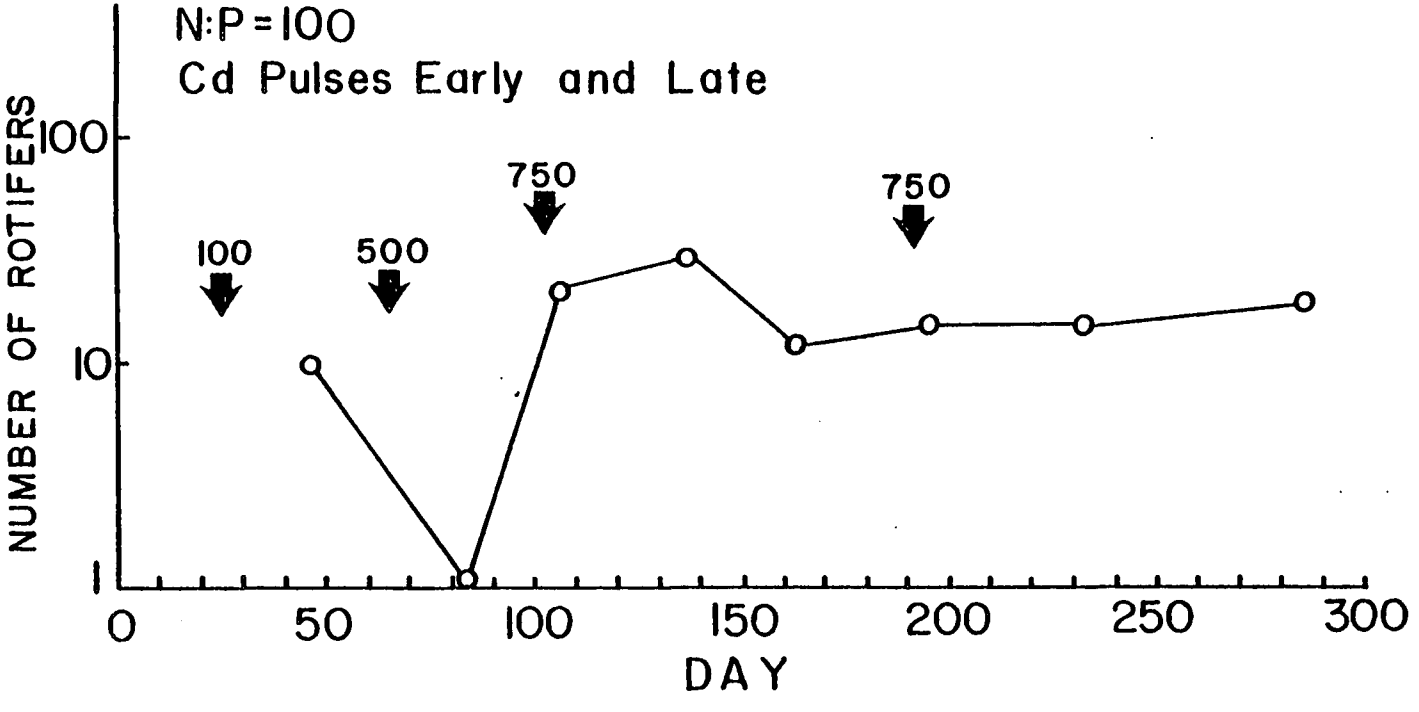

FIGURE 39. Rotifer abundance through time in flowthrough microcosms with input N:P= 100 and cadmium pulses as indicated in ppb Cd by arrows. Each point is based on a single microscopic count of a composite from four replicate microcosms.

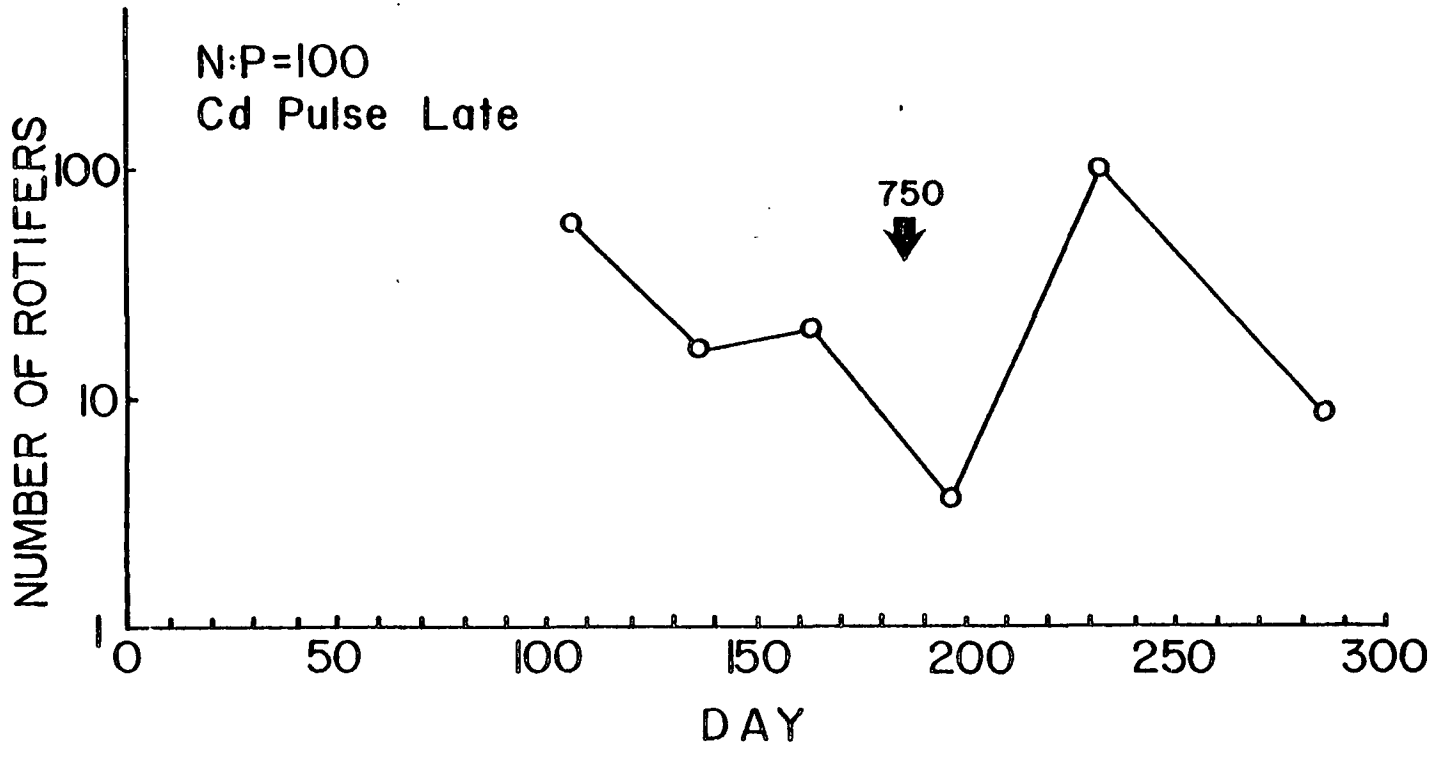

FIGURE 40. Rotifer abundance through time in flowthrough microcosms with input N:P = 100 and cadmium pulse as indicated in ppb Cd by arrow. Each point is based on a single microscopic count of a composite from four replicate microcosms.

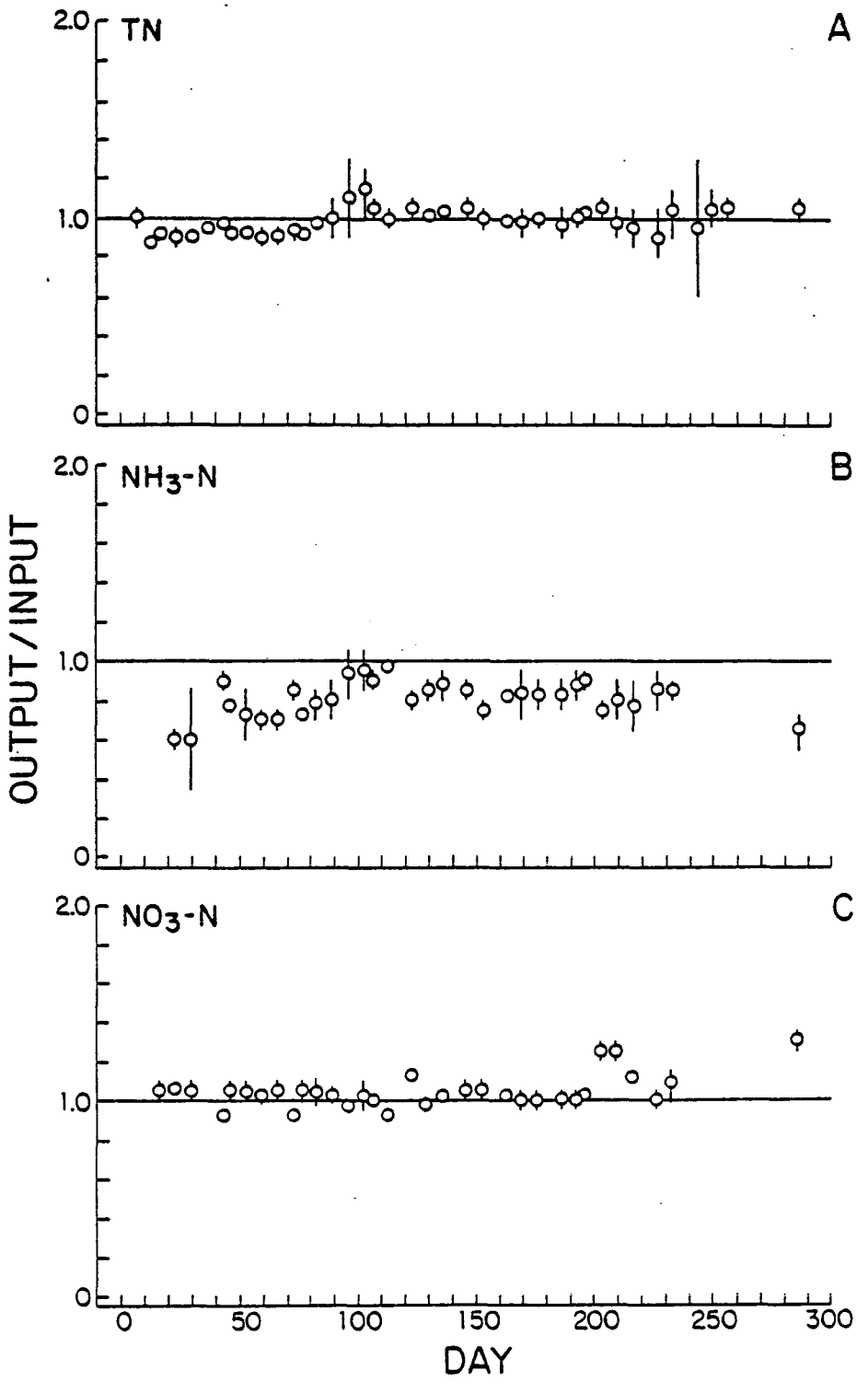

FIGURE 41. Total nitrogen (A), ammonia nitrogen (B) and nitrate nitrogen (C) output/input ratios through time in flowthrough microcosms with input N:P = 100 and no cadmium. Each point is the mean of four replicate systems with 95% confidence bars.

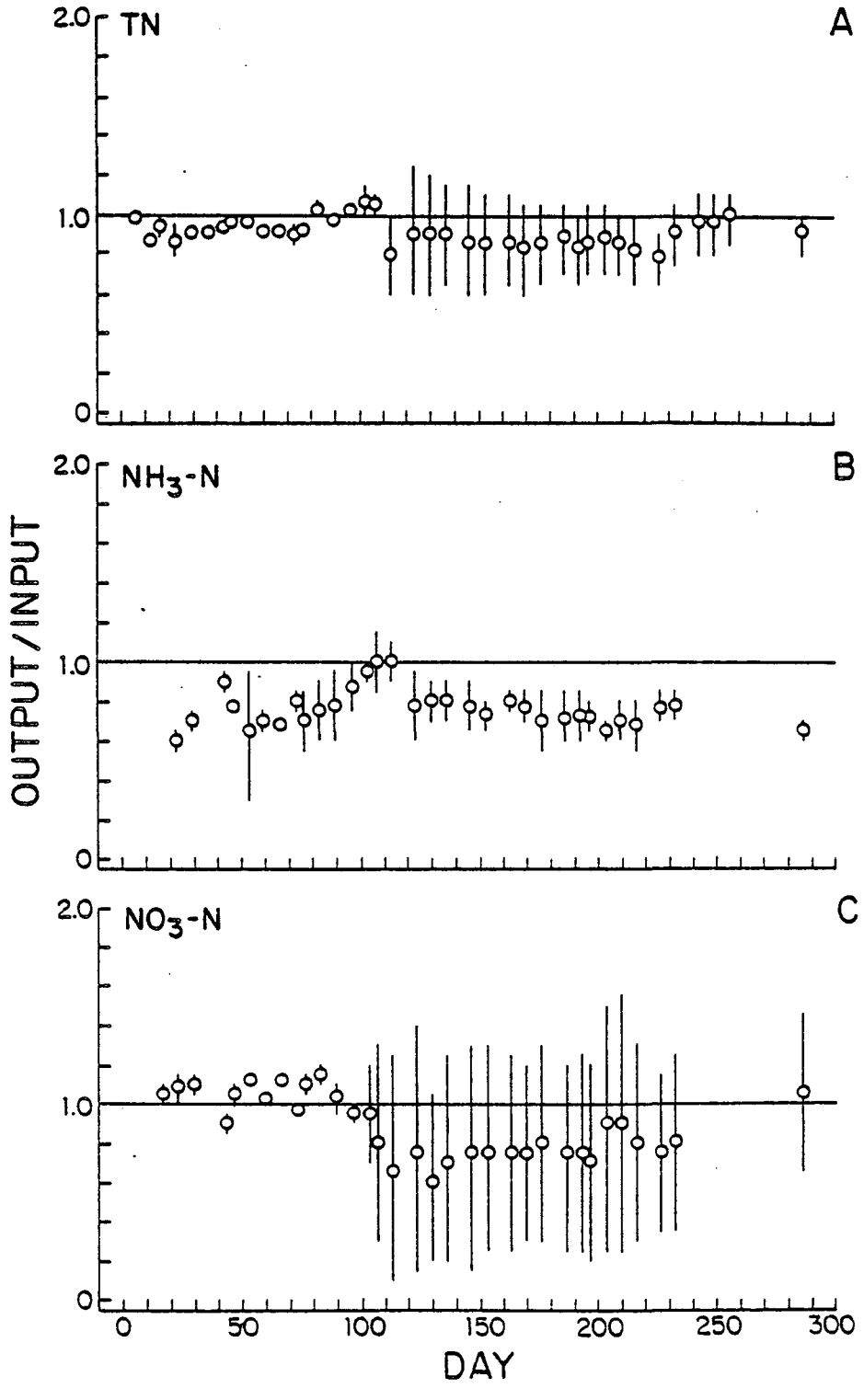

FIGURE 42. Total nitrogen (A), ammonia nitrogen (B), and nitrate nitrogen (C) output/input ratios through time in flowthrough microcosms with input N:P = 100 and continuous 10 ppb Cd inputs. Each point is the mean of four replicate systems with 95% confidence bars.

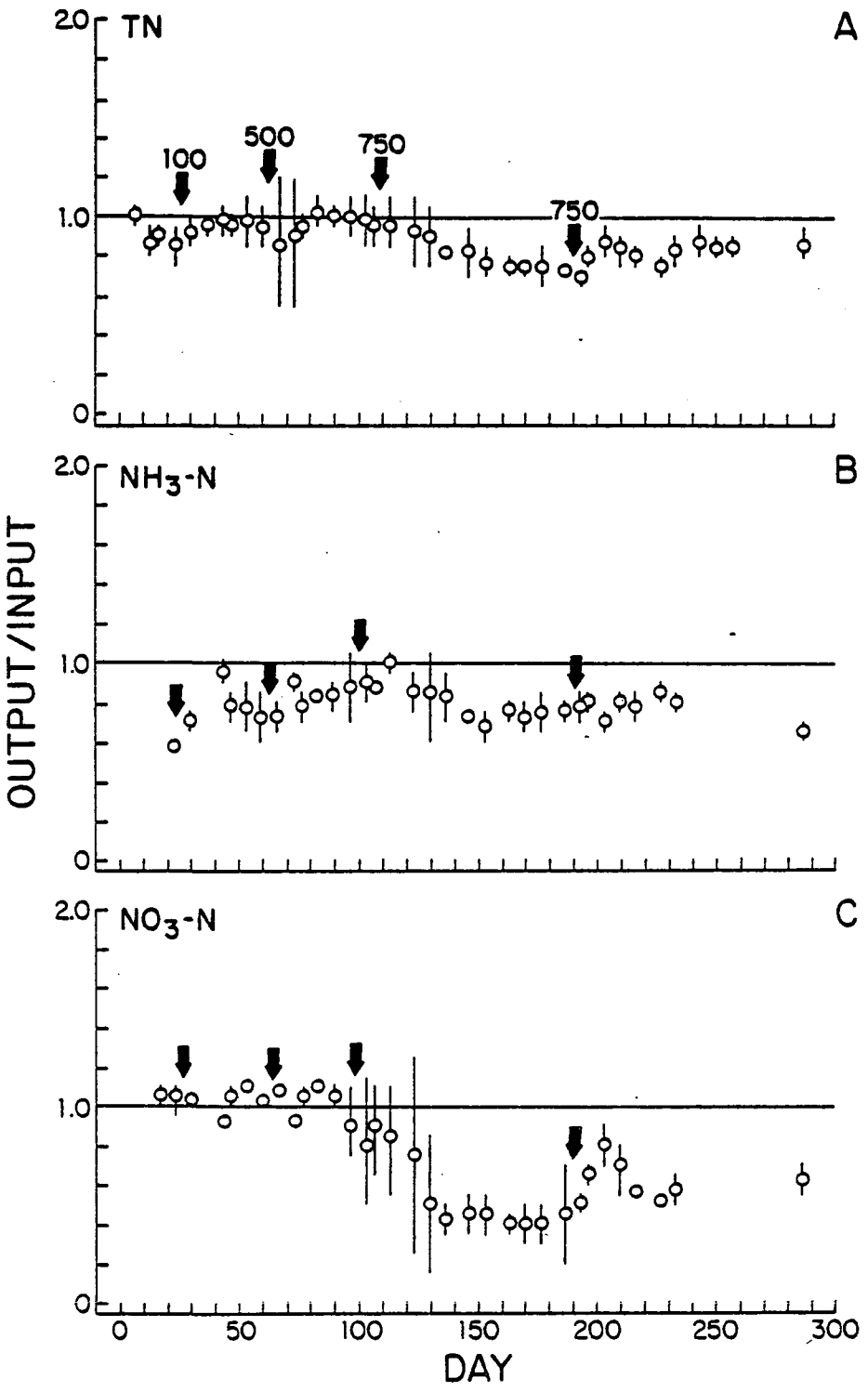

FIGURE 43. Total nitrogen (A), ammonia nitrogen (B), and nitrate nitrogen (C) output/input ratios through time in flowthrough microcosms with input N:P = 100 and cadmium pulses as indicated in ppb Cd by arrows. Each point is the mean of four replicate systems with 95% confidence bars.

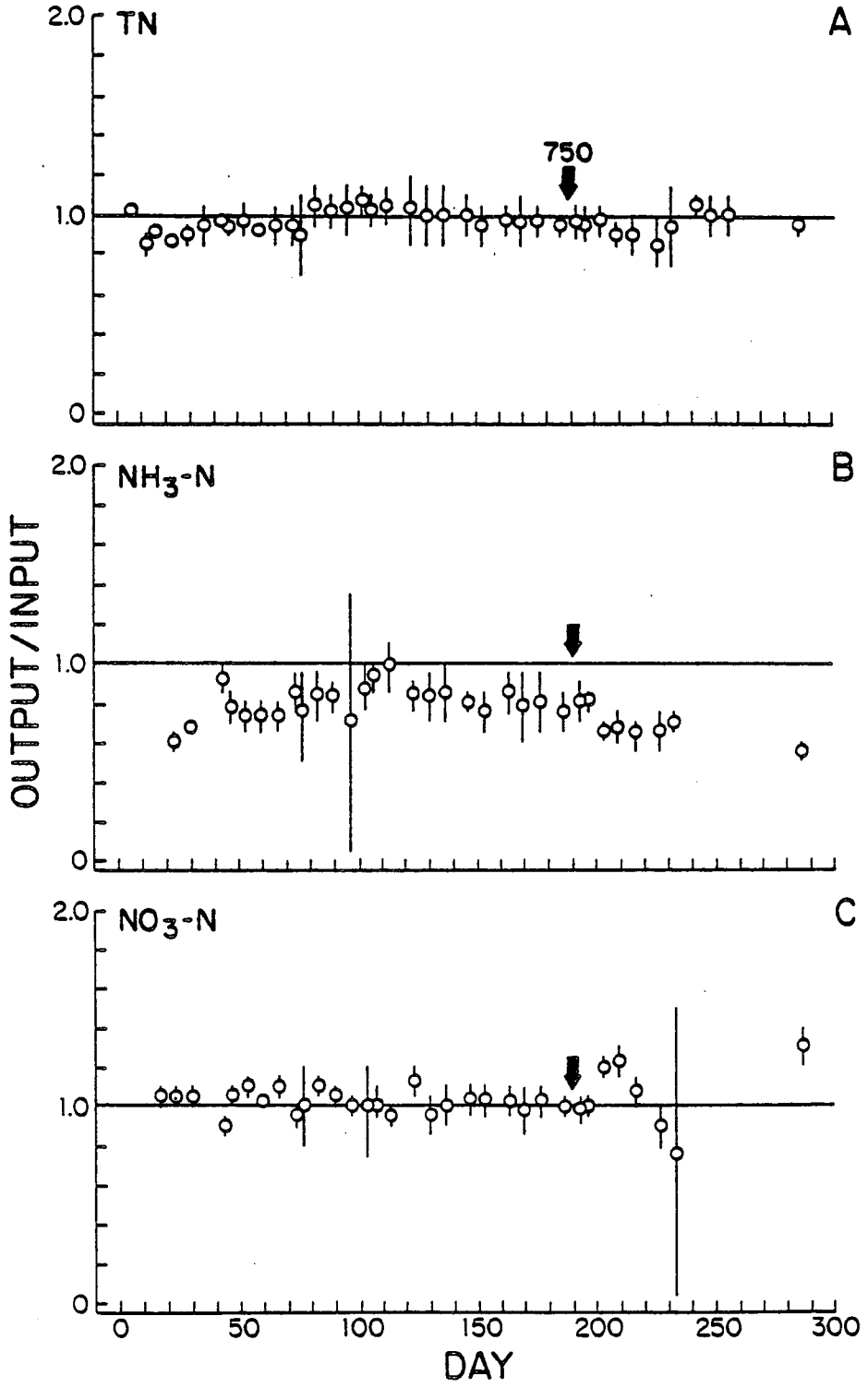

FIGURE 44. Total nitrogen (A), ammonia nitrogen (B), and nitrate nitrogen (C) output/input ratios through time in flowthrough microcosms with input N:P = 100 and cadmium pulse as indicated in ppb Cd by arrow. Each point is the mean of four replicate systems with 95% confidence bars.

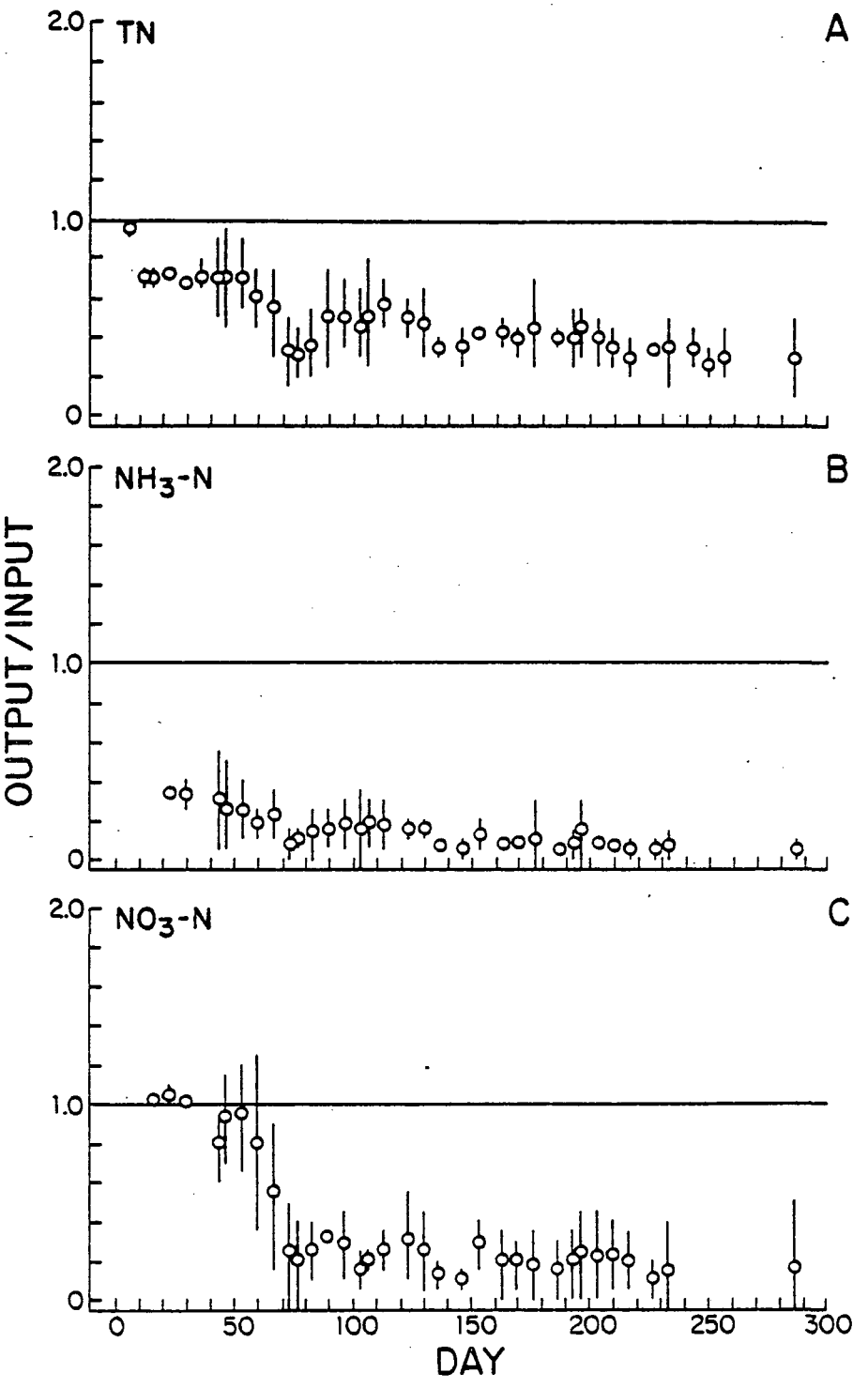

FIGURE 45. Total nitrogen (A), ammonia nitrogen (B), and nitrate nitrogen (C) output/input ratios through time in flowthrough microcosms with input N:P = 10 and no cadmium. Each point is the mean of four replicate systems with 95% confidence bars.

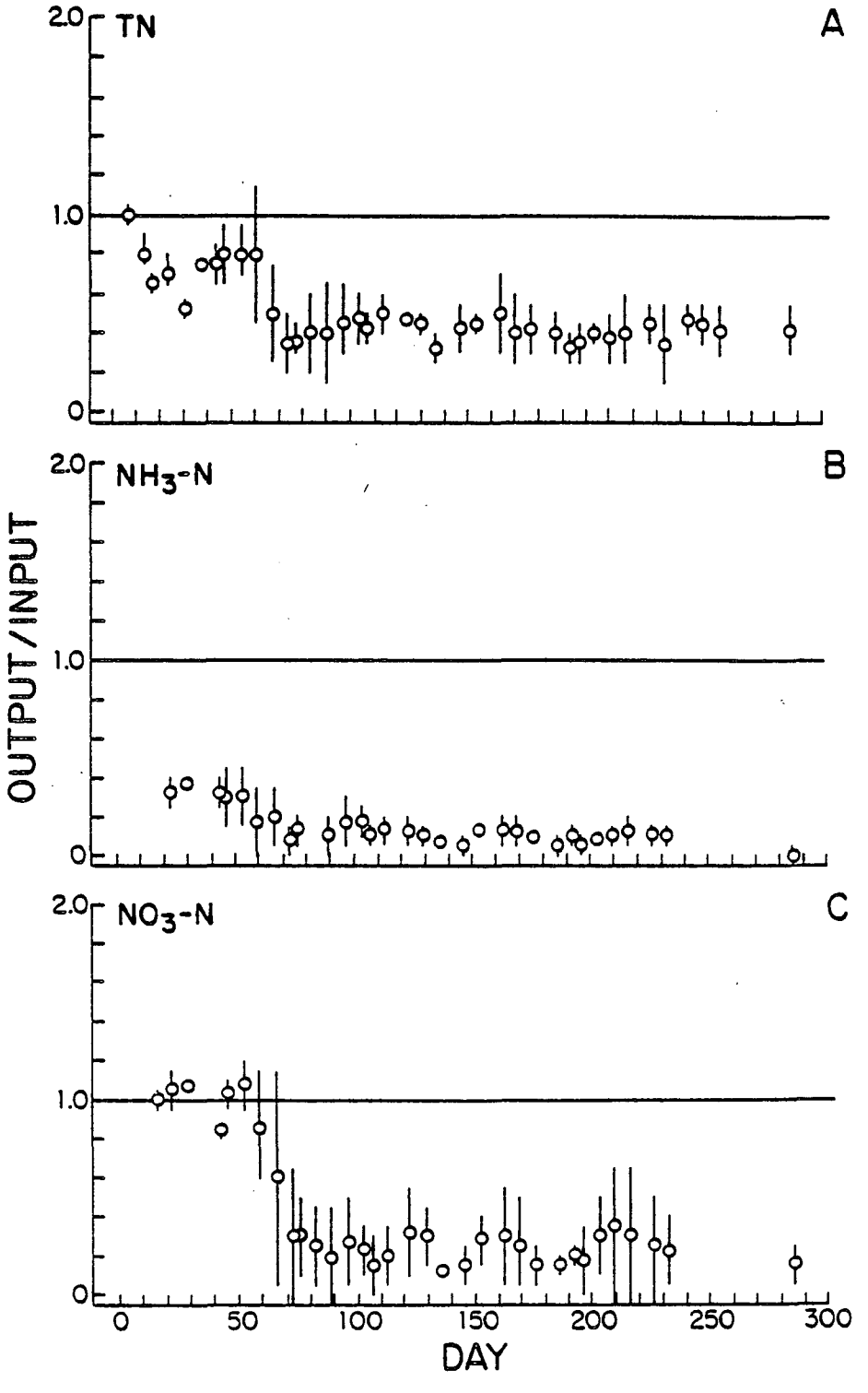

FIGURE 46. Total nitrogen (A), ammonia nitrogen (B), and nitrate nitrogen (C) output/input ratios through time in flowthrough microcosms with input N:P = 10 and continuous 10 ppb Cd inputs. Each point is the mean of four replicate systems with 95% confidence bars.

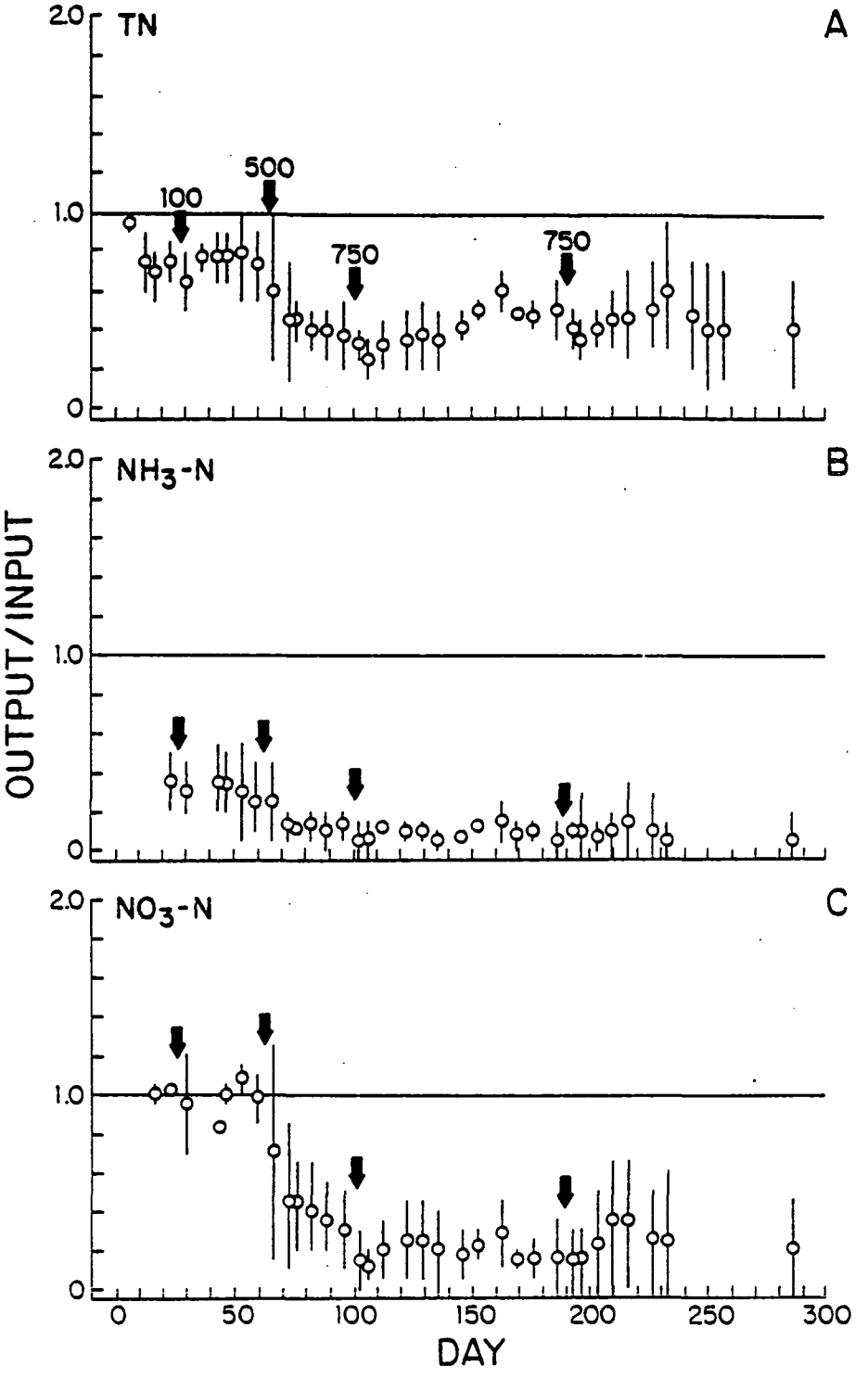

FIGURE 47. Total nitrogen (A), ammonia nitrogen (B), and nitrate nitrogen (C) output/input ratios through time in flowthrough microcosms with input N:P = 10 and cadmium pulses as indicated in ppb Cd by arrows. Each point is the mean of four replicate systems with 95% confidence bars.

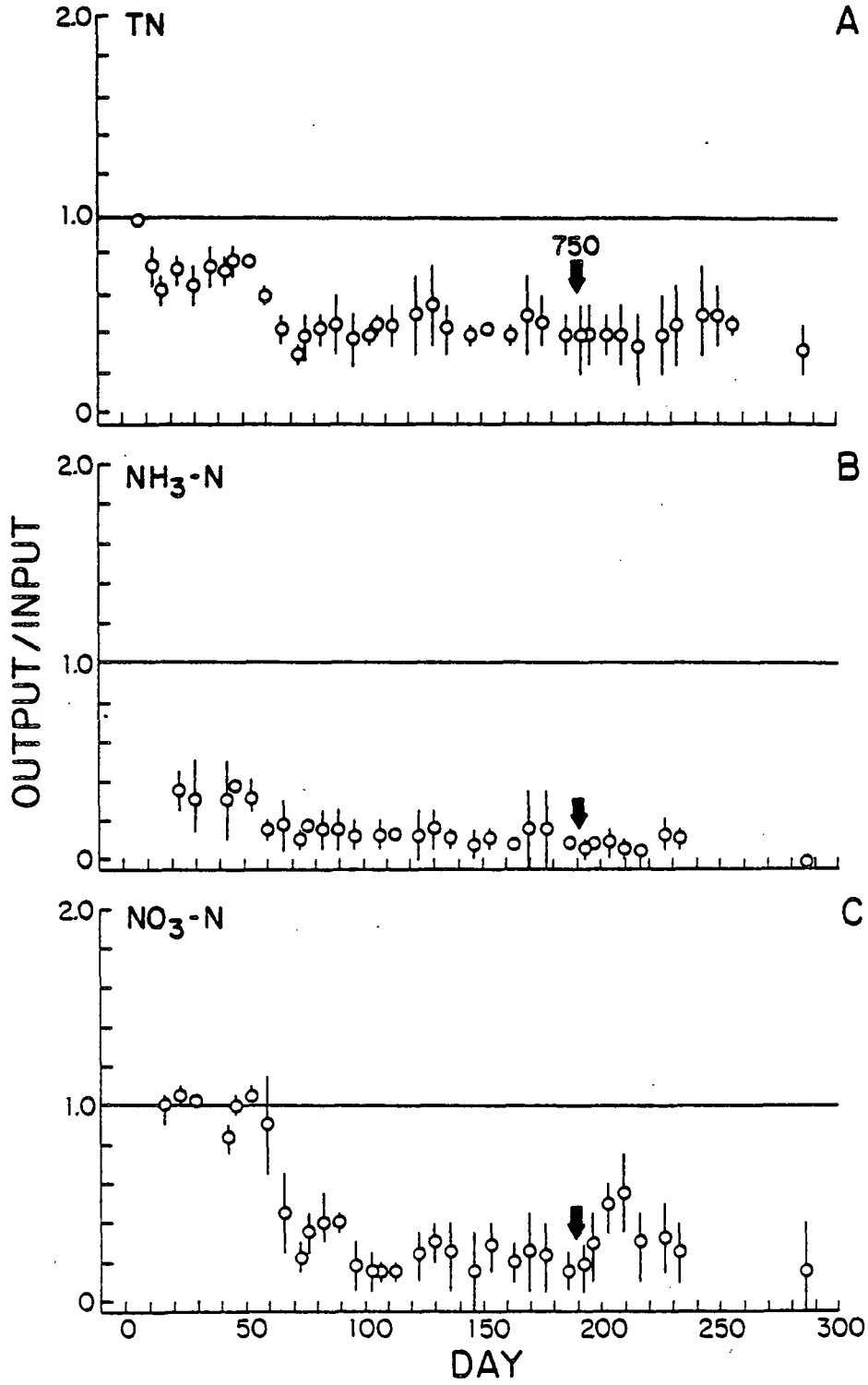

FIGURE 48. Total nitrogen (A), ammonia nitrogen (B), and nitrate nitrogen (C) output/input ratios through time in flowthrough microcosms with input N:P = 10 and cadmium pulse as indicated in ppb Cd by arrow. Each point is the mean of four replicate systems with 95% confidence bars.

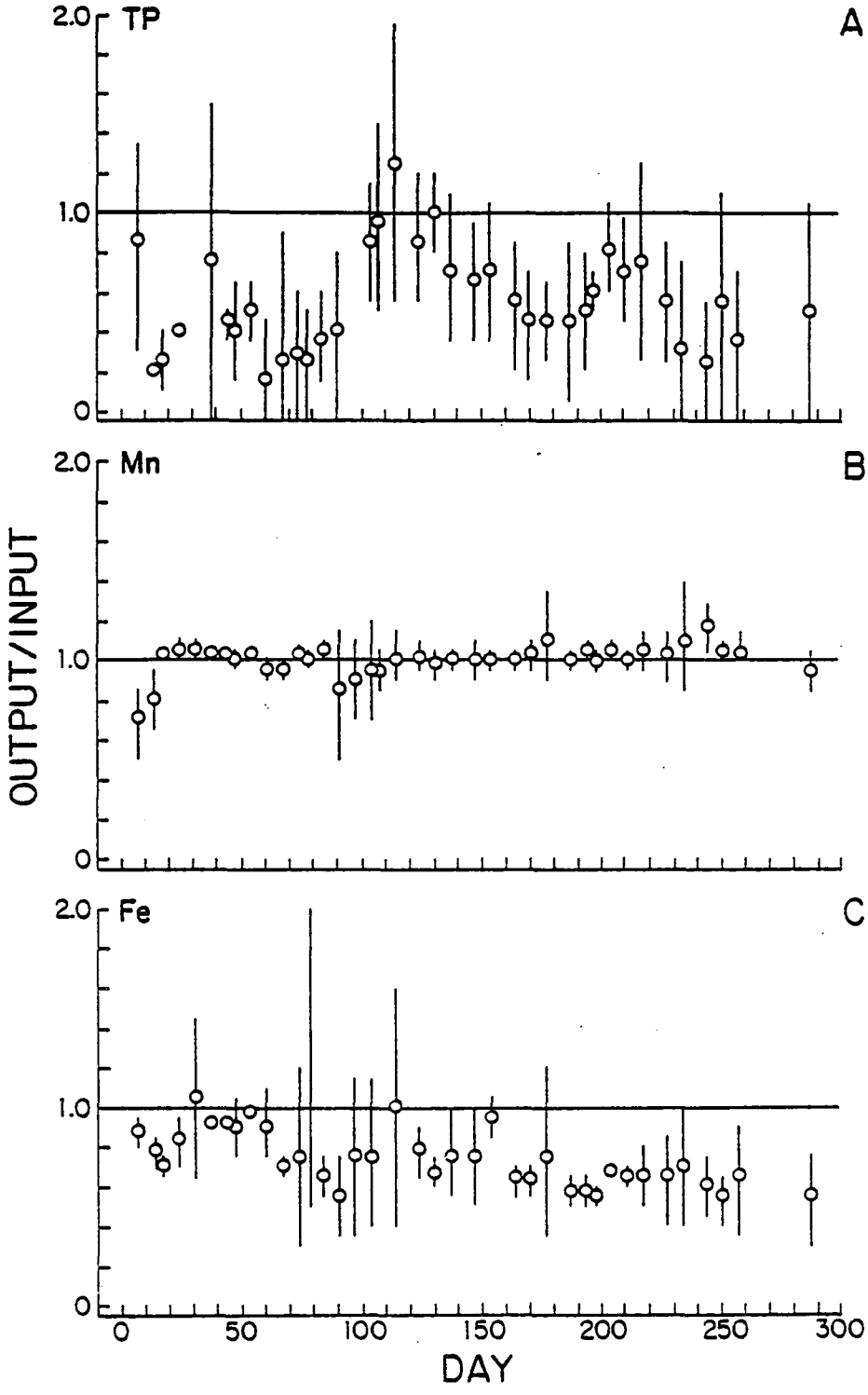

FIGURE 49. Total phosphorus (A), manganese (B), and iron (C) output/input ratios through time in flowthrough microcosms with input N:P = 100 and no cadmium. Each point is the mean of four replicate systems with 95% confidence bars.

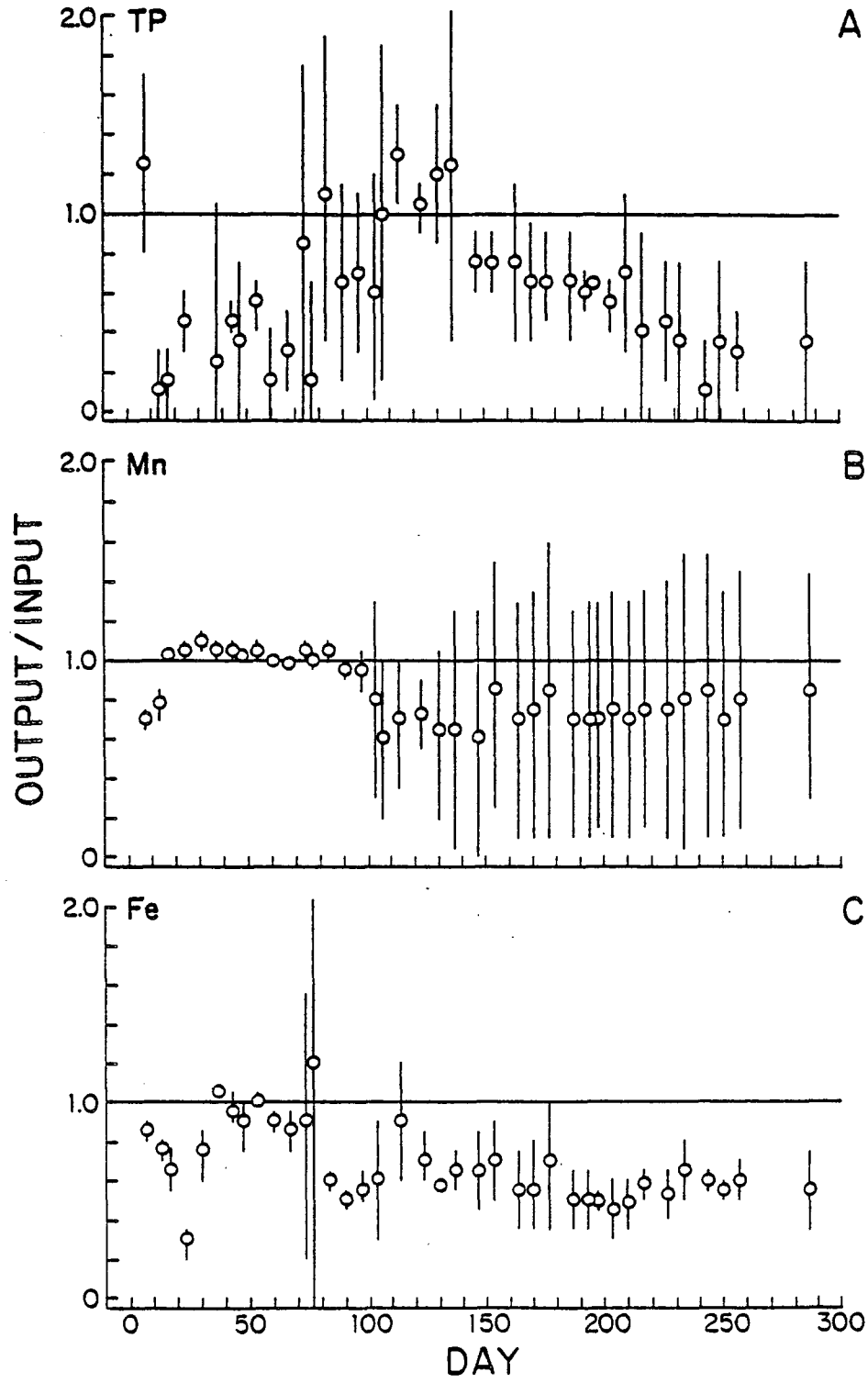

FIGURE 50. Total phosphorus (A), manganese (B), and iron (C) output/input ratios through time in flowthrough microcosms with input N:P = 100 and continuous 10 ppb Cd inputs. Each point is the mean of four replicate systems with 95% confidence bars.

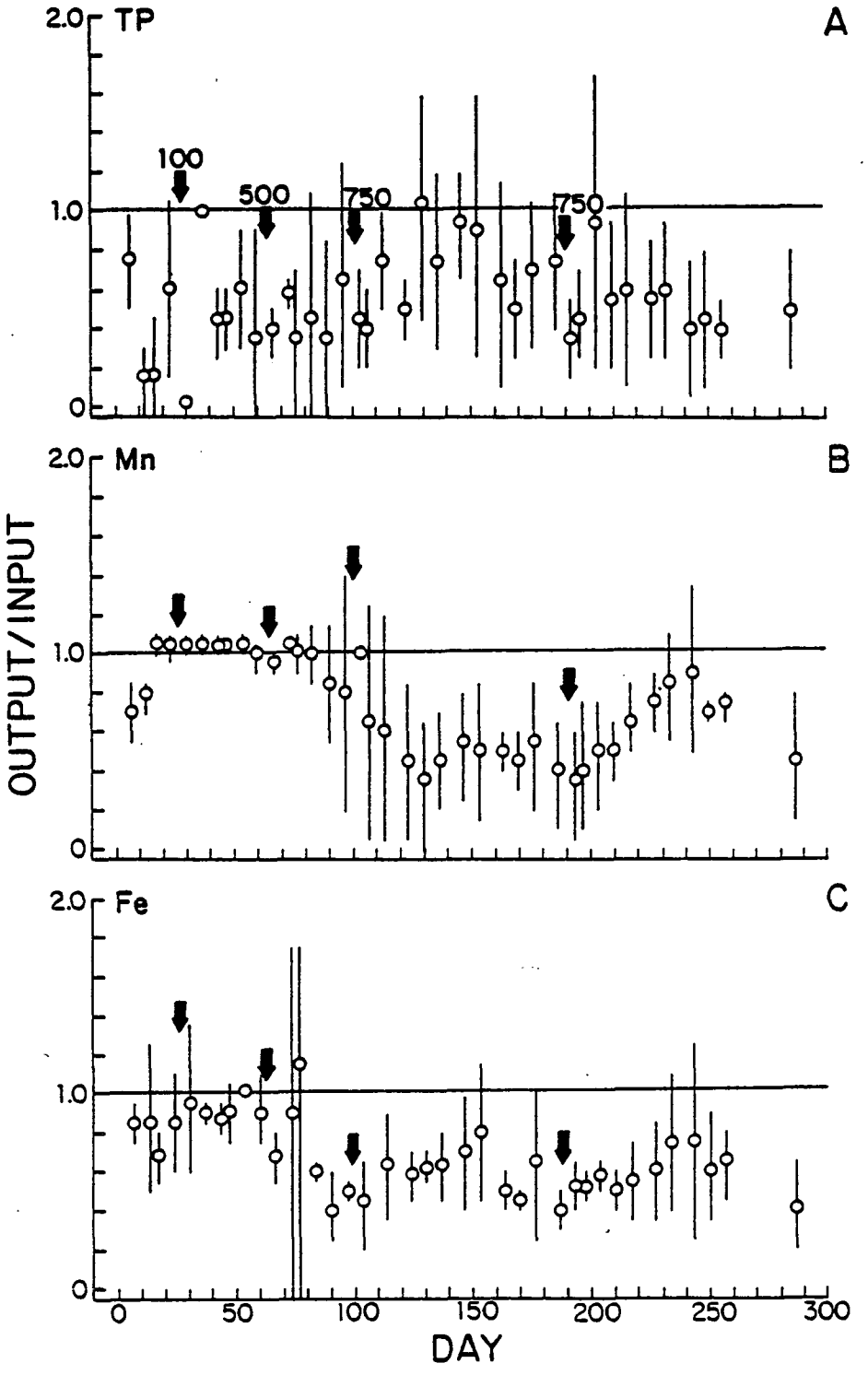

FIGURE 51. Total phosphorus (A), managanese (B), and iron (C) output/input ratios through time in flowthrough microcosms with input N:P = 100 and cadmium pulses as indicated in ppb Cd by arrows. Each point is the mean of four replicate systems with 95% confidence bars.

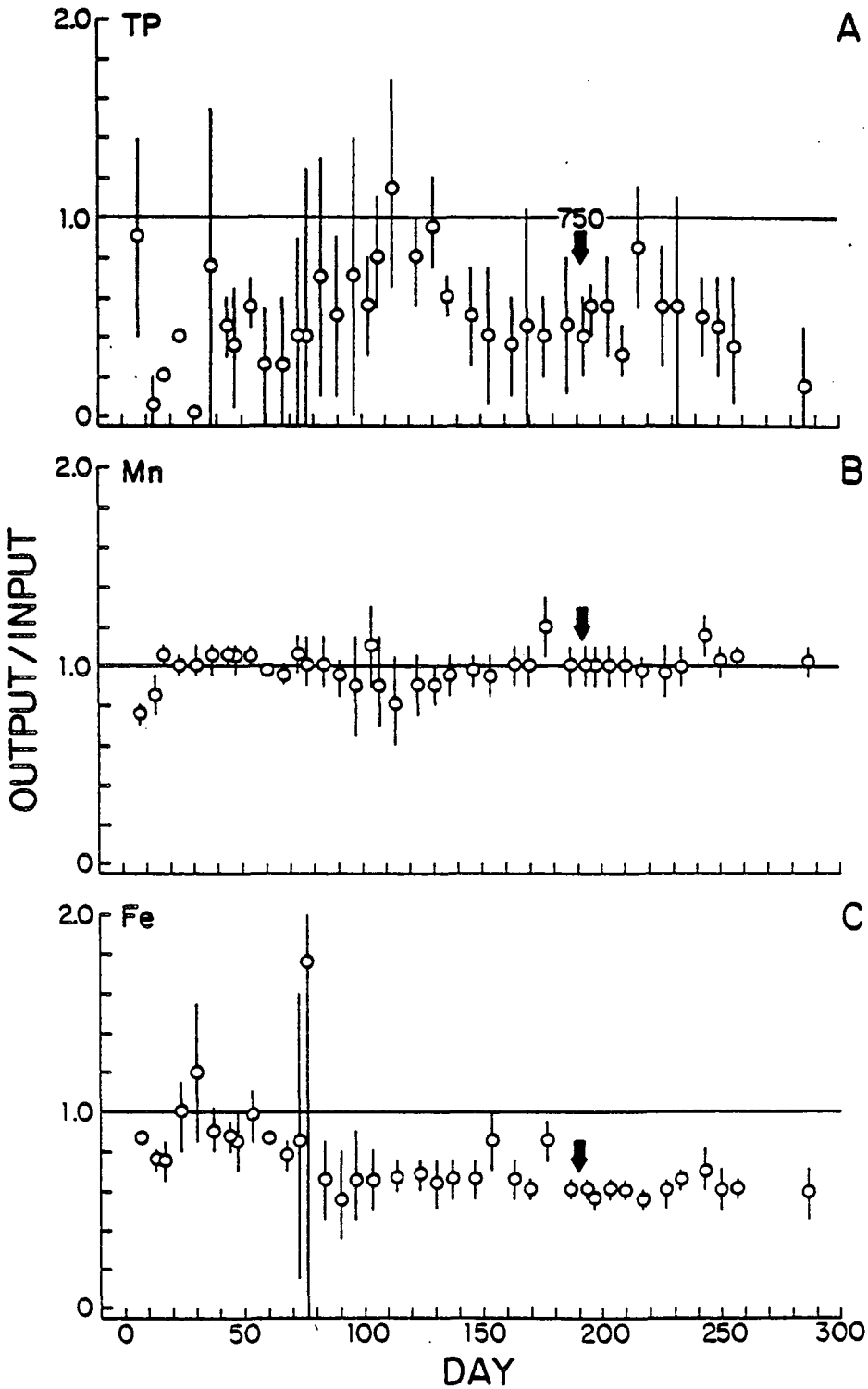

FIGURE 52. Total phosphorus (A), managanese (B), and iron (C) output/input ratios through time in flowthrough microcosms with input N:P = 100 and cadmium pulse as indicated in ppb Cd by arrow. Each point is the mean of four replicate systems with 95% confidence bars.

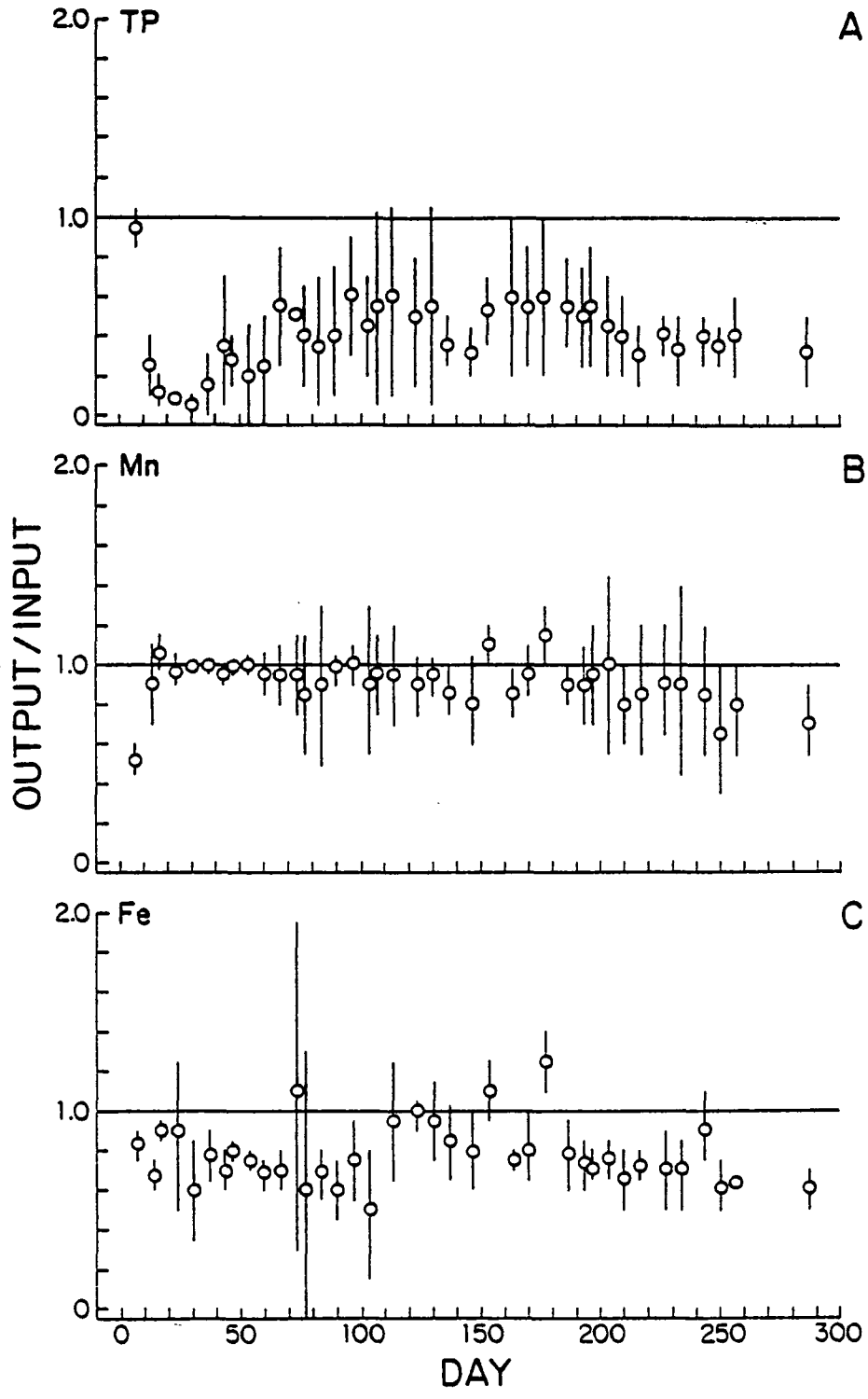

FIGURE 53. Total phosphorus (A), managanese (B), and iron (C) output/input ratios through time in flowthrough microcosms with input N:P = 10 and no cadmium. Each point is the mean of four replicate systems with 95% confidence bars.

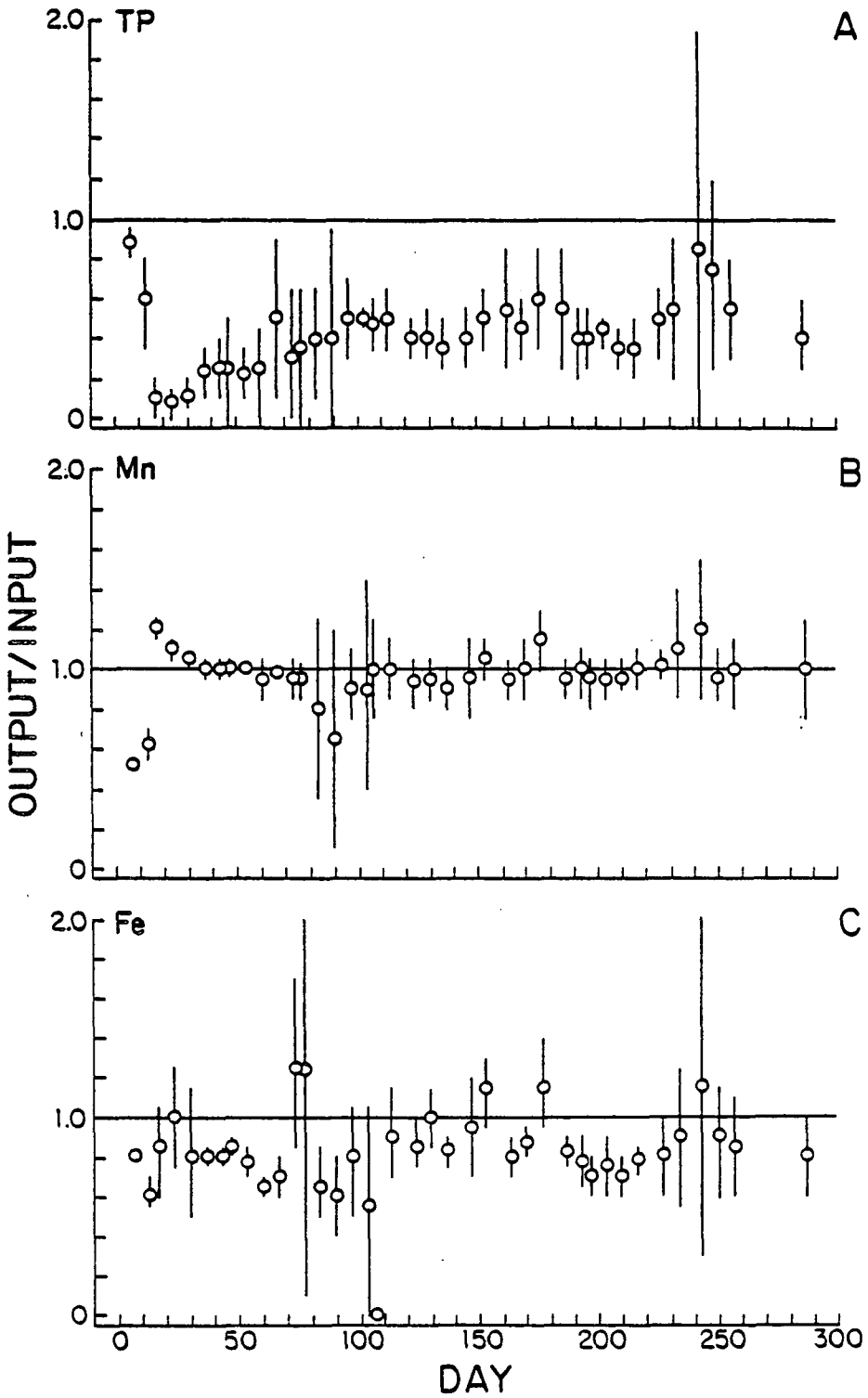

FIGURE 54. Total phosphorus (A), manganese (B), and iron (C) output/input ratios through time in flowthrough microcosms with input N:P = 10 and continuous 10 ppb Cd inputs. Each point is the mean of four replicate systems with 95% confidence bars.

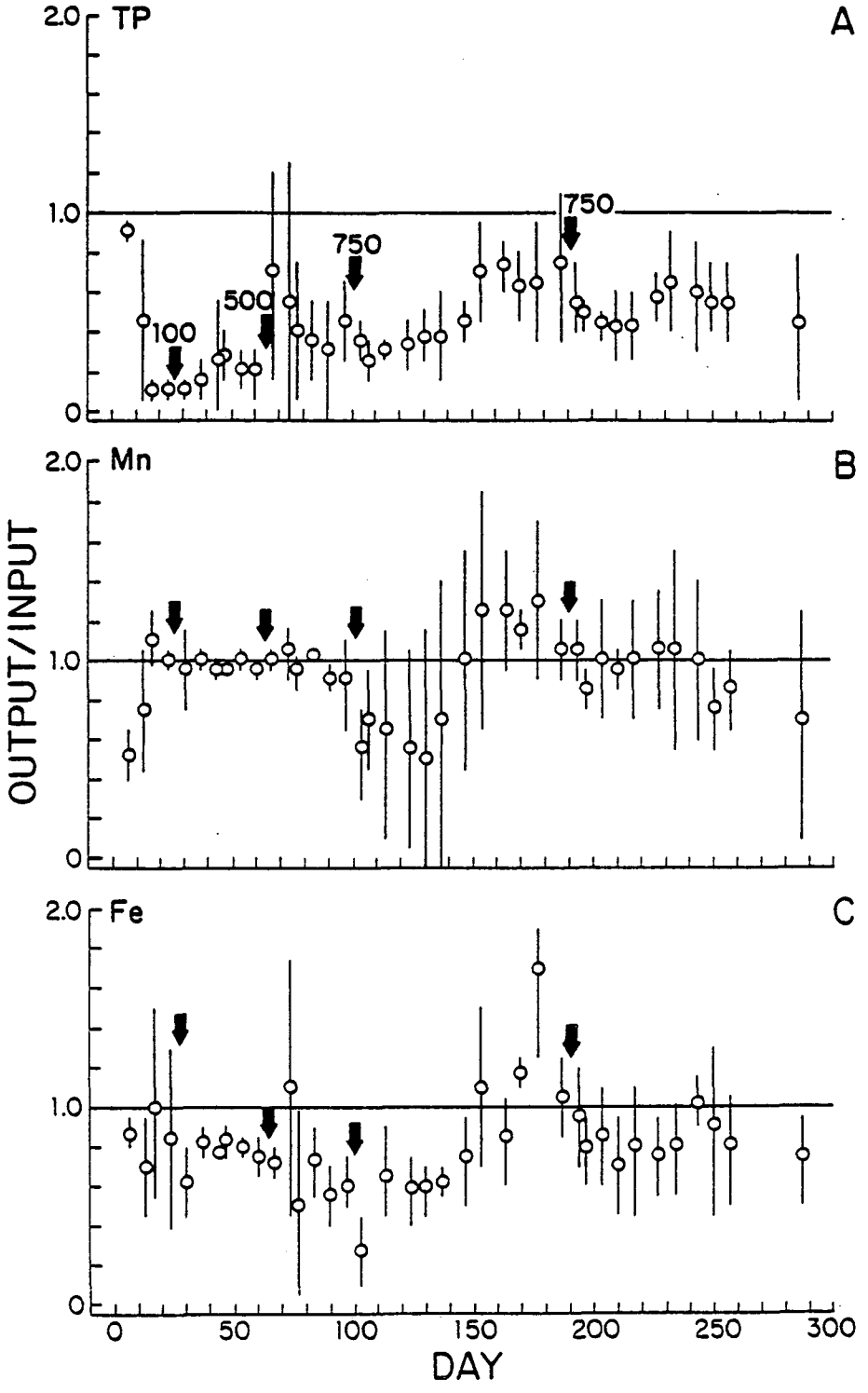

FIGURE 55. Total phosphorus (A), manganese (B), and iron (C) output/input ratios through time in flowthrough microcosms with input N:P = 10 and cadmium pulses as indicated in ppb Cd by arrows. Each point is the mean of four replicate systems with 95% confidence bars.

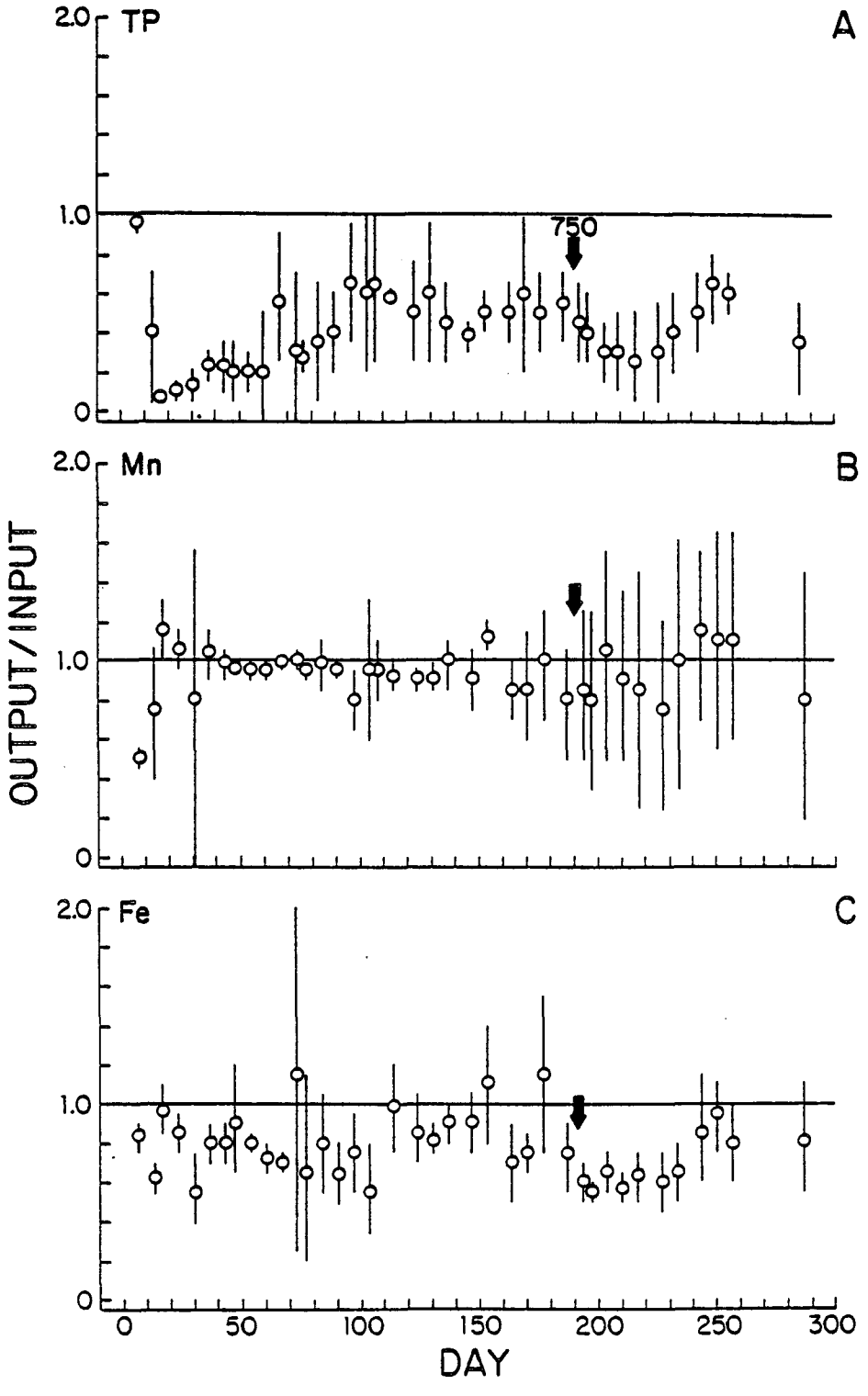

FIGURE 56. Total phosphorus (A), manganese (B), and iron (C) output/input ratios through time in flowthrough microcosms with input N:P = 10 and cadmium pulse as indicated in ppb Cd by arrow. Each point is the mean of four replicate systems with 95% confidence bars.

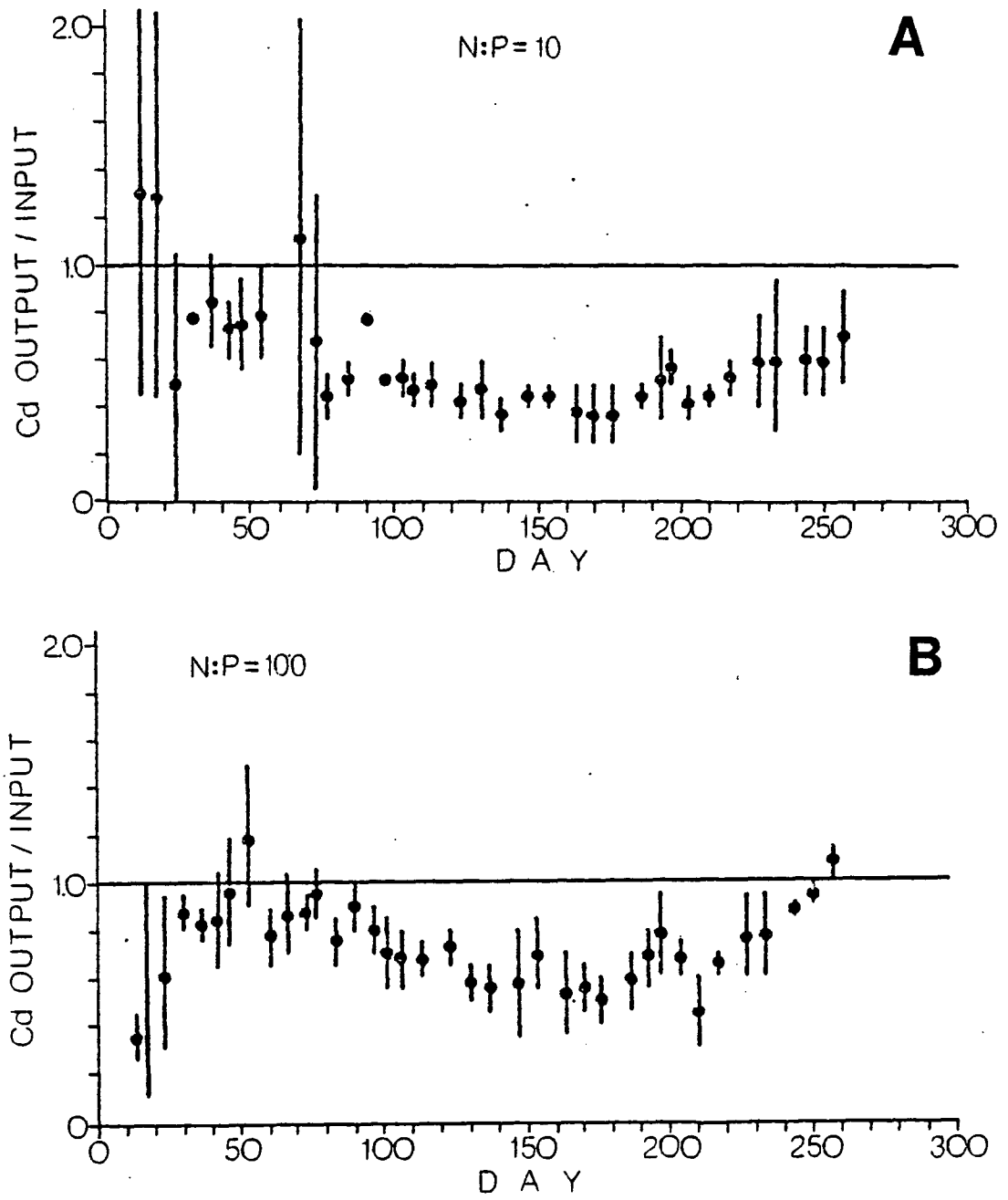

FIGURE 57. Cadmium output/input ratios through time in flowthrough microcosms with input N:P = 10 (A), and N:P = 100 (B). Cadmium input concentration was 10 ppb.

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NOTE: This bibliography is based largely on a computerized literature search of Biological Abstracts, Bio-Research Index, and Government Reports Announcements, conducted at the University of Georgia. The last search was conducted January 15, 1981.

APPENDIX A

Nutrient medium composition. Modified Taub and Dollar (1964) #36 medium. All values are in mg/l.

Compound	Phase I (Level 1)[1]	Phase II (N:P=100)[2]
CaCl	0.367	1.952
$MgSO_4 \cdot 7$ H 0	1.233	4.944
KH_2PO_4	0.046	0.276 (2.724)
NaOH	0.077	0.734 (1.309)
EDTA	0.162	1.631
$FeSO_4 \cdot 7\ H_2O$	0.156	1.556
$MnCl_2 \cdot 4\ H_2O$	0.050	0.990
H_3BO_3	0.046	0.927
$Co(NO_3)_2 \cdot 6\ H_2O$	0.007	0.145
$ZnSO_4 \cdot 7\ H_2O$	0.007	0.143
$CuSO_4 \cdot 5\ H_2O$	0.001	0.025
$NaMoO_4 \cdot 2\ H_2O$	0.006	0.121
KOH	0.026	0
NH_4NO_3	0.304	17.770
NaCl		4.380 (43.338)

[1]Level 2 = 5 X Level 1; Level 3 = 10 X Level 1; Level 4 = 100 X Level 1.

[2]N:P = 10 same as N:P = 100 except as indicated by values in parentheses.

APPENDIX B

Detection limits of elements analyzed on the Jarrell-Ash plasma emission spectrograph. Limits were determined as the lower point of linearity on standard curves containing the entire nutrient complex. All values are in µg/l.

Element	Lower Detection Limit	Nutrient Medium Input Concentrations (Phase II)
Boron	100	200
*Cadmium	10	10
Calcium	100	500
Cobalt	10	35
Copper	100	6
Iron	100	300
Potassium	1000	80
Magnesium	10	480
Manganese	10	350
Sodium	100	1700
Zinc	10	40

*Cadmium concentrations were determined independently by flameless atomic adsorption spectrophometry.

APPENDIX C

Results of Analysis of Variance. Where interactions were significant, F values for main effects were calculated using mean square of interaction as the denominator.

PHASE I:

Variable - Net Daytime Production
Model - P_D = NLEV + CDLEV + NLEV * CDLEV + Wk

Source	df	SS	MS	F	α
Model	32	263.61	8.24	34.33	.0001
NLEV	3	111.29	37.10	15.52	.001
CDLEV	3	3.02	1.01	.423	NS
CDLEV * NLEV	9	21.46	2.39	9.96	.0001
Error	1495	352.20	.24		

Variable - Nighttime Respiration
Model - R_N = NLEV + CDLEV + NLEV * CDLEV + Wk

Source	df	SS	MS	F	α
Model	32	241.95	7.56	42.00	.0001
NLEV	3	123.42	41.14	15.58	.001
CDLEV	3	33.38	11.17	4.21	.05
CDLEV * NLEV	9	23.77	2.64	14.67	.0001
Error	1494	270.86	.18		

Variable - Production/Respiration
Model - P/R = NLEV + CDLEV + NLEV * CDLEV + Wk

Source	df	SS	MS	F	α
Model	32	321.67	10.05	18.27	.0001
NLEV	3	3.91	1.30	2.36	NS
CDLEV	3	6.58	2.19	3.98	.05
CDLEV * NLEV	9	1.86	.21	.38	NS
Error	1459	795.42	.55		

Variable - Chlorophyll a
Model - Chl = NLEV + CDLEV + NLEV * CDLEV + Wk

Source	df	SS	MS	F	α
Model	30	114.91	3.83	13.68	.0025
NLEV	3	70.71	23.57	14.37	.001
CDLEV	3	19.31	6.44	3.92	.05
CDLEV * NLEV	9	14.74	1.64	5.86	.01
Error	730	203.37	.28		

Variable - Phaeo-pigments
Model - Pha = NLEV + CDLEV + NLEV * CDLEV + Wk

Source	df	SS	MS	F	α
Model	30	23.88	.80	4.00	.0001
NLEV	3	13.05	4.35	21.75	.0001
CDLEV	3	1.03	.34	1.70	NS
CDLEV & NLEV	9	4.08	.45	2.25	.10
Error	730	143.16	.20		

Variable - Biomass
Model - B = NLEV + CDLEV + NLEV * CDLEV + Wk

Source	df	SS	MS	F	α
Model	30	348,315,998.12	11,610,533.27	21.38	.0001
NLEV	3	140,496,382.06	46,832,127.00	86.25	.0001
CDLEV	3	2,868,906.34	956,302.11	1.76	NS
CDLEV * NLEV	9	3,796,917.61	421,879.73	0.78	NS
Error	734	398.569,829.97	543,010.67		

PHASE II:

Variable - Net Daytime Production
Model - P_D = NUT + CD + NUT * CD

Source	df	SS	F	α
Model	7	351.66	61.60	.0001
NUT	1	133.38	4.52	NS
CD	3	129.66	1.46	NS
NUT * CD	3	88.61	36.22	.0001
Error	1240	1011.18		

Variable - Nighttime Respiration
Model - R_N = NUT + CD + NUT * CD

Source	df	SS	F	α
Model	7	351.48	62.64	.0001
NUT	1	146.47	4.87	NS
CD	3	114.85	1.61	NS
NUT * CD	3	90.15	37.49	.0001
Error	1224	981.12		

Variable - Production/Respiration
Model - P/R = NUT + CD + NUT * CD

Source	df	SS	F	α
Model	7	0.84	3.13	.0029
NUT	1	0.53	13.93	.0002
CD	3	0.06	0.50	.6831
NUT * CD	3	0.25	2.16	.0891
Error	1224	46.83		

Variable - Chlorophyll a
Model - Chl = NUT + CD + NUT * CD

Source	df	SS	F	α
Model	7	904.65	144.65	.0001
NUT	1	900.52	1007.94	.0001
CD	3	0.76	0.28	.8397
NUT * CD	3	3.38	1.26	.2863
Error	1230	1098.91		

Variable - Phaeo-pigments
Model - Pha = NUT + CD + NUT * CD

Source	df	SS	F	α
Model	7	527.95	29.13	.0001
NUT	1	503.56	194.48	.0001
CD	3	10.88	1.40	.2399
NUT * CD	3	13.52	1.74	.1551
Error	1230	3184.72		

Variable - Biomass
Model - B = NUT + CD + NUT * CD

Source	df	SS	F	α
Model	7	53,277,320.91	108.84	.0001
NUT	1	53,065,507.29	758.83	.0001
CD	3	78,974.66	0.38	.7731
NUT * CD	3	132,838.96	0.63	.5977
Error	1235	86,364,454.86		

Variable - Total Phosphorus Output
Model - TP = NUT + CD + NUT * CD

Source	df	SS	F	α
Model	7	18.68	250.38	.0001
NUT	1	18.64	1,749.11	.0001
CD	3	0.02	0.59	.6288
NUT * CD	3	0.02	0.61	.6149
Error	1238	13.20		

Variable - Total Nitrogen Output
Model - TN = NUT + CD + NUT * CD

Source	df	SS	F	α
Model	7	3,124.24	338.75	.0001
NUT	1	3,059.94	198.35	.001
CD	3	18.02	0.39	NS
NUT * CD	3	46.28	11.71	.0001
Error	1238	1,631.11		

Variable - Ammonia Nitrogen Output
Model - NH_3N = NUT + CD + NUT * CD

Source	df	SS	F	α
Model	7	1,413.09	1,076.03	.0001
NUT	1	1,409.93	1,733.52	.001
CD	3	0.72	0.89	NS
NUT * CD	3	2.44	4.33	.005
Error	1173	1,633.15		

Variable - Nitrate Nitrogen Output
Model - NO_3N = NUT + CD + NUT * CD

Source	df	SS	F	α
Model	7	1,020.31	168.99	.0001
NUT	1	918.23	48.70	.01
CD	3	45.51	0.08	NS
NUT * CD	3	56.56	21.86	.0001
Error	1173	1,011.72		