REPORT TO THE NATIONAL AERONAUTICS AND SPACE ADMINISTRATION, FEBRUARY 15, 1967

Final Report on NASA Grant NSG-706

N67-25874

BIODYNAMICS OF MICROECOSYSTEMS

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Code CR-83884 pages 46

Cat 04

SUMMARY

This report covers the period between July 23, 1964, and July 23, 1966, the duration of NASA grant NSG 706. The first six months were spent mainly in the initial phases of the work. Most of the required items of equipment were purchased and delivered to either the Savannah River Plant or the University of Georgia in Athens. By January 23, 1965, only two major pieces of equipment remained undelivered. These were two walk-in constant temperature and humidity rooms. During this period the necessary routine procedures for microecosystem research were worked out and a technician trained to perform them. Only a few experiments were carried out and limited data were obtained. During the second six-month period delays in delivery and installation of the constant temperature rooms slowed the progress of the work. However, during the second year, several experiments were performed using several different approaches. Carryover into the third year will insure that the work originally projected will be completed.

The primary objectives of the research under this grant were, and are, to test the hypothesis that true stability in a life support system is obtainable only after the system becomes adjusted to its boundary conditions (i.e., outside environment and internal chemical and aspects composition) by the process of ecological succession, and only if there is a minimum diversity of components performing necessary ecosystem functions such as production,

consumption, decomposition, growth-promotion, etc. The importance of succession and diversity have been overlooked in the present emphasis on growth of single species high-yielding algal or bacterial strains which, by their very nature, cannot be maintained in steady state without a large outlay of associated plumbing. An expansion of these views was presented in a paper by the principal investigators and G. Dennis Cooke, given by them at the NASA Conference on Bioregenerative Systems. This paper is included as an appendix to this report, and may be considered as a summary of the work on laboratory microcosms as supported, in part, by NASA grant NSG 706.

Studies on succession in sub-cultures derived from microecosystems that have maintained themselves in a stable state in our laboratory for several years have revealed important differences between heterotrophic and autotrophic succession, processes commonly confused in the ecological literature. Furthermore, use of gamma irradiation as a stress factor has revealed sensitivity of the bacterial stage that is prerequisite to the algal bloom stage of heterotrophic succession. Studies on nutritive value of pelletized mixed as compared to pure culture material were inconclusive due largely to the lack of proper facilities and personnel for preparing large enough batches for the feeding experiments with mice. Experiments were done on the effects of photo period and medium composition on succession in the microcosms. Finally, two pre-doctoral students were attracted to the program and have begun training and thesis work on aspects of succession and diversity in microecosystems. A technician has been trained in the techniques of microecosystem culture, and Dr. Beyers received additional training in bio-space technology as a participant in the NASA training program held on Wallops Island, Virginia, in August, 1965.

In terms of theory and regenerative systems, our work may be summarized as follows: it was clearly demonstrated that "efficiency" in terms of ratio of primary productivity (P) (or rate O_2 production or CO_2 consumption) to biomass (B) or weight always decreases until stability is achieved, while the reciprocal "efficiency," namely, B/P, increases and is maximum as steady-state is achieved. In most thinking about regenerative space crafts, the emphasis has been on achieving a high ratio of P/B, as is characteristic of early succession in microecosystems (as well as in nature in general), with the idea that stability can be achieved in this basically unstable situation by mechanical means. Therefore, interest in experimental work has centered on very small "bloom type" organisms with rapid turnovers. It is our strong opinion that we also should investigate the feasibility of using systems with more "climax" (i.e., inherent stability) characteristics, even though this means a lower P/B efficiency.

INTRODUCTION

One aim of ecology is to study the structure and function of ecosystems. However, like everything else in nature, ecosystems tend to grade into one another and drawing a line between them is a difficult task indeed. One solution to the boundary problem is to enclose an ecosystem in some type of container. This encapsulation at least partially isolates a functional ecological unit from the rest of the biosphere. Such a deliberately isolated ecosystem has been called a microecosystem or microcosm.

As well as being difficult to delineate, natural ecosystems are often quite large and subject to variables in such environmental conditions as light intensity and duration, temperature averages and extremes, conditions of export or import of non-living materials and biota, and in aquatic

habitats materials suspended or dissolved in the fluid medium. These disadvantages often make natural ecosystems unsuitable for experimental work when control of such environmental conditions is essential. Where an ecosystem which has discrete physical boundaries and which is small enough to be conveniently subjected to experimental conditions is not available several researchers have resorted to the microcosm approach (Odum and Hoskins, 1957; Whittaker, 1961; Beyers, 1963a, b, c; Butler, 1964; McConnell, 1962; Copeland, 1965). The microcosm method allows the fabrication of replicate ecosystems (Abbott, 1966). Such duplicate ecosystems are almost impossible to find in nature. Microecosystems also permit investigation into the effects of gamma radiation upon aquatic ecosystems which would be almost impossible under field conditions. The high dosages required to elicit a response from small aquatic organisms are impractical and dangerous to give to natural bodies of water.

This report deals with an attempt to develop a laboratory "white mouse" type of ecosystem. That is, a natural assemblage of organisms and their abiotic environment about which a relatively large body of information is known and which is convenient to use as a laboratory tool in experimental ecology.

Ecological purists may object to calling the processes taking place in microecosystems succession on the grounds that there can be no succession without invasion of species from beyond the system in question. While it is true that the methods used to conduct the experiments described in this report did not permit the invasion of the microecosystems by other species, we feel that it was truly a succession which took place. The question here is a matter of point of view. Although all component species are physically

present in the microecosystem, at the start of the succession they are not functionally present. That is, a few organisms of each species are present as spores, eggs, or rare individuals, but they do not hatch or become abundant until the proper conditions are established within the flask. These conditions are brought about by the action of the biota in the previous seral stages. This point of view is supported by the classical experiment of Woodruff (1913) which involved the study of changes in the protozoan fauna of hay infusions. There was a regular sequence of species populations, each population entering a period of growth, followed by a period of decline, until a relatively stable end product was reached. Although she may have had some invasion, most of her protozoa were already on the hay in the form of spores. Oosting and Humphreys (1940) have demonstrated a somewhat similar situation in terrestrial ecosystems. They found the viable seeds of old field species to be present in climax forests, indicating that successional species may be physically but not functionally present, the same condition which occurs in our systems.

GENERAL MATERIALS AND METHODS

The system chosen for this study was originally isolated from a sewage oxidation pond in Austin, Texas, 1959. The plant community is made up of three species. The dominant alga is Chlorella. There is a subdominant blue-green alga, Schizothrix calciocola and a very rare Senedesmus. The largest animal is an ostracod, Cipradopsis vidua. The protozoa are represented by Paramecium bursaria and two species of flagellates. Two rotifers are present, Lepadella sp. and Philodina sp. Three different fungi and at least ten species of bacteria have also been isolated from this system. The microecosystem will live well on a defined medium and has survived, in the climax situation, in the laboratory for several years with light as the only energy input.

If it is desired to increase the volume or numbers of the experimental system, it must be put through an ecological succession. The usual procedure is to inoculate about 5 ml of the climax system containing all the representative organisms into sterile, fresh 1/2 strength Taub algal medium #36. (Taub and Dollar, 1964) with additives. The choice of additives depends on the type of succession the microcosms are to undergo. If amino acids or peptones are added, a heterotrophic succession will take place. This succession is defined as heterotrophic because the activities of the heterotrophs are very important in the first few days' increase in biomass. Bacteria and fungi initially utilize the nitrogenous organic matter as a substrate and produce a great deal of turbidity in the flask. After the bacterial bloom, there is an algal bloom. The system then begins to function autotrophically, with the plants providing the fixed carbon and energy necessary for the other members of the community. Subsequent to the algal bloom, the particulate organic matter settles to the bottom of the flask, and the system assumes a biogeochemical steady state which persists indefinitely. This is the climax state of the microecosystem.

If thiamine and inorganic fixed nitrogen are added to the system, an autotrophic succession will occur. This succession is defined as autotrophic because the biomass increase is brought about by the photosynthetic efforts of the autotrophs. The thiamine must be added to satisfy the Chlorella's requirement for this vitamin. In the heterotrophic succession, the thiamine is produced by the bacteria, and the additional nitrogen comes from the amino acids or peptones. The end product of this succession is also the climax state.

In studying either type of succession, most of the experiments involve the sacrifice of replicate systems at given time intervals. Enough flasks

are prepared to last for the duration of the experiment. The systems are placed in constant temperature growth chambers or on lighted shelves and held under a 12-hour photoperiod. A system is sacrificed by filtering the contents of the whole flask through a 0.45 micron pore size membrane filter of known weight. The filters are dried below 60°C and weighed to determine the particulate biomass. The filters may also be extracted with acetone for spectrophotometric determinations of chlorophyll and other photosynthetic pigments. The filtrate is dried below 60°C and weighed to determine total dissolved solids. Ashing the dried filtrate yields data as quantity of ash and ash-free dry weight of the total dissolved solids. Particulate materials can be scraped from the membrane filter and burned in a micro-bomb calorimeter for energy measurements. Calorific values for dissolved organic matter may also be made. Assays of population numbers are made with direct microscopic counts, plate counts, or serial dilution. Measurements of net community photosynthesis and nighttime community respiration are made using the pH-CO_2 diurnal curve method of Beyers (1963a) and Beyers, et al. (1963).

IRRADIATION METHODS

The irradiations involved in this study were performed at the 11,500 curie ^{60}Co source belonging to the Savannah River Laboratory (Ahrens and Boudreaux, 1962). The dose levels used were 10^4 Rads, 10^5 Rads, 10^6 Rads, 2×10^6 Rads, 3.5×10^6 Rads and 5×10^6 Rads. These doses were delivered within 0.6 min., 6 min., 1 hr., 2 hr., 3.5 hr., and 5 hr., respectively. In the successional work only the first three doses were used and exposures were carried out on successive days beginning with the 10^4R exposure. On the day of the irradiation, two 500 ml samples were taken from a climax microecosystem. One of these samples was put in a one liter Erlenmyer

flask and placed in the growth chamber for use as a control. The other was partitioned between two 250 ml glass stoppered bottles and taken to the Savannah River Laboratory for irradiation. This partition was necessary as the 250 ml bottle was the largest container that could be placed in the source and receive a uniform dose. Following irradiation, the microcosms were returned to the laboratory where they were recombined, put into a one liter flask and placed in the growth chamber. The next day successions were started by inocula from the control and irradiated microcosms. Successions with inocula from the control and irradiated microecosystems were also set up at weekly intervals following the first succession (8, 15, and 22 days after irradiation). This procedure was followed for each of the exposure intensities and both types of succession. Thus, there were 12 control and 12 experimental successions for the autotrophic and heterotrophic studies. All successions were run in the constant temperature rooms under the conditions mentioned above.

Additional 250 ml aliquats of climax microcosms were irradiated at 1, 2, 3.5, and 5 x 10^6 R in an attempt to achieve total sterilization of the system. After irradiation the microecosystems were returned to the constant temperature room and inspected visually as to color. Samples were taken from control and irradiated systems for determination of the most probable number (MPN) of bacteria present by the Multiple-tube fermentation technique (APHA, 1960).

RESULTS

Autotrophic succession: An investigation was conducted on the effects of added phosphorus on the autotrophic succession. Three levels of phosphate phosphorus were used (Table 1); the normal concentration in half-strength

Taub #36 medium; one half the normal concentration; and double the normal concentration. After fifty-four days the greatest biomass occurred in the highest phosphorus concentration. The other two levels had biomasses proportional to the amount of phosphorous present. However, the total dissolved solids were in inverse proportion to the phosphorus concentration. Thus, the total water production was approximately the same at all three levels.

These results may be interpreted as a secretion of primary photosynthate into the medium when phosphorus is not available for the formation of particulate organic matter from the first products of photosynthesis.

TABLE 1. Phosphorus concentration, biomass, dissolved solids and total solids in laboratory microecosystems 54 days after start of autotrophic succession. All values given in milligrams per liter.

PO_4-P concentration	1.55	3.10	6.20
Particulate biomass	856	924	1022
Dissolved solids	1304	1032	872
Total solids	2160	1956	1894

Heterotrophic succession: An intensive study of the first 30 days of the heterotrophic succession under 150 to 200 foot candles and at 27°C was conducted. The parameters investigated were: metabolism of the system, species numbers, biomass, dissolved inorganic material, and dissolved organic material.

The microecosystem metabolism was found to increase with time. pH changes were as great as 4-1/2 units in late succession (Fig. 1). The diurnal pattern of metabolism was similar to those reported for other microecosystems under laboratory light conditions (Beyers, 1963b). Net photo-

synthesis was maximal in the first half of the light period and nighttime respiration was maximal in the first half of the dark period (Fig. 1). Chlorella cells increased approximately logarithmically for the first five days reaching 1.5×10^7 cells per cubic centimeter. Subsequently, the rate of increase gradually leveled off. The final concentration was 6×10^7 cells per cubic centimeter at 30 days. The two flagellates peaked in numbers around 16 days. Scenedesmus appeared sporadically in the samples. Rotifers were not present in the first 30 days, but reappeared later. The ostracods increased to 80 per liter on day 5 then decreased to 0 by day 15. However, eggs were present and the ostracods reappeared in the samples on day 17, 22 and 28, indicating that some hatching was taking place. Schizothrix abundance was measured in terms of meters of filament per liter. The biomass of this blue-green alga varied around 6.3 meters per liter.

Total particulate biomass increased from 50 mg per liter on day one to 900 mg per liter on day 30, while dissolved organic material decreased rapidly from 500 mg per liter to 50 mg per liter in the first 8 days. Subsequently, values for this quantity remained more or less stable at a somewhat low figure (Fig. 2). Dissolved inorganic salts decreased rapidly during the first 12 days of the succession and then leveled off at about 450 mg per liter.

Another series of heterotrophic experiments was performed in an attempt to simplify the medium. The following amino acids were tested as the single organic component of the medium: methionine, cystine, arginine, valine, lysine, leucine, isoleucine, hydroxyproline, proline, histidine, tyrosine, tryptophan, phenylalanine, glutamic acid, aspartic acid, alanine, glycine, serine. Alanine was most effective in supporting algal life over a period of more than 30 days. It most resembled the proteose-peptone controls in

biomass production. However, no ostracods survived. The microecosystems raised on the other amino acids with the exception of arganine all turned yellow after about 30 days indicating algal death. Cipradopsis survived only in the lysine and cystine systems. Glucose plus nitrate was also tested as the basis of the heterotrophic medium. Glucose produced the highest biomass of any media but most of it was in fungal growth and the algae did not survive.

Based on these and earlier data, the following combinations were tested: 1) arginine, lysine, glycine and tyrosine; 2) alanine, cystine, tryptophane and histidine; and 3) all of these amino acids together. Media 1 supported an almost normal heterotrophic succession but turned yellow two months later. Media 2 underwent an almost continual algal bloom after 98 days. No ostracods were visible. Media 3 produced a normal succession with a slightly higher biomass than Media 1 but no ostracods survived. Thus, at the present writing, no medium has been found which will replace peptone as an effective medium for the heterotrophic succession. Even vitamin-free caseamino acids will not provide support for a normal succession for periods over 120 days. Experiments are continuing to determine a simpler medium.

Irradiation experiments: In the autotrophic succession the growth of the microcosm biota is produced by the photosynthetic fixation of carbon, while the initial biomass increase in heterotrophic succession is due to the growth of bacteria and fungi on the organic matter added to the medium. Thus, biomass increase in the autotrophic succession is the net community production of the system. This is not true in the heterotrophic succession, at least in the early stages, where biomass increase is a combination of net community production and heterotrophic growth.

Subsequent work with these systems has indicated that they may not reach climax, as indicated by stable biomass values, until later than 40 days. However, in this irradiation study the system at 40 days is considered to be at climax at least for comparison of effects. This position is supported by the fact that the rate of growth in both types of succession drops two orders of magnitude between early succession around day 8 and late succession at day 38.

Figures 3 and 4 show a plot of biomass versus time in the autotrophic and heterotrophic successions. In general, the control autotrophic succession has a longer lag phase, but achieves a higher biomass than the control heterotrophic succession. Three parameters of succession affected by irradiation were studied. They are 1) the lag time between innoculation, and the time of maximum rate of growth, 2) the maximum rate of growth, and 3) the terminal standing crop. Rate of growth has been calculated as the milligrams produced per milligram biomass per day to eliminate the effect of increasing system biomass during succession.

With the exception of the death of the metazoods at 10^5 Rads, there were no gross visible effect on the climax system at or below 10^6 Rads. At 2×10^6 Rads the algae bleach 40 days after irradiation. At 3.5×10^6 Rads they bleach after four days and at 5×10^6 Rads, they bleach after two days. After doses greater than 10^6 Rads, no climax system could be used to initiate either an autotrophic or heterotrophic succession. To investigate non-visible effects of irradiation at 10^6 Rads and lower doses, successions were set up one day after irradiation. Figures 3 and 4 show plots of biomass against time for autotrophic and heterotrophic successions at 0, 10^4, 10^5 and 10^6 Rads; and Table 2 gives the pertinent successional parameters

for the two types of succession and the three treatments. It should be pointed out that in all data presented in this report the control values are the average of the control runs for all three treatments. As pointed out above, the initial biomass increase in the heterotrophic succession is due mainly to heterotrophic growth on the organic matter added to the medium. Thus, it is not true net production. Because this growth is very rapid, the lag time in the heterotrophic successions was too short to be measured by the technique used except in the first succession from the microcosm irradiated at 10^6.

The recovery of the irradiated microcosms, as indicated by the growth of "daughter" microecosystems innoculated from them, was studied by following the three successional parameters in experiments that were set up at weekly intervals after irradiation. Each succession had its own control innoculated from a portion of the original mature system which had not been irradiated and had subsequently been under the same environmental conditions as the irradiated climax system which was recovering.

The lag time we define as the length of time between innoculation and the time of maximum rate of growth. In the autotrophic successions innoculated from the microecosystem irradiated at 10^4 Rads, the lag time returned to within the range of the controls in the succession started one week after irradiation. The lag times in those successions from microcosms irradiated at 10^5 and 10^6 Rads returned to normal after two weeks. There was no apparent effect of radiation on the lag times in the heterotrophic successions except at the 10^6 Rad level where it returned to normal in the succession set up one week after irradiation. The maximum growth rate of the successions in autotrophic medium innoculated from irradiated climaxes all were at normal

levels by one week after irradiation. The maximum growth rates of the heterotrophic successions from the microcosms irradiated at 10^6 and 10^5 Rads are consistently lower than those of the controls. The maximum growth rates of the successions from the microcosm irradiated at 10^4 Rads return to within the range of the controls three weeks after irradiation. The 10^5 Rads values do not quite achieve the control level. Those from the successions of the 10^6 Rads microcosm gradually increase but again never quite reach the controls.

The climax biomasses for the autotrophic successions from the microecosystem irradiated at 10^4 Rads were higher than those from the controls until the succession of the third week. Perhaps this indicates a temporary stimulatory effect of irradiation. The autotrophic successions from the microcosm irradiated at 10^5 Rads show a gradual increase in climax biomass until the second week, after which the values level off at about 2/3rds that of the controls. Irradiation at 10^6 Rads appears to have a similar effect on the successions. Although the rate of recovery was greater, the climax biomass also leveled off at about 2/3rds the value of the controls.

The terminal standing crop of the heterotrophic successions set up one week after irradiation appear anomalous (10^5 Rads too high and 10^4 Rads too low). Otherwise, the data show that the climax standing crop of the heterotrophic successions from each of the irradiated microcosms recover after two weeks from the time of irradiation.

Attempts at total sterilization: The viable bacterial cell count of the climax microecosystem is 9,300,000/cells per milliliter. After a dose of 2×10^6 Rads the count is 430 cells; after 3.5×10^6 Rads the count is reduced to 210 and a dose of 5×10^6 reduces the count to 150 viable cells

TABLE 2. Lag Time, Maximum Rate of Growth, and Terminal Standing Crop in Autotrophic and Heterotrophic Successions Innoculated from Control and Irradiated Microecosystems.

Dose in Rads	Lag Time in Days After Irradiation			
	0	8	15	22
	Autotrophic			
0	6	6	6	10
10^4	6	6	6	14
10^5	26	18	14	10
10^6	30	26	14	14
	Heterotrophic			
0	< 4	< 4	< 4	< 4
10^4	< 4	< 4	< 4	< 4
10^5	< 4	< 4	< 4	< 4
10^6	14	< 4	< 4	< 4
	Maximum Rate of Growth in Mg/Mg/Day			
	Autotrophic			
0	0.324	0.249	0.258	0.310
10^4	0.237	0.289	0.240	0.227
10^5	0.155	0.261	0.321	0.231
10^6	0.242	0.2[illegible]	0.335	0.228
	Heterotrophic			
0	0.339	0.393	0.399	0.403
10^4	0.363	0.364	0.369	0.409
10^5	0.361	0.368	0.343	0.376
10^6	0.130	0.265	0.294	0.373

(Table 2 cont'd)

	Terminal Standing Crop in Mg/l			
	Autotrophic			
0	930	844	874	893
10^4	1029	961	1051	900
10^5	500	555	625	607
10^6	234	348	516	558
	Heterotrophic			
0	416	444	353	330
10^4	350	291	344	324
10^5	302	469	322	322
10^6	213	354	265	304

per milliliter. Of the bacteria surviving the 2,000,000 Rad dose, 36% survive a 5,000,000 Rad dose. Thus, it appears impossible to attempt total sterilization of the microcosm with any practical level of gamma radiation.

OTHER MICROECOSYSTEM EXPERIMENTS

Nutritional Experiments: Experiments were conducted during the period of this grant to determine whether or not whole, dried microecosystems were nutritionally suitable as a diet for the harvest mouse (*Reithrodontomys humulis*) or juvenile cotton rats (*Sigmodon hispidis*), and if so, whether or not a matter balance could be worked out between the rodents and the microecosystems in such a way that the non-gaseous wastes of the rodents might be processed by the flora and fauna of the systems. It was hoped that these waste products would be converted into biomass of producers and primary consumers and once again be available to the rodents as food. However, due mainly to lack of facilities to grow a sufficient amount of material and the absence of a competent nutritionalist to supervise the work, these studies met with only limited success. For additional information the reader is directed to the report of Mr. Craig P. Markham which was submitted to NASA as part of the Third Semi-Annual Report from this grant.

Short photoperiod experiment: Autotrophic and heterotrophic successions were performed on systems placed on the normal 12-hour photoperiod and on a 45 min. photoperiod. Biomass data as well as production and respiration measurements were taken. As of this writing, the metabolic data is still being manipulated by the computer. However, the biomass data is very interesting. In both cases the experimental data is much

more variable than the controls. In the heterotrophic succession the experimental biomasses remain consistently below the controls, while in the autotrophic succession they are higher during early succession and lower after climax has been obtained.

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Appendix

THE CASE FOR THE MULTI-SPECIES ECOLOGICAL SYSTEM, WITH SPECIAL REFERENCE TO SUCCESSION AND STABILITY

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ABSTRACT

This paper presents an evaluation of proposed life support systems based on ecological theory. The two organism life support system (i.e. algae - man) is compared with a multi-species life support system as to stability, structure, and energy flow. It is concluded that the multi-species system is ecologically more sound. This position is supported with data taken from laboratory microecosystems.

A man in a space capsule is a member of an ecosystem, consequently, will be affected by all that goes on in this ecosystem. The success of long-term space flight may well depend on our success in developing a life supported system which is stable and long-lived. It is the purpose of this paper to discuss some properties of ecosystems which promote stability and longevity, and to propose that life support systems must be developed within the conceptual framework of the mature multi-species ecosystem.

Several types of life support systems have been designed or suggested to handle the following aspects of astronaut metabolism: gas exchange, food production, waste disposal and nutrient and water regeneration. Of those proposed, only the storage system, designed for short flights, has been successfully tested. For flights of long duration, only bio-regenerative systems appear to be feasible. The two-species gas exchange and/or food production model has received much attention. These have been described as the unialgal-man gas exchanger (Myers, 1960; others) and the Hydrogenomonas - man life support system (Bongers and Kok, 1964; others). In addition, Oswald, et al. (1965) have discussed the feasibility of an algae-bacteria-mammal system. One other type of life support system has been suggested. This is the multi-species climax ecosystem as proposed by H. T. Odum (1963), and which will be the topic of this paper.

There are at least two approaches to the development of life support systems. One of these consists of the testing and later assembling of separate biological, chemical and mechanical components. The second consists of allowing groups of species known to occur together to re-assemble and reorganize in a new environment into an integrated, self-maintaining system. This system we call an ecosystem. Nature operates

by the second method. Man uses the first in constructing his machines. We submit that the first is ecologically unsound and will prove to be unsuccessful. The balance of this paper will present evidence to show that the multi-species approach will provide the greatest chance of a successful long-term life-support system.

An ecosystem is any assemblage of organisms and their abiotic environment which have the following characteristics (E. P. Odum, 1959, 1963): structural organization, interdependency of components, homeostasis and regulation (either external or internal or both), limits and thresholds, and a development toward a steady state with increasing adaptation with and control of the physical environment (succession). There are four components of an ecosystem: (1) abiotic substances (organic and inorganic), (2) producers, or autotrophs, (3) consumers or phagotrophs which feed on larger particles, and (4) decomposers or osmotrophs, which derive their support from smaller or molecular size particles. Both of these latter categories decompose organic material and release products usable by producers.

One of the most important attributes of ecosystems is the unidirectional flow of energy from green plants through food webs to consumers and decomposers. The amount of photosynthate stored in excess of daytime community respiration is termed net community photosynthesis. At night, part or all of this net storage is consumed by community respiration. A continued excess of community photosynthesis over community respiration leads to an accumulation of biomass. Eventually this accumulation of biomass stops as limits of utilization of light input are reached or nutrients becoming limiting, or some physical threshold such as space requirements is reached.

Ecosystems have structure. By this we mean biomass, stratification of both living and non-living substances, and biochemical and species diversity. Depending on age and limitations of the physical environment, structure is more or less apparent in terms of the numbers of species. An ecosystem with many species per unit number of individuals may have a very complex food web as a result of niche ("way of life") specialization by these species. Also, as the number of species increases, the number of homeostatic or regulatory mechanisms increases, and the organisms within and between the various trophic levels become more independent. There is increasing evidence to show that diverse ecosystems are also diverse biochemically (Margalef, 1963b).

The truly unique feature of ecosystems, however, is not structure or regulation, since these might be accomplished through external mechanical means, but the ability of ecosystems to develop, to come to a steady, self-maintaining, mature stage, often called a climax ecosystem. Some examples of mature systems adapted to particular physical factor regimes are temperate North American Stipa-Biutelous perennial grassland, eastern deciduous oak-hickory forest, intertidal mangrove forest (Colley, et al. 1962), tropical rain forest and coral reef (Odum and Odum, 1959). Oriental rice culture represents an agricultural system maintained by man which is more mature and stable than, for example, shifting row crop tropical agriculture. The mature ecosystem tends to exhibit the maximum in structure and stability, within the limits imposed by the physical environment.

It is the mature ecosystem which we propose as the theoretical basis for the development of life support systems. We believe that long-term stability, which is the result of the development of many homeostatic mechanisms through succession, must be the underlying concept in the

development of a dependable life support system. In other words, a multi-species system, with its associated high stability, has a far higher probability of survival than, for example, a two-species system.

A two-species system represents what we call "young nature." It has characteristics of early developmental stages of succession. A multi-species system, the result of a long developmental period, represents what we call "old nature" or a mature developmental stage (E. P. Odum, 1962a).

One of the authors of this paper (E. P. Odum) has prepared a tabular model of succession (table 1) with which we can compare the characteristics of old and young nature. Using some of the concepts of this model, we intend to compare two-species life support systems and multi-species systems. We will show in greater detail some properties of ecosystems which demonstrate why we believe that a system with the characteristics of a mature ecosystem must be the basis of future life support systems.

Not all of the ecosystem attributes of the model shown in table 1 are applicable, at present, to life support systems. For example, no one envisions the possibility of man completing a life cycle in space. Other attributes are not well documented and need further research. Our remarks here will be confined primarily to attributes of ecosystem energetics and structure.

Many of the data which we will use during this paper to demonstrate the functional and structural events during succession has been obtained from the study of laboratory microcosms. These microecosystems are at least partially physically isolated from other ecosystems and in this respect are unnatural, since there is no export or import, other than light and gas exchange with the atmosphere. However, the data obtained from these systems has particular applicability to the topic in question here, since a space capsule is a microecosystem.

Table 1. A tabular model of ecological succession.* Trends to be expected in the development of ecosystems.

		Ecosystem Attributes	Developmental Stages	Mature Stages
Community Energetics	1.	gross production/ community respiration	P/R ratio or one	approaches one
	2.	gross production/ standing crop biomass	P/B ratio high	low
	3.	net community production (yield)	high	low
	4.	food chains	linear, predominately grazing	web-like, predominately detritus
Community Structure	5.	standing crop biomass & organic matter	small	large
	6.	Species diversity	low	high
	7.	biochemical diversity	low	high
	8.	stratification	undeveloped	well developed
Life History	9.	niche specialization	broad	narrow
	10.	size of organism	small	large
	11.	life cycles	short, simple	long, complex
Nutrient Cycling	12.	free inorganic nutrients	large	small
	13.	mineral cycles	open	closed
	14.	nutrient exchange rate, organisms-environment	rapid	slow
	15.	role animals in nutrient regeneration	unimportant	important
Overall Homeostasis	16.	internal symbiosis (interdependence of organisms)	low	high
	17.	Nutrient conservation	poor	good
	18.	stability (resist external pertubation)	poor	good
	19.	Entropy	high	low
	20.	Information	low	high

*Prepared by Eugene P. Odum

The microcosm method has been described by Beyers (1963a, 1964). Briefly, materials from a natural ecosystem are brought into the laboratory and divided equally among a group of containers. Cross-seeding minimizes any possibility of divergence between microcosms. The systems are then placed on the desired regime of physico-chemical variables. Metabolism is measured by recording diurnal pH changes and these data are translated into total CO_2 changes through the use of a graph depicting the relationship between microcosm pH and CO_2 changes. Microcosm biomass is determined by pouring an ecosystem into a tared weighing dish or through a tared Millipore filter. The materials are then dried and weighed. Similarly, total ecosystem chlorophyll is measured by filtering all or part of the system, reading the acetone extract at the appropriate wave lengths for the various pigments, and calculating the amount of chlorophyll according to Strickland and Parsons (1965). These and other measurements are made at intervals during development or succession of the microcosm, and from these data, we have been able to show the course of some of the events of metabolic and structural succession.

In comparing the structure and function of old and young nature, we intend to emphasize these main points. (1) The two-species system represents young nature and has the advantage of a high rate of productivity per unit biomass, but has low stability. The multi-species system has a low ratio of photosynthesis to biomass and thus must be large to support an astronaut, but has the distinct advantage of multi-channel stability. (2) The astronaut is part of a microecosystem, whether we are considering a two-species or a multi-species system, and is therefore part of the structure and function of the system. Depending on system stability, he will be more or less influenced by perturbations in its structure and function.

In Figure 1 and 2 some data on succession in laboratory microcosms are plotted. In these experiments succession was initiated by innoculating material from a mature system into new medium. In young communities the rate of day-time photosynthesis exceeds that of night respiration and biomass accumulates. Total or gross photosynthesis is high in the early stages. After about 70 days of succession, the ratio of day-time photosynthesis to night respiration approaches one, and biomass reaches a stable value. At this point, the efficiency of the system is maximum, under a given set of environmental conditions, in that the highest level of biomass is maintained per unit of gross photosynthesis. Notice also that the rates of respiration and photosynthesis are steady.

In our comparison of young and old nature, we are actually comparing two types of efficiency (Figure 2). In early developmental stages such as the two-species life support system, the ratio of gross photosynthesis to biomass is very high--a small amount of structure is maintaining a high rate of photosynthesis. This is one type of efficiency, and is that which has been emphasized by proponents of the two-species system. If succession is allowed to proceed, whether by design or accident, the ratio drops. The trend in succession is to develop as large and diverse a structure, per unit of energy flow, as possible. Thus in early stages, the ratio biomass/photosynthesis is low; in a mature stage the ratio is high. At climax a more complex structure, with a reduced waste of energy, allows the maintenance of the same biomass with a lower expenditure of energy or cost to the system (Margalef, 1963). The more stable the system, both externally and internally, the less energy needed to maintain this biomass (Connell and Orias, 1964). In other words, as the system ages and develops structure, it becomes more

efficient at maintaining that structure. This is the other type of efficiency, and is that which we propose to be the basis of a stable life support system.

The important point is that stability in these rates and ratios has been developed and will be maintained without external controls at maturity, while in young stages, stability must be constantly maintained through external controls. Mature microecosystems in the laboratory of Beyers have maintained themselves for years.

Another development during succession is the shift from an early planktonic-open water system to a detritus system in later stages. Recent studies (Engelmann, 1961; MacFayden, 1961; Odum, 1963b) have shown that up to 90% or more of the metabolism of natural mature systems is in the detritus layer. The consequence of this in the use of a mature multi-species life support system is that the astronaut must become a detritus-feeder, or a consumer of detritus-feeding organisms. This may, in fact, prove to be far more palatable than bacteria or algae since a great variety of vertebrates and invertebrates are detritus-feeders.

As communities develop, there is an increase in species diversity and this has been assumed to contribute to stability (Connell and Orias, 1964). In a young ecosystem, there are a large number of unexploited ways of life, or niches. During succession, organisms from other ecosystems invade such structually simple communities or organisms which have been dormant or rare in the early stages become active and numerous. With time, the number of species per unit number of individuals, which we may call a species/number diversity index, increases. It is assumed on incomplete evidence that an increase in the diversity index favors the establishment of homeostasis in terms of checks and balances. During the early stages of succession there

may be "blooms" of the invader populations, often at the expense of one or more established species. Such "blooms" create perturbations that may seriously upset the balance within systems as does a "cancer" growth in individuals. For instance, in the development of unialgal life support systems Miller and Ward (1966) have remarked on the difficulty of preventing the establishment of large populations of grazing zooplankton in their cultures. In a mature ecosystem, with most or all niches filled, the probability of blooms, or even the successful invasion by a new species, is very low (Elton, 1958). That is, the system now possesses stability. For example, the probability of invasion by extra-terrestrial species or a bloom of a mutated form of some component species in a climax system would be much less than in an unsaturated system.

To summarize, the presence of many species not only means a diversity of energy pathways, but also the presence of a great many regulatory and symbiotic relationships. We cannot envision a two-species mechanical-bioregenerative system with this sophistication of control.

Another important trend from young to mature ecosystems, which is a direct result of increasing diversity, is the increase in complexity of food webs. In young stages, the number of species is small and, therefore, the number of pathways of energy transfer between producers and consumers is limited. In the two-species life support system this pathway is linear. In older stages, a great many species have had an opportunity to become established and the food web becomes more complex -- so complex, in fact, that few have been completely described for nay large natural area. Figures 3 and 4, based on the data of Paine (1966), illustrates food webs of a simple and a complex ecosystem. The importance of food web complexity to ecosystem stability is very apparent here. The top consumer in the more

mature food web has the choice of ten prey and most of these prey also have several food chains from which to graze, whereas in the less mature system, the number of interactions is much lower. This is analogous to the back-up systems built into the circuitry of space vehicles. In the microecosystem, the investigator has some choice about the number of species in the system, at least initially. During succession, several of the original groups of species may become extinct. For example, truly planktonic species do not survive succession to the climax stage.

Several examples will illustrate our point about the stability of climax ecosystems. In a climax forest, the outbreak of a pest is rare (Elton, 1958), but in a corn field (an ecosystem much like the two-species life support system) large numbers of pests are common. In the forest a system of checks and balances exists such that an increase in insect population density is automatically followed by an increase in predator density. No such system exists in the corn field and the farmer has to resort to pesticides or mechanical devices. With increasing insecticide resistance, he must resort to more and more potent chemicals. In practice, a combination of biological and physical control is usually optimum from man's standpoint. Our point is that we should fully utilize all possible. self-regulation in order not to have to create unnecessary artificial substitutes.

Beyers (1962) has shown that the metabolism of a complex climax ecosystem is considerably more independent of temperature than the metabolism of a simpler sewage community or a single organism. He postulated that the closer a living system approaches the integration of a balanced ecosystem, the less it is affected by temperature. This hypothesis may be expanded to state that the more complex the ecosystem, the less it

will be affected by temperature extremes, adding stability to the system as a whole.

A mature ecosystem is also stable metabolically. Golueke and Oswald (1964) have pointed out that the CO_2/O_2 exchange ratio of the plant used in setting up a biological gas exchanger must match that of the crew, since a very slight mismatch between human RQ and plant AQ would lead to the accumulation or loss of a certain fraction of the human oxygen demand and carbon dioxide output per day. In the multi-species system, the RQ's of several kinds of heterotrophs would balance the AQ's of the several autotrophs so that a temporary imbalance with one species would be compensated for by other species.

Additional evidence for the increased stability for a multi-species system is shown by the data presented in Figure 4. A climax microcosystem was irradiated with 10^6 R in an acute dose. With the exception of the loss of one species (an ostracod) there was no visible effect on the system. However, when the system was used to initiate a new autotrophic succession, the results of radiation became apparent. As can be seen in Figure 4, the rate of growth of the system was decreased in comparison to the non-irradiated controls. However, this effect decreased with time, indicating the system's capacity for self repair. The curve for each innoculation, made at weekly intervals after irradiation, shows progressive recovery.. The greater the time after irradiation, the closer the curve approaches that of the controls. The principal primary producer and the organism accounting for the maximum biomass in this microcosm was a Chlorella. It is interesting to note that Posner and Sparrow (1964) found that 90% of their pure culture Chlorella died after a dose of 23,000 R. Our Chlorella showed no effects of radiation until they were

irradiated at 2,000,000 R and then took 40 days to die. These results may indicate that the system confers some radiation protection to its member organisms.

The interdependency of components in a climax microecosystem was clearly illustrated in a recent investigation in our laboratory by Mr. Robert Gorden. Gorden has shown that a bacterium also present in the climax is an important source of thiamine, a requirement for the growth of the Chlorella. Close symbiosis between pairs of taxonomically unrelated species is an outstanding characteristic of the most successful natural communities, for example, lichen growths in the arctic or coral reefs in the tropics.

Although little information is presently available, it appears that during succession, both the variety and amount of biochemicals increase (Margalef, 1963b). Many of these extra-metabolites apparently have the properties of inhibitors or of growth promoters (Saunders, 1957). These substances then are environmental hormones and act as regulators (Margalef, 1963b). Another biochemical change during succession is the increase in the quantity of accessory photosynthetic pigments, thus affording the ecosystem with more complete utilization of light as well as a complement of more stable pigments. The increased ability of mature systems to regulate themselves by internal chemical feedback means that less outside energy need be applied by man to achieve stability.

Beyers (1963a, 1965) has shown that there is a general pattern in the metabolism of aquatic ecosystems correlated with the onset of light and dark. The maximum metabolism occurs in the first half of the day or night period. The implications of this pattern for multi-species life

support systems have been discussed elsewhere (Beyers, 1963b). It must be admitted that there is the possibility of deleterious effects on an astronaut by this periodic reduction of photosynthesis and respiration. However, it does seem that the intensity of this phenomena decreases as the species diversity increases (Beyers, 1963a), adding another bit of evidence for the use of complex systems to support man in space.

Our main point in this discussion of ecosystem structure and function is high diversity and high stability in mature systems, low diversity and low stability in early stages. The more mature system has a built-in set of checks and balances which prevent internal disturbances and buffer the system against most external disturbances. Of course, no system is immune to severe perturbations, and, in fact, the limits of ecosystem stability are strongly related to the stability of the physical environment (Dunbar, 1960).

There are certain distinct advantages to young nature, when viewed as life support systems. These advantages are primarily energetic. That is, young ecosystems have high productivity rates per unit biomass which means that they are more efficient gas exchangers in terms of O_2 produced or CO_2 absorbed per unit of biomass. As we have pointed out, however, there are serious disadvantages to young systems as well. It should now be apparent that in the development of a life support ecosystem for man, we must first select for system stability and longevity and then turn to the development of maximum productivity per unit biomass consonant with this stability. We cannot, as has been suggested by Miller and Ward (1960), simply select organisms as needed on the basis of certain desirable functional characteristics and hope successfully to integrate them into a system. This attitude implies that the addition of new species will have no effect

on resident species and this, of course, is ecologically unsound. It should also be apparent that homeostatic mechanisms of ecosystems are far more sophisticated and reliable than their mechanical counterparts. As H. T. Odum (1963) has pointed out, man has yet to develop the miniaturization of circuitry that is found in ecosystems.

The area of a multi-species life support ecosystem capable of supporting an astronaut has been estimated at two acres (H. T. Odum, 1963). This estimate is based on an expenditure of all but about 2% of the photosynthetic production on respiratory requirements of other components of the system. Obviously, practicality dictates some compromise between two-species mechanical systems and the multi-species system which depends on natural self-regulation.

To date, the major emphasis in the development of life support systems has been on single components. These data are valuable and such work should be supported in the future. However, we believe, based on our knowledge of the properties of ecosystems, that future work must stress the development of a multi-species system.

Since such a system will necessarily be larger than proposed two-species systems, we need to determine which processes can be satisfactorily supplemented or replaced by mechanical or chemical devices. For example, the reduction of fecal material to small particles might best be handled by some mechanical method, thus eliminating the need for populations of consumers which ordinarily would fill this role. In other words, we may be able to reduce the predicted size of a multi-species life support ecosystem without reducing the built-in stability of the system.

Finally, it is clear that a great deal of work must be directed towards an analysis of properties of ecosystems before we attempt to advise a multi-species life support system. Part of the controversy regarding the simple vs. complex system may be resolved by a set of experiments. Laboratory microecosystems ranging in complexity from a single alga and consumer to a highly complex system containing several representatives of each trophic level could be cultured under identical conditions. The climax systems and successional stages could be tested for metabolic and species stability under various stresses. Such stresses could include thermal manipulations, ionizing radiation, invasion by foreign species, and mechanical and photoperiodic stresses. We propose to perform such experiments in the future.

Acknowledgements

Preparation of this manuscript was supported by a United States Public Health Service (Division of Water Supply and Pollution Control) Post-doctoral Fellowship, contract AT(38-1)-310 between the U. S. Atomic Energy Commission and the University of Georgia, and grant NSF-706/11-003-001 from the U. S. National Aeronautics and Space Administration to the University of Georgia. The authors wish to express their appreciation to Drs. Frank B. Golley, Richard G. Wiegert, and Mr. Peter C. Fraleigh for their criticisms and comments. Figures were prepared by Mr. M. E. Chavis.

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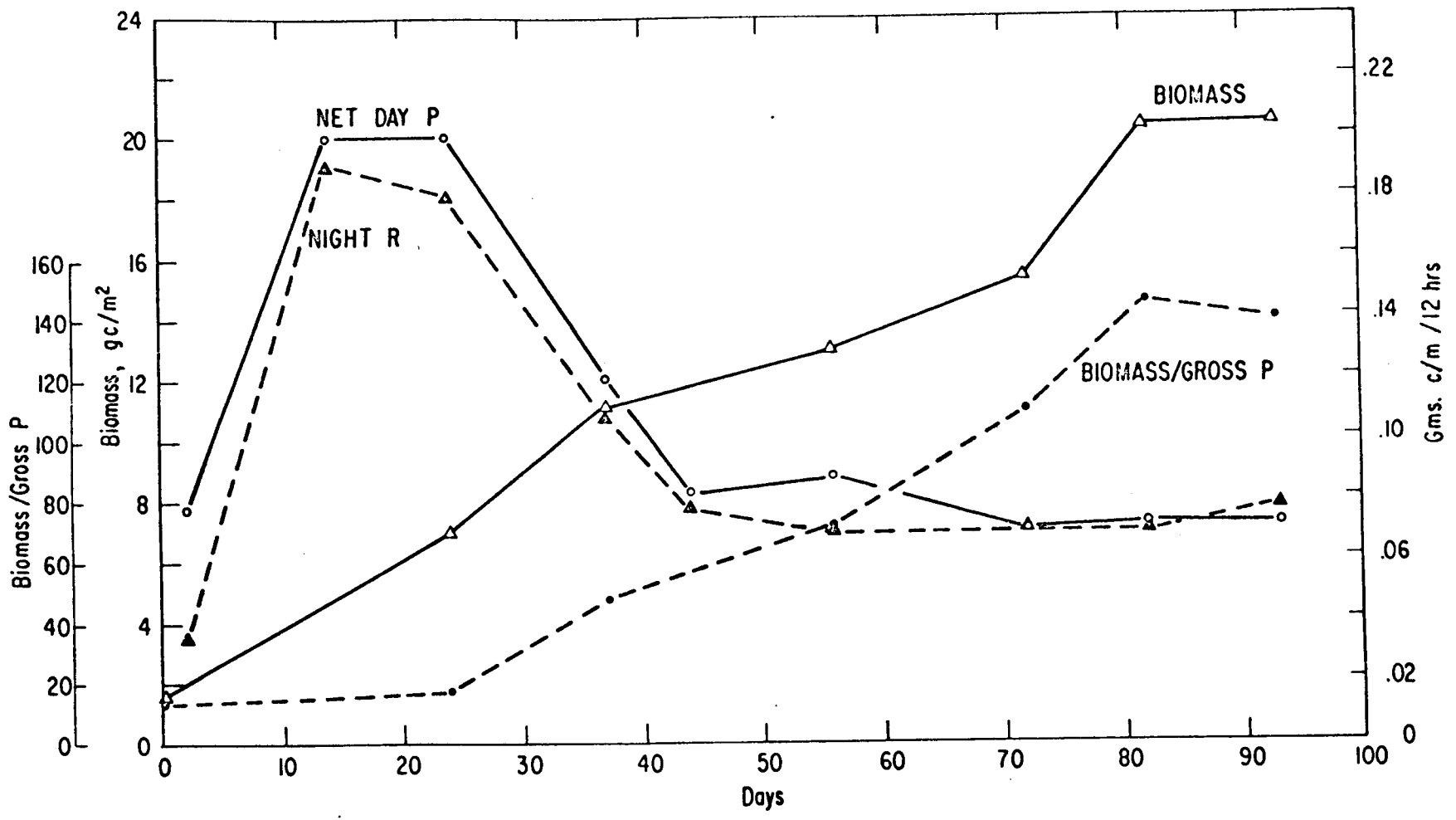
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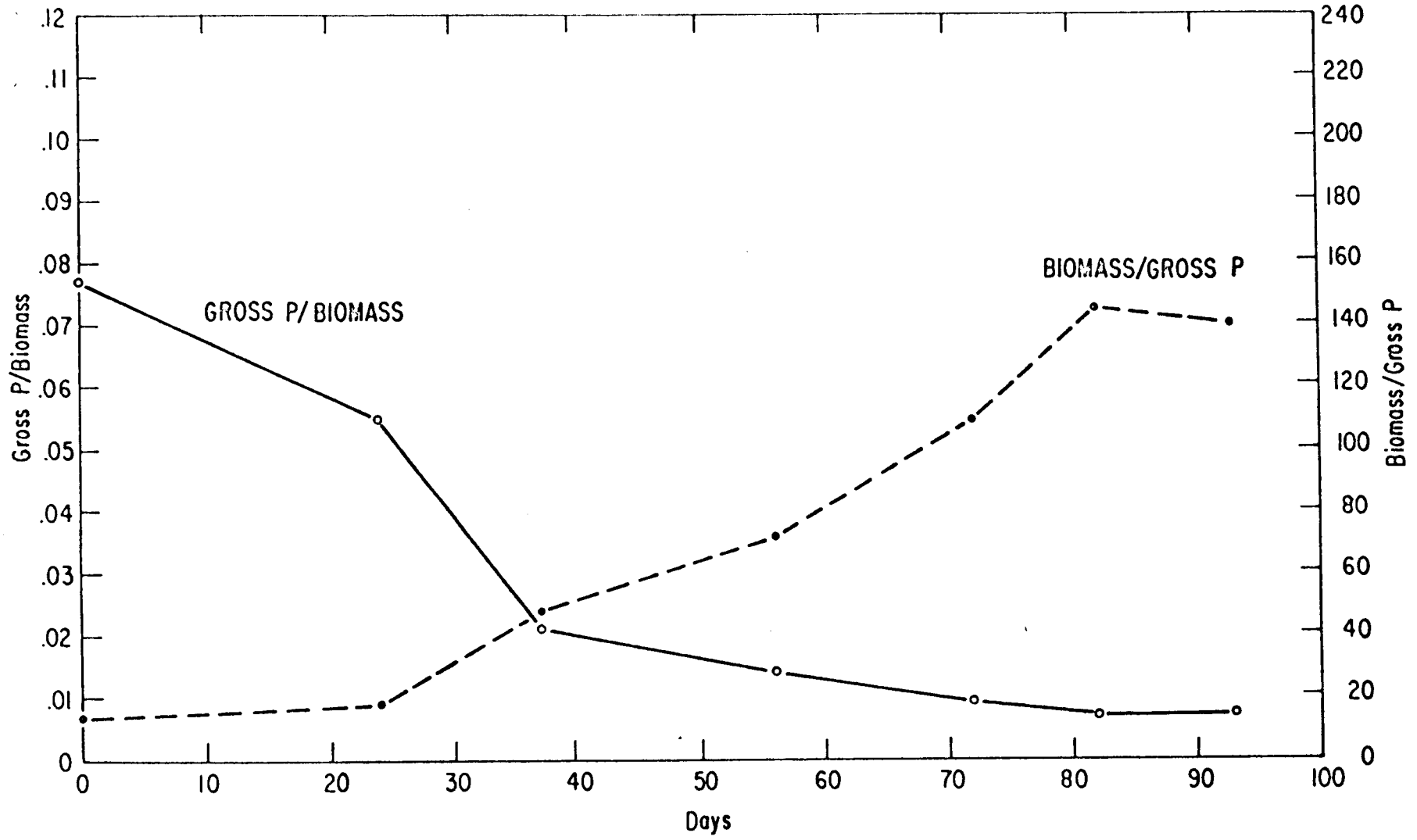
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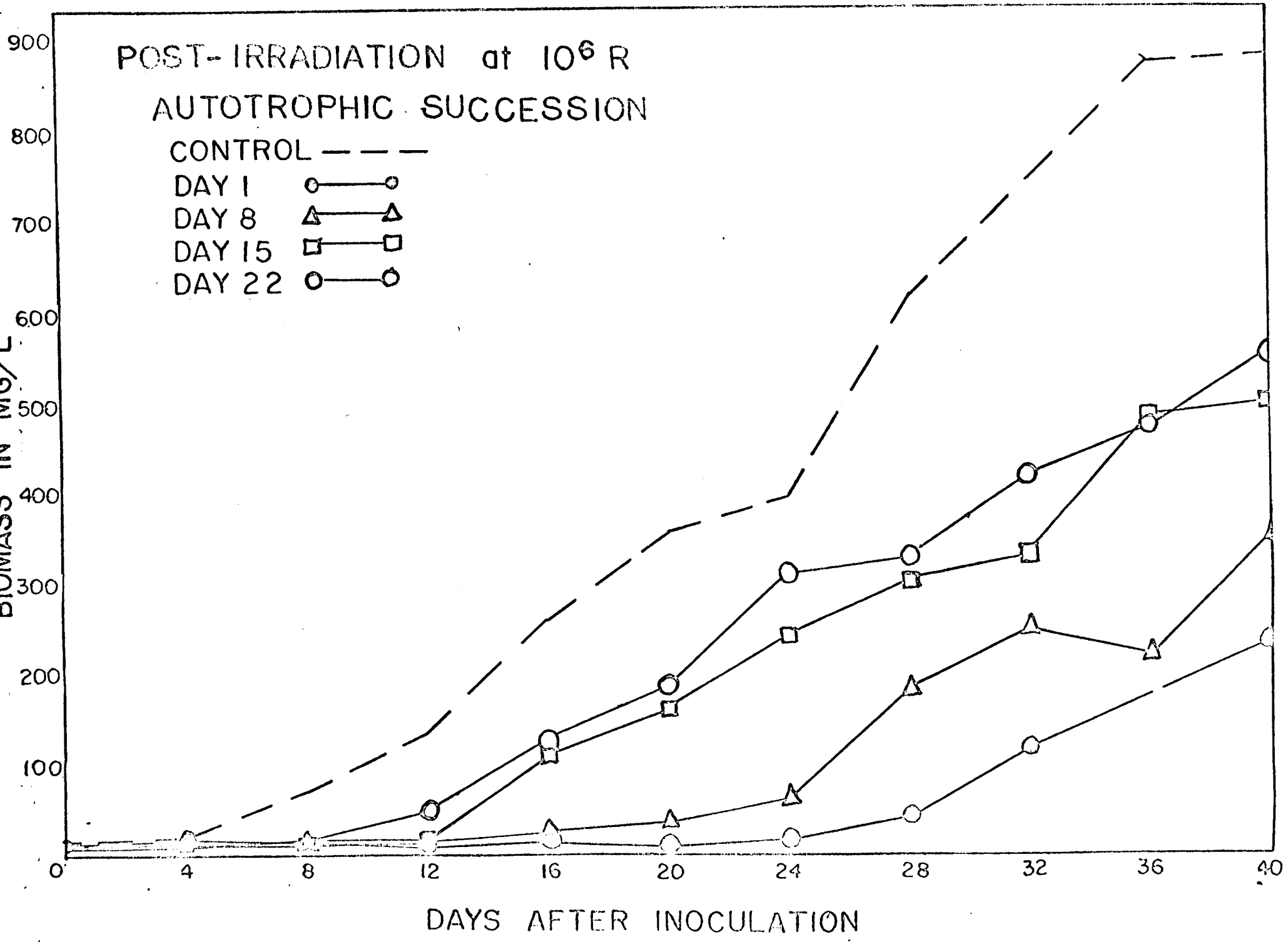
POST-IRRADIATION at 10^6 R
AUTOTROPHIC SUCCESSION
CONTROL
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DAY 8
DAY 15
DAY 22
BIOMASS IN MG/L
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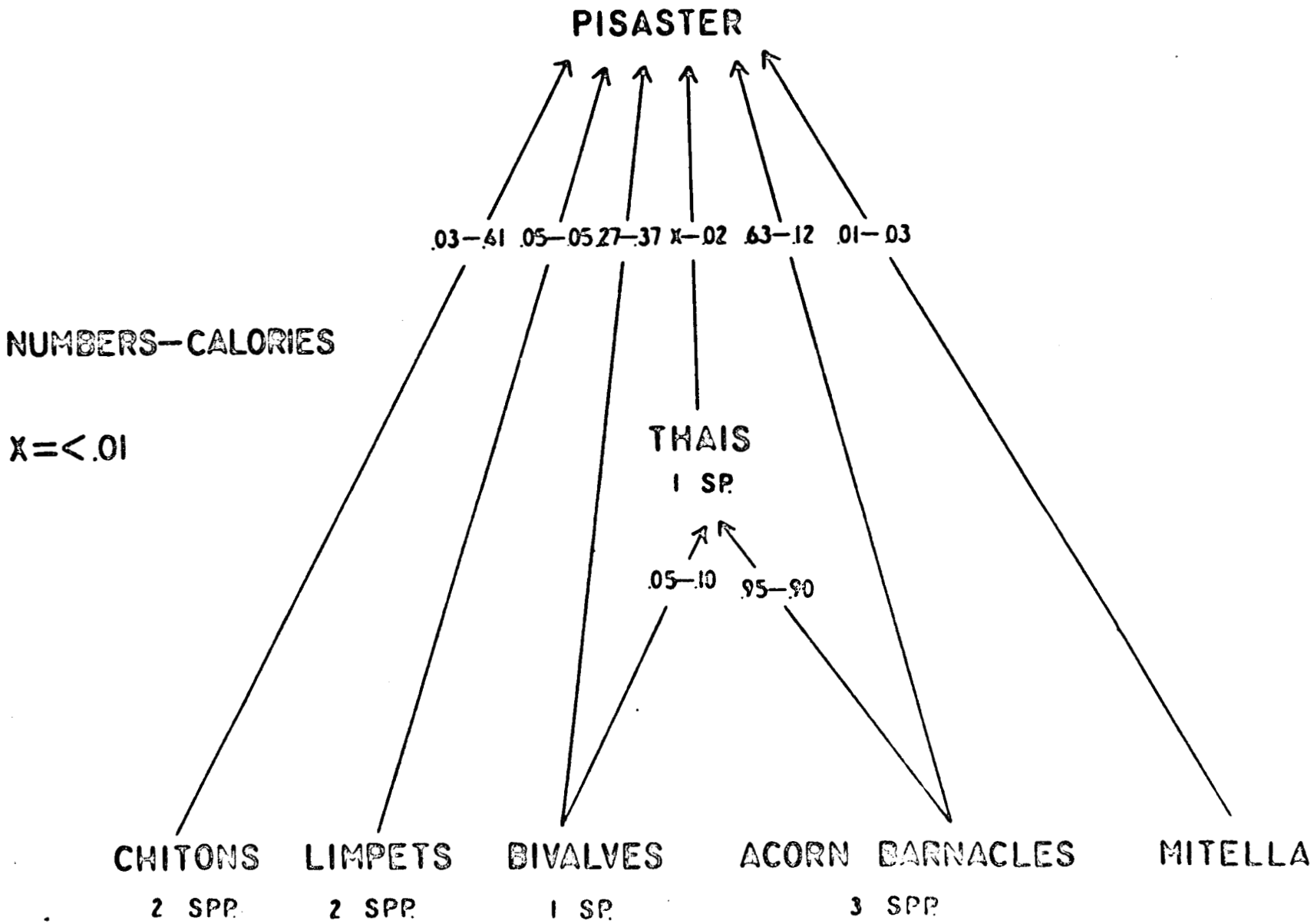
DAYS AFTER INOCULATION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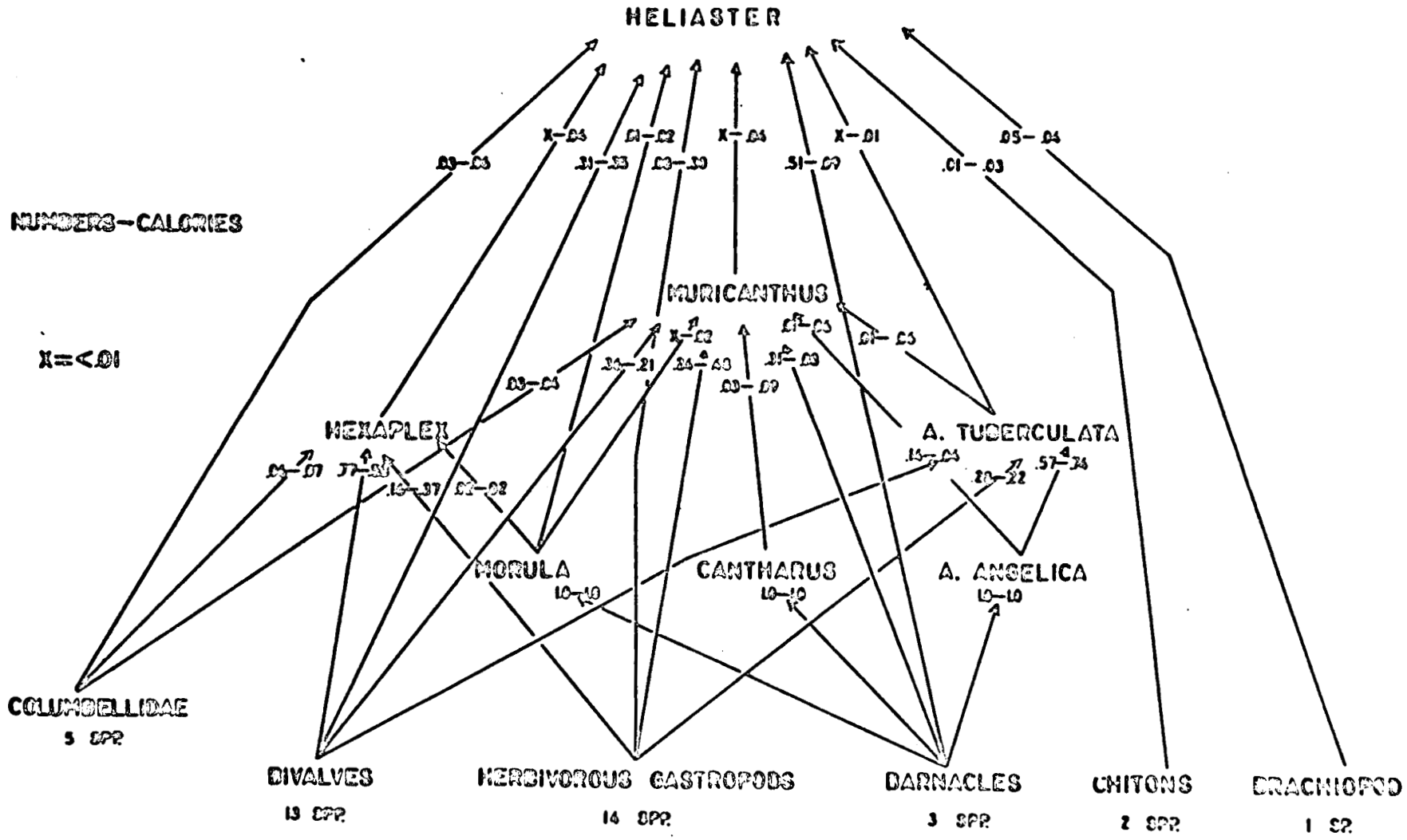
HELIASTER
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COLUMBELLIDAE
5 SPP.
DIVALVES
13 SPP.
HERBIVOROUS GASTROPODS
14 SPP.
BARNACLES
3 SPP.
CHITONS
2 SPP.
BRACHIOPOD
1 SP.

Figure Legends

Figure 1. Plots of net daytime photosynthesis, nighttime respiration, biomass and the ratio between biomass and gross or total photosynthesis against time in a microecosystem undergoing autotrophic succession. All data has been reduced to aerial dimensions.

Figure 2. Plots of the ratios of gross or total photosynthesis to biomass and vice versa against time in a microecosystem undergoing autotrophic succession. This figure illustrates the two types of efficiency outlined in the text.

Figure 3. The feeding relationships by numbers and calories of the *Piaster* dominated food web at Mukkaw Bay, Washington. *Piaster*, N = 1049, *Thais* = 287 where N is the number of food items observed eaten by the predators. The specific composition of each predator's diet is given as a pair of fractions: numbers on the left, calories on the right. (From Paine, 1966).

Figure 4. The feeding relationships by numbers and calories of the *Helmster* dominated food web in the northern Gulf of California. *Helmster*, N = 2245; *Muricanthus*, N = 113; *Hexaplex*, N = 62; *A. tuberculata*, N = 14; *A. angelica*, N = 432; *Morula*, N = 39; *Cantharus*, N = 8. See Figure 3 for further explanation (from Paine, 1966).

Figure 5. Course of biomass increase with time in an autotrophic succession in a laboratory microecosystem irradiated at 10^6 Rads. Successions were initiated by inoculating samples of the irradiated mature microecosystem at 1, 8, 15, and 22 days after irradiation. Control curve is from non-irradiated microecosystems.