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RELATIONSHIPS BETWEEN INORGANIC NUTRIENT INPUT, ALGAL DENSITY, HERBIVORE DENSITY, AND RESIDUAL INORGANIC NUTRIENT

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The relationships between inorganic nutrient supply and the first two trophic levels have long been understood in a very approximate manner but the dynamics of such a system cannot be explored adequately by simple arithmetic when nonlinear relationships exist. An exploration of such a system was accomplished by the use of a mathematical model based on experimental data from a pair of two-stage continuous cultures of the alga *Chlamydomonas reinhardti* and the herbivorous protozoan *Tetrahymena vorax*.

METHODS

To interpret the data, one needs a few details of the culture method. The inorganic culture media were designed to have nitrate as the sole limiting nutrient; the phosphate concentration was varied along with the nitrate concentration in a molar ration of 12.5 N to 1 P, and phosphate and all other requirements were assumed to be present in excess. The algal cells provided the nutritional support for the protozoa since the protozoa could not grow in the initial inorganic media nor in the cell-free, spent medium. The two-stage culture unit had an axenic algal culture in the upstream flasks which overflowed into the downstream flasks. In one of the two-stage culture units, protozoa also had been added to the downstream flask. Thus the algal cells were protected from predation in the upper flask and could be introduced into the downstream flask in high concentration. The flow served both to import nutrient and to export cells. The culture volume in each flask was 500 ml. The culture method has been described in detail in Taub and McKenzie 1972. The results of batch and continuous cultures of these organisms, which formed part of the basis for this model, have been published (Taub 1969*a*, *b*, *c*). For reviews of continuous culture methods and the calculations for multistage continuous cultures, see Kubitschek (1970) and Herbert (1964), respectively.

One needs to understand also the major assumptions and parameters of the model. The algal growth rate was based on a modified Michaelis-Menten equation that included the effects of nitrate concentrations and the effective light concentration as calculated by Beer's law to account for self-shading. The maximal growth rate (but not a standard μ_{max}) was 4.13; the K_S was 2.25×10^{-3} mM NO_3^-; and the K_L was 5500 (arb. light units). The protozoan growth rate was based similarly on the Michaelis-Menten relationship with algal cell concentration as a substrate: the μ_{max} was 1.3, and the K_S was 7.2×10^5 algal cells. The resultant relationship was similar to an Ivlev saturation curve (Sushchenya 1970). The relationships between the algae and protozoa were basic Lotka-Volterra equations modified to include the effects of inflow and washout to represent the chemostat environment. These basic relationships were modified by numerous interactions as indicated by experimental data. A portion of the algal cell protein consumed by the protozoa was assumed excreted as ammonia, and this, in turn, was assumed available for algal uptake preferentially to available nitrate. The protein of the algal cell varied with the available nitrate concentration. The percentage of protein in the algal cell modified the μ_{max} of the protozoa and the number of algal cells consumed per protozoan produced. A light-induced mortality affected the protozoa. Time lags and several other minor features

were included in the model. The model generally preducts a smooth approach to a steady-state condition; major predator-prey cycles do not occur. Under some conditions, e.g., very slow flow rates, the true steady state is approached so slowly that a practical time limit of 24 days was used. The details of the model are described elsewhere (D. H. McKenzie, Ph.D. thesis in preparation).

RESULTS

The results, shown in Figures 1-15, should be considered as provisional model results of approximate steady states, not as experimental data. The model was run until densities appeared to be stable, maximum 24 days. Somewhat different values would have occurred if the model had been run to the true stability, but these long time periods would be impractical to verify experimentally. The figures demonstrate how a system would respond if the organisms behaved according to the assumptions and estimated parameters of the model. Although virtually all of the assumptions and parameters were experimentally derived, they do not reflect all of the adaptive capabilities of organisms.

At the lowest concentration of limiting nutrient, 0.05 mM NO_3^- (Figure 1), it can be seen that the maximum algal concentration would occur only under the restricted conditions of extremely low flow rates, almost independently of light intensity. Although the protozoa reduced the maximum algal densities (Figure 2), they had virtually no effect on the algal concentrations under the remainder of the environmental conditions. The protozoan densities (Figure 3) were quite low, but they were greatest at extremely low light intensities and extremely low flow rates. The residual nitrate (Figure 4) was appreciable only where cells could not accumulate to use it, where light was low and flows high. The effect of the protozoan on residual nitrate (Figure 5) occurred only under restricted environmental conditions and at concentrations difficult to detect. For broad expanses of environmental conditions stability existed, i.e., concentrations remained relatively unchanged despite changes in light or flow. These results occurred because at these very low nutrient concentrations the algae grow slowly and accumulate only at low dilution rates. Similarly, at these low algal densities, the protozoa grow slowly and cannot persist at high dilution rates.

A tenfold increase in the concentrations of limiting nutrient to 0.5 mM NO_3^- increased the maximum algal density 4.7-fold and shifted the conditions yielding the maximum density (Figure 6). The decrease in density at low flow rates was due to the reduced input of nutrient and slow replacement of dead cells. At higher flow rates, the density was very responsive to changes in light intensity. At the plateau of maximum density, relative stability prevailed. The presence of the protozoa had a marked effect on algal density over much of the environmental range (Figure 7). Comparing Figures 6 and 7, we see that although the same maximum density could be obtained, it could be maintained in the presence of the protozoa only over a much smaller environmental range: very high flow rates and very high light intensities. The protozoan density (Figure 8) that obtained at the lower nutrient concentration was 7.7-fold; the distribution of the density relationship was shifted so that the maximum occurred at moderate light intensities and 100-ml/day flows, and decreases in density occurred in all other directions.

Since the protozoa were able to have a major effect on the algal density over most of the range, they were able also to have a major effect on the residual nitrate concentration, as can be seen by a comparison of Figures 9 and 10. Under environmental conditions where the protozoa had little effect on the algae, they also had little effect on the residual nitrate.

Another tenfold increase in the limited nutrient to 5.0 mM NO_3^- resulted in a 4.8-fold increase in maximum algal density and another shift in the position of the maximum (Figure 11). The protozoa were able to reduce the concentration of algae over the entire range of environmental conditions (Figure 12). The protozoan density distribution was very much like that at the moderate nitrate concentrations although the densities were 1.4-fold higher. The residual nitrate concentration was most dramatically increased over those ranges where the algal concentration was most reduced. Part of the shift in nitrate concentration due to protozoan feeding lies in the assumed preferential uptake of the ammonia that would arise from excretion by the protozoa and the comparatively smaller number of cells that would pick up the residual nitrate.

DISCUSSION

As can be seen from these inclusive model results (it would have taken almost 20 years of experimental data to collect enough values for these relationships to have been drawn empirically), universal general relationships could not have been obtained at any single light intensity, any single flow rate, or any single nutrient concentration. The relationships between the concentration of nutrient and the densities of algae and protozoa are not linear. The systems tended to remain stable under changes in flow rate only as long as the organisms had unutilized capacity to grow. As they approached their maximal growth rates, further increases in flow resulted in lower concentrations of organisms and higher concentrations of residual nutrient (F. B. Taub MS in preparation).

Although these data are only provisional model results based on constants derived from cultures of the single alga *Chlamydomonas reinhardti* and the single protozoan *Tetrahymena vorax*, the relationships are extremely similar to those postulated generally between an alga and an herbivore. Therefore it is felt that these results have a general significance and that the model can be used as a means of exploring the probable relationships between other kinds of organisms.

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FIGURE LEGENDS

Figures 1-5. The concentrations predicted by the model for the lowest nutrient concentration, 0.05 mM nitrate. The isopleths represent the concentrations at approximate steady states (24 days).

Figure 1. Algal densities in the absence of herbivores (shown as isopleths). The maximum density areas are shaded. A high density of lines indicates instability, i.e., a rapid change in cell density due to small environmental changes, whereas an absence of lines indicates stability, i.e., a plateau over which changes in cell density would be slight despite major changes in the environmental conditions.

Figure 2. The algal density in the presence of an herbivore.

Figure 3. Protozoan density in the community shown in Figure 2.

Figure 4. The residual nitrate concentration in the axenic algal community shown in Figure 1.

Figure 5. The residual nitrate concentration in the algal-herbivore community shown in Figures 2 and 3.

Figures 6-10. The concentrations predicted by the model for the moderate nutrient concentration, 0.5 mM nitrate.

Figure 6. Algal densities in the absence of herbivores.

Figure 7. Algal density in the presence of an herbivore.

Figure 8. Protozoan density in the community shown in Figure 7.

Figure 9. Residual nitrate in the axenic algal community shown in Figure 6.

Figure 10. Residual nitrate in the presence of the algal-herbivore community shown in Figures 7 and 8.

Figures 11-15. The concentrations predicted by the model for high nutrient concentrations, 5.0 mM.

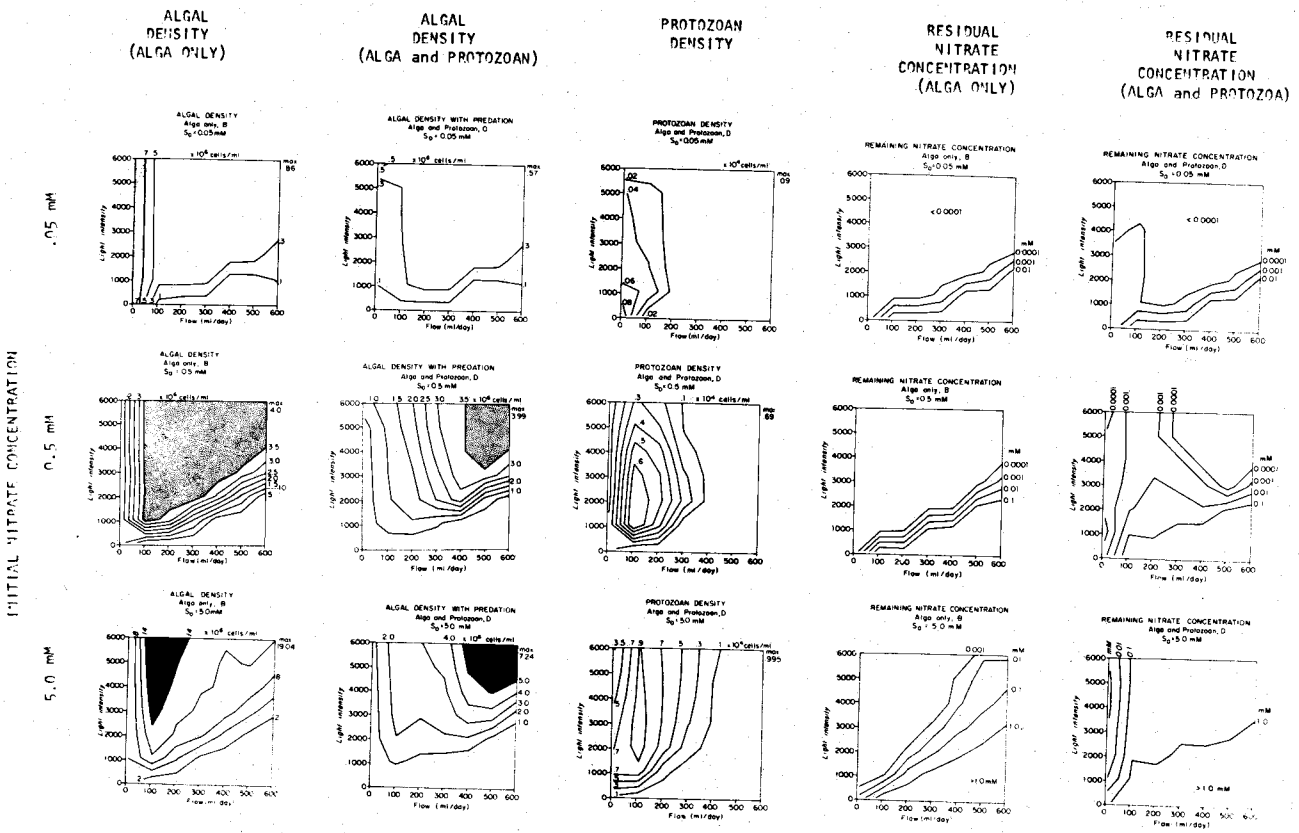
Figure 11. Algal densities in the absence of herbivores.

Figure 12. Algal density in the presence of an herbivore.

Figure 13. Protozoan density in the community shown in Figure 12.

Figure 14. Residual nitrate in the axenic algal community shown in Figure 11.

Figure 15. Residual nitrate in the presence of the algal herbivore community shown in Figures 12 and 13.



Figures 1-15. Left to right: top row, figures 1-5; middle row, figures 6-10; bottom row, figures 11-15.