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by

John Harry Vandermeer

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John Harry Vandermeer

Chairman: Nelson G. Hairston

A classification of communities is suggested based on average amount and kind of niche overlap as reflected in competitive interactions. The major dichotomy is based on the existence or non-existence of higher order interaction terms in the Gause multi-species competition equations. The major dichotomy is interactive and non-interactive communities. Non-interactive communities may be thought of as forming a continuum between completely open and completely additive based on the number of interactions per species.

Derivations are presented for two approximate measures of relative openness based on the covariance of the community matrix.

The expected number of species in a community is discussed with reference to the distribution of the saturation densities (K's) of the individual populations.

The probable effects of higher order interactions are discussed, and it is concluded that they are important but that it is difficult to predict their exact effects.

An empirical test of the existence of higher order interactions was carried out using four ciliate protozoans, Paramecium caudatum, P. bursaria, P. aurelia, and Blepharisma sp..

All four ciliates were cultured individually and their population histories were described quite well by the simple logistic equation.

Attempts to explain minor deviations of the data from the logistic by use of the one or two time lag logistic failed. It was concluded that a more complicated time lag phenomenon must be operative.

Every possible pair of the four ciliates was cultured and a trial and error procedure was used to estimate α and β of the Gause equations. In all cases the simple Gause equations seemed to adequately describe the data.

All four ciliates were cultured together and compared to predictions made by use of the competition coefficients estimated from pair-wise competition and population parameters estimated from single species population growth. The correspondence between prediction and data suggest that the higher order interactions have slight or no effect on the dynamics of this artificial community.

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INTRODUCTION

The central goal of community ecology is to understand the dynamics of community organization. Most likely that goal would be best approached from the point of view of mechanism, beginning with basic principles and deducing how communities should behave. However, such attempts have in the past been stifled by certain methodological difficulties, diverting the attention of community ecologists toward more empirical observations. These empirical observations have usually taken the form of measuring the relative abundance of species (number of species with a given number of individuals).

Most of the work concerned with the latter may be dichotomized as follows. One series of papers [Fisher, Corbet, and Williams (1943); Preston (1948, 1962a, b); Hairston and Beyers (1954); Hairston (1959)] emphasizes underlying mathematical distributions and causes of deviance from these distributions. Another series, stimulated by Margalef (1957), and rigorously formalized by Pielou (1966a, b), is concerned with measuring the relative abundance of species usually to compare communities to each other.

There have also been a few attempts at building either conceptual or mathematical models of communities using supposedly basic components. Kendall (1948) has shown how certain patterns of population growth will lead to Fisher's logarithmic series. MacArthur (1955) discussed several aspects of community stability as deduced from considerations of energy transfer among populations, and Watt (1964) later tested some of these ideas. MacArthur (1960) suggested mechanisms whereby

lognormal distributions should arise. Hairston, Smith, and Slobodkin (1960) presented a general explanation for the structure of terrestrial communities which stimulated a recent controversy (Murdoch, 1966; Ehrlich and Birch, 1967; Slobodkin, Smith, and Hairston, 1967). Garfinkel (1967) studied stability properties of theoretical systems using the Lotka-Volterra predator-prey equations.

These approaches to community ecology have established the basic attitude for the following theoretical formulations and empirical tests. Simple assumptions are made, namely that populations grow according to the logistic equation, and populations on the same trophic level obey the Gause equations of competition. I shall be concerned with communities which derive their structure through inter- and intra-species competition. Predators, parasites, and weather all play the same role in this model -- they are the environment which determines the parameters of the equations. The purpose of the theoretical formulation is not to describe in detail particular realities of nature, but rather to establish theoretical consequences which may be suggested as possible general trends.

By way of illustrating further the limits of applicability of the theory developed herein, I suggest an analogy with the law of gravitation. The fact that two objects do not usually fall at the same rate in any real situation -- e.g., their physical configurations may be such that wind friction may act differentially between them -- has not led physicists to discard Newton's theory of gravity. Rather, they argue that the theory assumes objects falling in a vacuum. Complete vacuums are not particularly commonplace in the real world. Still no one rejects Newton's theory of gravity. In the same sense,

observing that populations do not in general follow the logistic is not evidence for rejecting the logistic as a basic model. If the interest is in parachuting, frictional components might be more important than if the interest were in free fall. Similarly, if the interest is in optimization of yield from a small fishery, frictional components might be more important than if the interest were in competitive outcome. Just as one must add friction components to predict in any precise way the exact course of a falling object, one must add "friction components" -- e.g., time lags, age structure, immigration -- to the basic logistic equation if one is to predict the precise course of a growing population (Slobodkin, 1953).

It is in keeping at least with historical tradition to begin the development of a theory by considering the frictionless case, hoping that this development will suggest broad trends which can be observed in nature. To compare any part of the theory with nature -- as opposed to observing general trends -- would require the addition of those factors that are necessary to make the basic premises match up with the realities of nature.

THEORETICAL DEVELOPMENT

Basic models: In elucidating the following formal identities it is convenient to develop a graphical method of presentation. Such a method is immediately suggested by Hutchinson's formalization of the concept of the ecological niche (Hutchinson, 1957). In Hutchinson's model a niche is thought of as a hyperspace. This hyperspace is a subspace of a larger hyperspace, the coordinates of which are all the factors that affect the species in question. The niche hyperspace is delimited by the extremes on each coordinate that mark the upper and lower tolerance of the species as a function of that particular factor.

Consider the ecological niche of any species as a subspace of an arbitrary two dimensional niche space. The relative amount of overlap of two niches is proportional to the competitive pressure felt by both of these species. It will be convenient to draw niches as circles either overlapping (competition) or not overlapping (not competition).

The fundamental model for this paper is the basic Lotka-Volterra competition equations, given as

$$\left.\begin{aligned} dN_1/dt &= r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1}\right) \\ dN_2/dt &= r_2 N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2}\right) \end{aligned}\right\} \quad (1)$$

where r_1 and r_2 are the intrinsic rates of natural increase for species 1 and 2, K_1 and K_2 are the saturation population densities of species 1 and 2, N_1 and N_2 are the abundances of species 1 and 2, and α and β are competition coefficients. Setting derivatives equal to zero and

rearranging we have

$$N_1 = K_1 - \alpha N_2$$

$$N_2 = K_2 - \beta N_1$$

which are the equations of two straight lines in N_1, N_2 space (See figure 1.). There are four cases of competitive outcome predicted by these equations, depending on where the lines intersect (Gause and Witt, 1935; Slobodkin, 1962).

The lines representing the equilibria of equation 1 are K_1/α, K_1 and K_2/β, K_2. Let the acute angle formed by the line K_1/α, K_1 and the vertical be "a," and the acute angle formed by the line K_2/β, K_2 and the horizontal be "b." These relationships are pictured in figure 1.

Now we also have the identity

$$\alpha = \tan a$$

$$\beta = \tan b$$

It follows that when $a + b = 90^\circ$ (i.e., the lines are coincident),

$$\alpha\beta = 1$$

since

$$\alpha\beta = (\tan a)(\tan b) = [\tan a][\tan (90^\circ - a)] = 1$$

The determinant of the coefficient matrix (here called the community matrix) is

$$\begin{vmatrix} 1 & \alpha \\ \beta & 1 \end{vmatrix} = 1 - \alpha\beta$$

and is zero when the lines are coincident.

We may now forget about the axes and consider the lines defined by the angles a and b. The line that used to be K_1/α, K_1 will be called I and the line that used to be called K_2/β, K_2 will be called II.

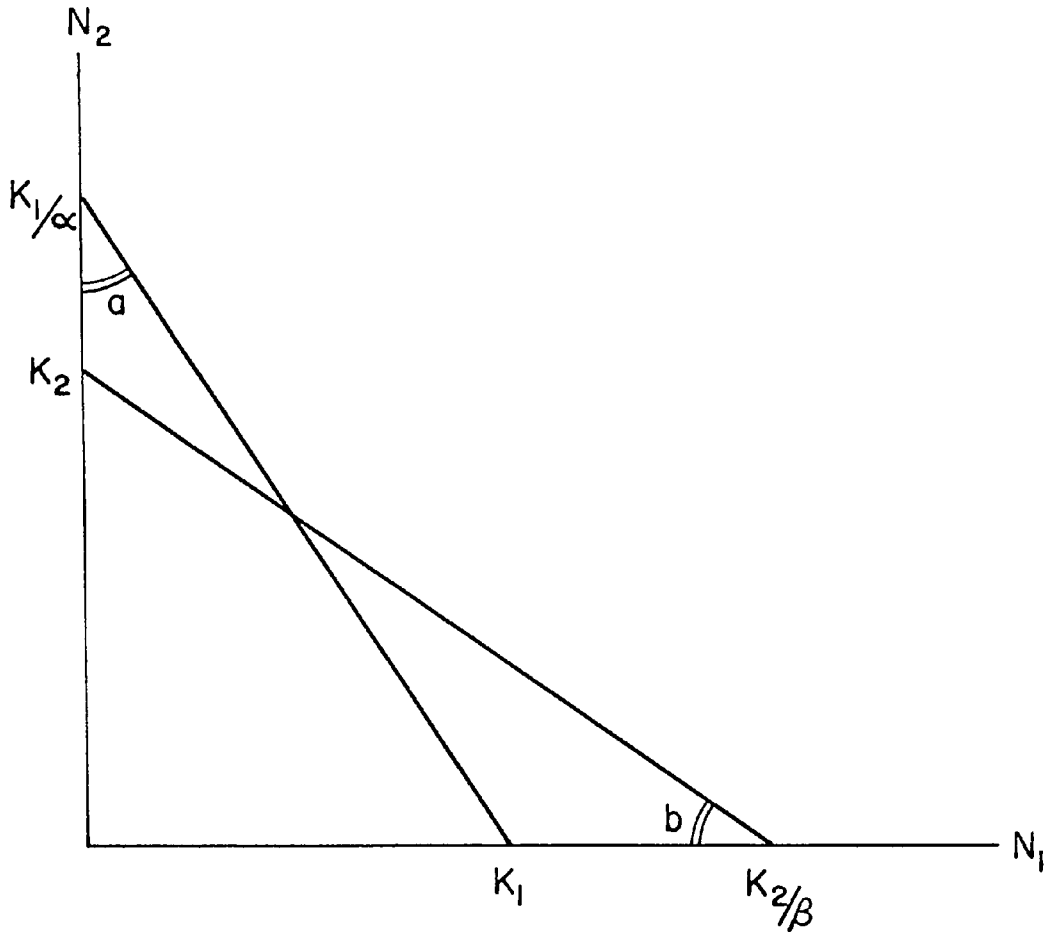


Figure 1. Locus of points in the phase plane (N_1, N_2) for which $dN_1/dt = dN_2/dt = 0$. (equations 1).

We still have a reference point for the solution to equations 1. If the lines are rotated such that $a + b < 90^\circ$ we have a stable solution; if they are rotated such that $a + b > 90^\circ$ we have an unstable solution. Figure 2 clarifies these relationships. Beginning with the case of concurrent solutions ($a + b = 90^\circ$) if the line I is rotated clockwise, a stable solution is created; if it is rotated counterclockwise an unstable solution is created.

The above analysis of the Lotka-Volterra equations tells us the criteria for the existence and stability of a mathematical solution. However, the biological outcome -- does one or the other species win or does there exist an equilibrium point for which both equilibrium population densities are positive -- requires consideration of the K values. To determine which species wins and/or where the equilibrium point is, we must add coordinates to the system. That is, it has been shown that the stability of the solution depends only on $a + b \lesseqgtr 90^\circ$ (or $\alpha\beta \lesseqgtr 1$), and not on the values of K. Values of K can be specified by positioning the N_1, N_2 coordinates as illustrated in figure 3. Thus, with fixed values of α and β a variety of results may be obtained by changing K_1 and/or K_2 (displacing the axes).

Classification of communities: Consider the possible qualitatively different ways in which a single species can be added to a community of two species. There are clearly three different ways in which this can happen (ignoring the trivial case of no competition). Figure 4 depicts these obvious relationships.

We now define three types of communities (an admittedly arbitrary classification), based on their competitive structure. An open

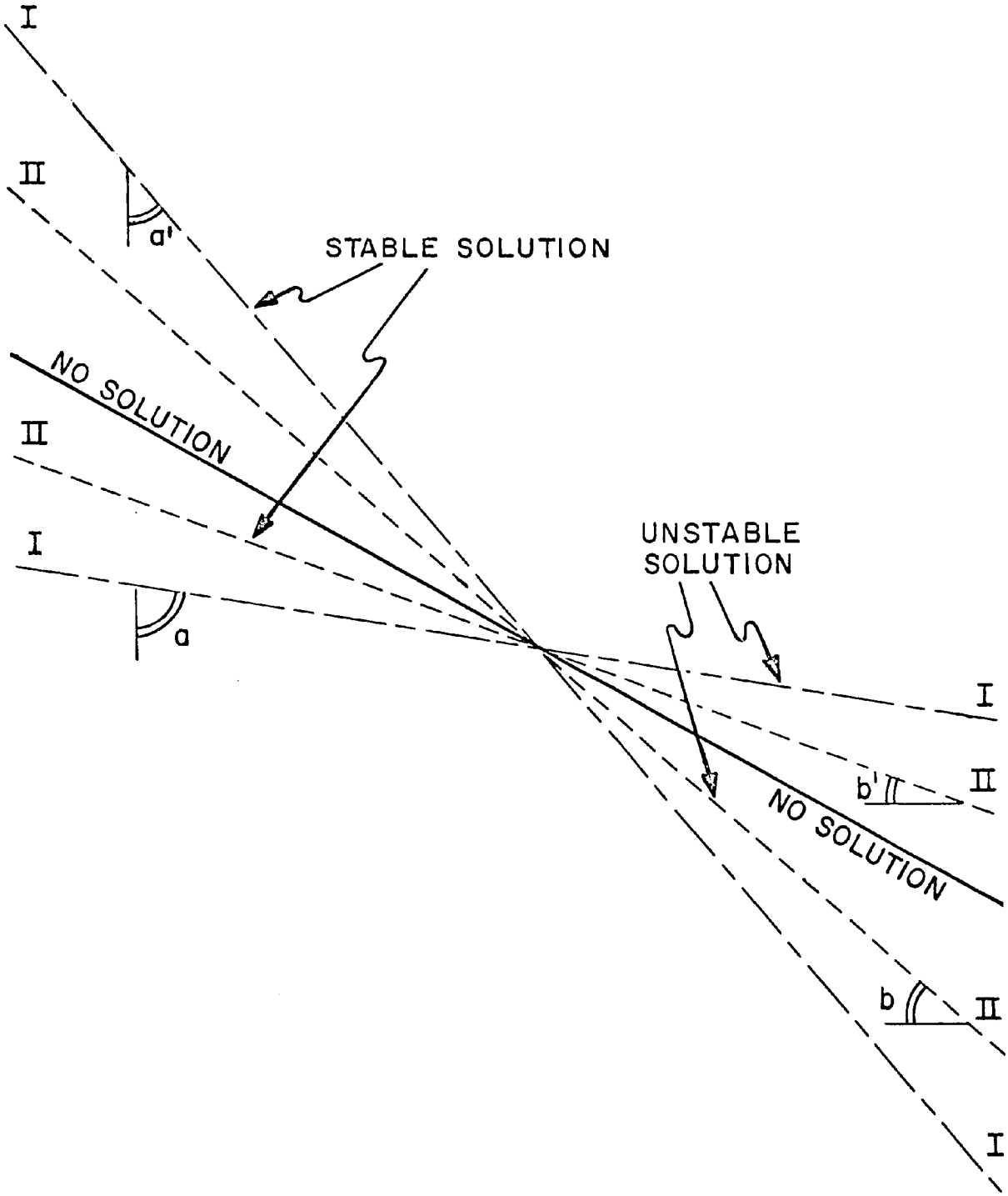


Figure 2. The two kinds of equilibria of equations 1.

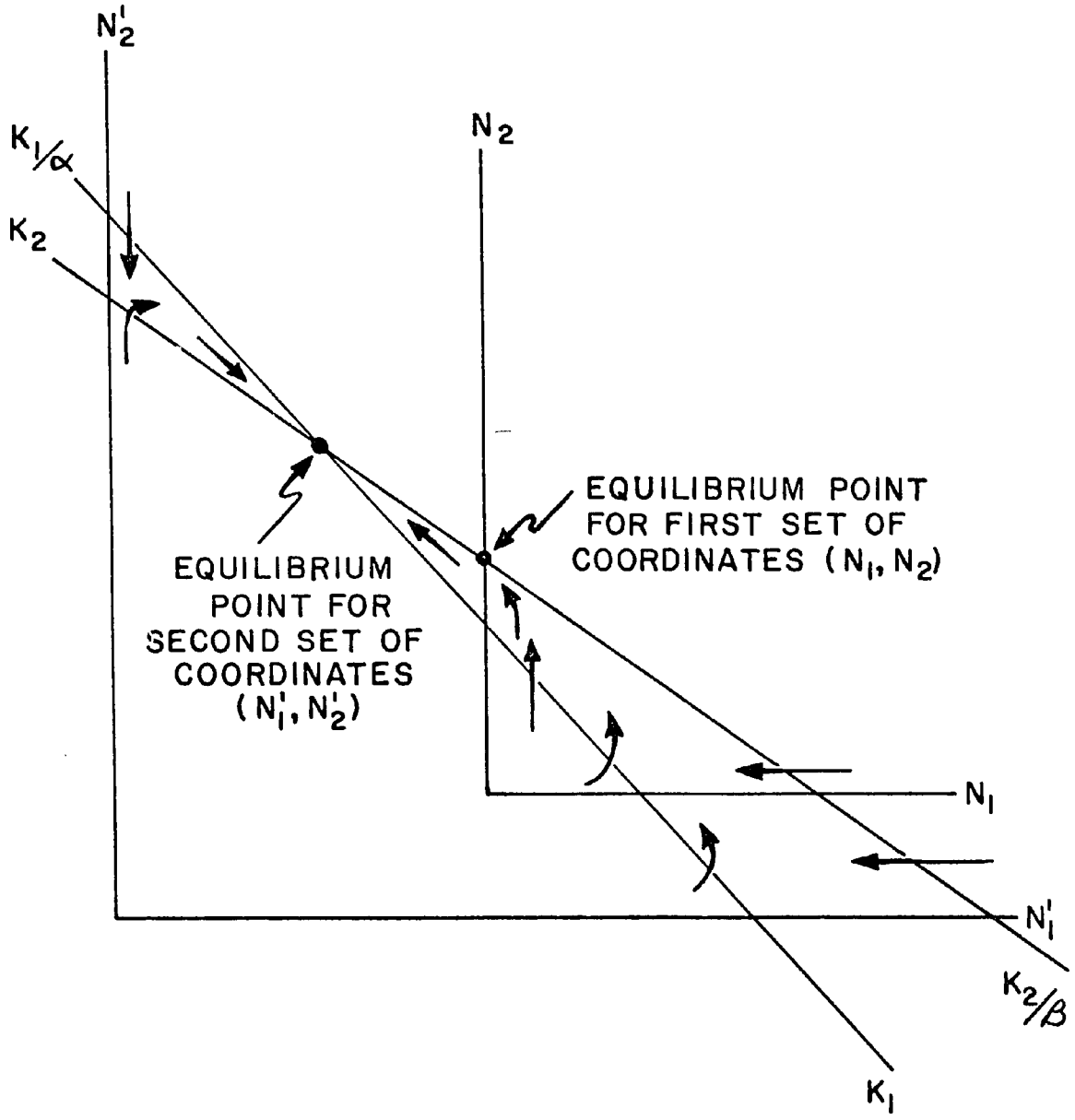


Figure 3. Changing the outcome of competition by displacing the axes. The first set of coordinates (N_1, N_2) results in N_2 winning in competition. The second set of coordinates (N_1', N_2') results in stable equilibrium, with both species persisting.

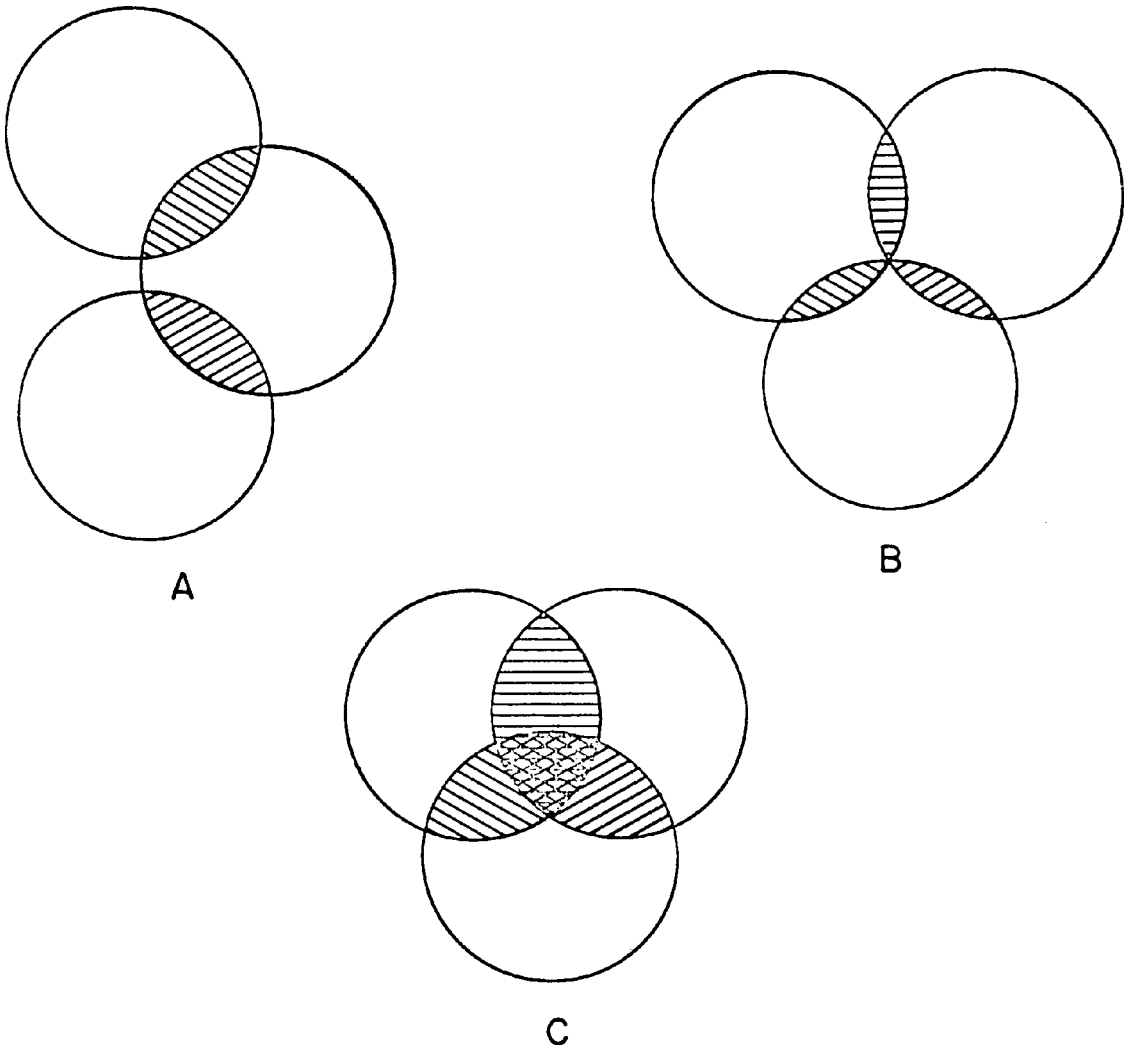


Figure 4. The three basic kinds of communities, a = open, b = additive, c = interactive.

community is one in which every species interacts with at most two other species in the community and two of the species interact with only one other (figure 4a). An additive community is one in which every species interacts with every other species in the community, with no higher order interactions (figure 4b). An interactive community is one in which every species interacts with every other species and also experiences all higher order interactions (figure 4c). Obviously all communities will not fall into one or another of these categories but usually will be intermediate. Some simple communities may be open and some highly organized communities may be interactive, but probably most communities will be partly open, partly additive and partly interactive.

The relationships among these three types are easily seen if an analogy is drawn between species colonizing a new area and circular discs dropping randomly upon a table. At first only a few of the discs overlap, but as more and more discs are added many of the discs are overlapped by more than one other disc. Further addition of discs results in further piling up, or an effect of higher order interaction coefficients. Thus, we can view these three community types as merely stages in an apparent succession, from open to additive to interactive.

Putting these graphical models into a more analytical form allows deduction of further consequences. I first consider the additive and open communities as special cases of each other (collectively termed non-interactive), and then discuss problems associated with the theoretical study of interactive communities.

We can write the solutions to equations 1 in matrix form as follows:

$$k = An \qquad (2)$$

where

$$k = \begin{bmatrix} K_1 \\ K_2 \end{bmatrix} \qquad A = \begin{bmatrix} 1 & \alpha \\ \beta & 1 \end{bmatrix} \qquad n = \begin{bmatrix} N_1 \\ N_2 \end{bmatrix}$$

The general non-interactive case of equations 1 may be expressed as in MacArthur and Levins (1967) for the ith species,

$$\frac{dN_i}{dt} = r_i N_i \left(\frac{K_i - N_i - \sum_{j=1}^{m} \alpha_{ij} N_j}{K_i} \right) \qquad j \neq i \qquad (3)$$

where there are m species in the community and α_{ij} is the effect of the jth species on the ith species. In matrix notation k is the column vector of the saturation densities, n is the column vector of the equilibrium densities and A is the community matrix (Levins, 1968), as follows:

$$\begin{bmatrix} 1 & \alpha_{12} & \alpha_{13} & \cdot & \cdot & \cdot & \alpha_{1m} \\ \alpha_{21} & 1 & \alpha_{23} & & & & \cdot \\ \alpha_{31} & \alpha_{32} & 1 & & & & \\ \cdot & & & & & & \cdot \\ \cdot & & & & & & \cdot \\ \cdot & & & & & & \\ \alpha_{m1} & & \cdot & & \cdot & & 1 \end{bmatrix}$$

A perfectly open community is a special case of the above. The column vectors k and n remain the same and the community matrix becomes

$$\begin{bmatrix} 1 & \alpha_{12} & 0 & 0 & 0 & \cdot & \cdot & \cdot & 0 \\ \alpha_{21} & 1 & \alpha_{23} & 0 & 0 & \cdot & \cdot & \cdot & 0 \\ 0 & \alpha_{32} & 1 & \alpha_{34} & 0 & \cdot & \cdot & \cdot & 0 \\ 0 & 0 & \alpha_{43} & 1 & \alpha_{45} & & & & \cdot \\ \cdot & & & & & & & & \cdot \\ \cdot & & & & & & & & \cdot \\ \cdot & & & & & & & & \\ 0 & & \cdot & & \cdot & & 1 & & \alpha_{m-1,m} \\ 0 & & \cdot & & \cdot & & \alpha_{m,m-1} & & 1 \end{bmatrix}$$

As the community becomes more additive, the zeroes in the above matrix disappear. However, as long as some zeroes remain -- some species are completely independent of some other species -- equations (3) may be arranged in such a way that the matrix more or less retains its "band" structure (This concept will be clarified in a later section.).

The above discussion treats the difference between additive and open communities as a discontinuous phenomenon, with each step from open to additive as a discrete step (i.e., adding one more non-zero diagonal). Another, perhaps more realistic way, of viewing the relationship between open and additive communities is to consider a continuum of the following sort. Suppose each diagonal of the community matrix has some mean value. Suppose further that the mean α decreases, the further the diagonal is positioned from the principal diagonal. The implied functional relationship between mean α and position away from principal diagonal is graphed in figure 5 for a perfectly open community, a perfectly additive community, and a community intermediate between the two.

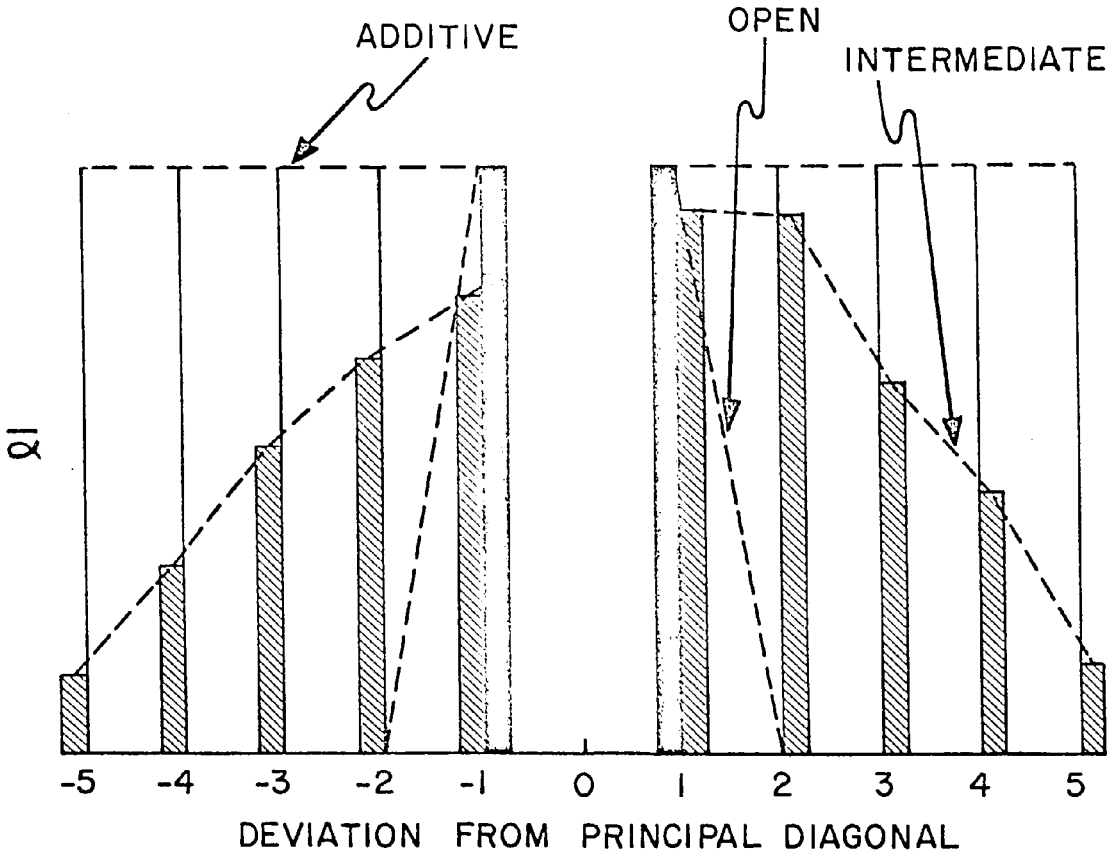


Figure 5. Functional relationship between mean α and deviation from principal diagonal for three cases; a = additive community, b = intermediate between additive and open, c = open community.

Many difficulties are encountered in attempting to force on the interactive case a notation analogous to the above. These difficulties are easily seen by writing out the general equations for a completely interactive system of m species. After setting derivatives equal to zero and cancelling constant multipliers, the equation for the ith species is,

$$K_i = N_i + \sum_j \alpha_{ij} N_j + \sum_{jk} \beta_{ijk} N_j N_k + \ldots + \sum_{jk\ldots m} \omega_{ijk\ldots m} N_j N_k \ldots N_m \quad (4)$$

where $j \neq i$, $k \neq i$, ... , $m \neq i$, and the Greek letters are interaction coefficients of increasingly high order. Obviously the terms $N_i + \sum \alpha_{ij} N_j$ represent the first element in the column vector k of equation 2. The higher order terms cannot be represented so simply, and if the entire system were forced into a form like equations 2, the community matrix would contain elements that are functions of the equilibrium densities. This fact leads to some rather frustrating complications, most of which remain unsolved.

A measure of relative openness: A completely open community has a community matrix with only three diagonals (the principal diagonal and each adjacent diagonal) non-zero. Clearly, how the species are ordered — an artificial consideration — will dictate whether or not the matrix has a band structure. For instance, if A and C interact, and B and C interact, but A and B do not interact, if the species are ordered N_1 = A, N_2 = B, N_3 = C, the resultant matrix will not have a band form. But, under the same circumstances, the ordering N_1 = A, N_2 = C, N_3 = B will yield a band-structured community matrix.

Thus, before a community matrix can be compared to figure 5 it must be transformed in such a way as suggested above so that it conforms to a band structure as closely as possible. To actually transform a matrix in such a way is similar to the construction of a phylogenetic tree from a difference matrix, except the present solution is much simpler. The criteria for the transformation are that the species must be connected to each other such that any one species interacts with at most two others (see figure 4a). This gives a string of species and the ordering of these in the community matrix gives the most "band-like" structure to the matrix, if the string was constructed to maximize the interactions included in it. After the matrix has been transformed, the mean α for each diagonal may be computed and plotted as in figure 5. Thus, the degree of band structuring in a community matrix will not be immediately apparent until the species are arranged in the proper order.

However, we need not in any real case reorder the species to determine the relative openness or additivness of the community. The same thing may be accomplished with the aid of the covariance of symmetrical terms. The covariance is defined as

$$\text{Cov}\ (\alpha_{ij}, \alpha_{ji}) = E\left[(\alpha_{ij} - \bar{\alpha})\ (\alpha_{ji} - \bar{\alpha})\right] .$$

This quantity can be related to the graphical approach of figure 5, and more specifically to the schedule put forth above of communities becoming more additive as more species are included.

There are at least two ways to look at the relationship between the additivity of a community and the covariance of the community matrix. Both ways rely on the idea of a maximum covariance, realized when the community is at a perfectly open state, and the requirement

that the alphas within a diagonal and between symmetrical diagonals are independent. The latter requirement is needed in the development that follows, but may be relaxed in real situations with a minimal loss in accuracy.

Given the above two assumptions, I proceed by holding the total variance of the community matrix -- excluding of course the principal diagonal -- constant. In the completely additive case α_{ij} is independent of α_{ji} for all ij and thus by definition the covariance is zero. The maximum covariance occurs when the community is perfectly open. Symbolizing the non-zero elements as α_i in a community of m species, we have,

$$Cov_{max} = \frac{\sum_i (\alpha_i - \bar{\alpha})^2 + (m-1)(m-2)\bar{\alpha}^2}{m^2 - m - 1}$$

which is equal to the total variance of the community matrix. Under the above stated restrictions, as a community goes from completely open to completely additive, the covariance changes from being equal to the variance to being equal to zero. If we divide the covariance of any community matrix by the maximum covariance, we have a measure of the relative position of the community between complete openness and complete additivity. In the present case, dividing the covariance by the maximum covariance is identical to dividing it by the variance, making the relative measure equal to the correlation coefficient relating symmetrical terms in the matrix.

An alternate approach to the measurement of relative openness is obtained by changing the assumption relating to the total variance of the matrix. Instead of holding the variance over the entire matrix constant, we assume that the variance of non-zero terms is constant.

That is, if the organisms interact at all, they are just as variable in their interactions if they are interacting with two other species as they are when they are interacting with m other species. It follows that the variance over the entire matrix decreases as the community goes from open to additive. The appropriate equation for the maximum covariance is

$$Cov_{max} = [2(m - 1) \text{ var } \alpha + (m - 1)(m - 2)\bar{\alpha}^2] / (m^2 - m - 1)$$

where m is the number of species in the community, and var α is the variance of alpha as computed from the community matrix in question. As in the above case, the real covariance may be divided by cov_{max} for a relative measure of the degree of openness.

The many assumptions made in deriving the two measures of relative openness render these measures as approximations or definitions. In either case the measure of relative openness has a firm biological basis and is not meant to be a statistical convenience. Past attempts at measuring community structure [e.g., Fisher et al. (1943)., Margalef (1957)] usually have been frank in admitting some arbitrariness either in curve fitting or pure mensuration. The concept of openness and the related measures as discussed above, hopefully will provide new insights into natural communities. In addition to asking for measures of the relative abundance of species, we might ask for measures of relative openness. The former are usually arbitrary statistics that reflect a particular emergent consequence of the community's structure. The latter purport to be uncontrived descriptions of a certain aspect of the internal organization of the community.

One obvious drawback to the above argument is the difficulty in measuring interaction coefficients. Hopefully, only rough approximations will be needed. Indeed, it would be useful to know just how rough the approximation to alpha may be before the biology -- in this case relative openness -- becomes obscured.

The number of species in a community: The foregoing theoretical development leads to several interesting consequences. One of these is that from a knowledge of the community matrix one could specify in some sense how many species should be in the community. Levins (1968) suggests holding the mean value of α and the covariance of symmetrical terms constant, and adding species to the community until the determinant becomes negative. If a solution exists it will be stable if the determinant is positive, and unstable if the determinant is negative. As Levins pointed out, the above procedure gives an upper limit to the number of species in an equilibrium community. The K values, and more important, the distribution of the K values -- envisioned earlier as a displacement of the N_1, N_2 axes -- are important in determining which species have an expected equilibrium population density greater than zero. It is quite possible that the displacement of the coordinates necessary to insure a "real" solution (all equilibrium densities positive) may in some cases be biologically unrealistic. The conditions of the K vector which dictate the number of species allowable in the community must now be considered.

Returning to equation 2 we can write

$$A^{-1}k = n$$

The inverse of A can be written as

$$(\det A)^{-1}\ \mathrm{adj}A = A^{-1}$$

where detA is the determinant of the matrix A and adjA is the adjoint of matrix A. The adjoint of a matrix is the mxn matrix C, where $c_{ij} = \Gamma_{ji}$ and Γ_{ji} is the cofactor of a_{ji} in detA, or by definition

$$\Gamma_{rs} = (-1)^{r+s} \det A_{rs}$$

where A_{rs} is the submatrix of A formed by deleting the rth row and sth column. So we have,

$$(\det A)^{-1} \begin{bmatrix} \Gamma_{11} & \Gamma_{21} & \cdots & \Gamma_{m1} \\ \Gamma_{12} & \Gamma_{22} & \cdots & \Gamma_{m2} \\ \cdot & & & \cdot \\ \cdot & & & \cdot \\ \cdot & & & \cdot \\ \Gamma_{1m} & \cdot & \cdot & \Gamma_{mm} \end{bmatrix} \begin{bmatrix} K_1 \\ K_2 \\ \cdot \\ \cdot \\ \cdot \\ K_m \end{bmatrix} = \begin{bmatrix} N_1 \\ N_2 \\ \cdot \\ \cdot \\ \cdot \\ N_m \end{bmatrix}$$

After completing the multiplication in the left hand side of the above we can write the equation for one species (the ith) as

$$N_i = [\det A]^{-1} [K_1 \Gamma_{ij} + K_2 \Gamma_{2i} + \ldots + K_m \Gamma_{mi}]$$

This is the ith element of the n vector. Substituting the definition of cofactor we have,

$$N_i = [\det A]^{-1} [K_1(-1)^{1+i} \det A_{ij} + K_2(-1)^{2+i} \det A_{2i} + \ldots + K_m(-1)^{m+i} \det A_{mi}]$$

Replacing N_i with zero, replacing the equal sign with <, and cancelling detA, it can be seen that the equilibrium number of individuals for the ith species will be greater than zero whenever

$$-K_i \det A_{ij} < \sum_{j=1}^{i-1} K_j(-1)^{j+i} \det A_{ji} + \sum_{j=i+1}^{m} K_j(-1)^{j+i} \det A_{ji} \quad (5)$$

The above relation may be used to test methodically each expected equilibrium for various distributions of K. However, further insight into the general relationship between the distribution of K and α

in determining the number of species at equilibrium may be gained by replacing each individual α in the matrix by the expected value $\bar{\alpha}$. The importance of the covariance has already been established, and it is now desirable to determine, at least qualitatively, what the importance of the K vector might be. We thus set the covariance to zero by substituting the expected value of α into all of the cells of the matrix. If the α's are replaced by $\bar{\alpha}$, we have the following,

$$\det A_{ji} = - \det A_{j,\, i+1} \qquad i \neq j$$

That is, the cofactors are equal whenever $i \neq j$. For example, if $n = 3$

$$A_{12} = \begin{bmatrix} \bar{\alpha} & \bar{\alpha} \\ \bar{\alpha} & 1 \end{bmatrix} \quad \det A_{12} = \bar{\alpha} - \bar{\alpha}^2$$

$$A_{13} = \begin{bmatrix} \bar{\alpha} & 1 \\ \bar{\alpha} & \bar{\alpha} \end{bmatrix} \quad \det A_{13} = \bar{\alpha}^2 - \bar{\alpha}$$

We now define the following relation,

$$(-1)^{i+j} \det A_{ij} = \begin{cases} -P_m & \text{for } i = j \\ Q_m & \text{for } i \neq j \end{cases}$$

where m = number of species in the system. Substituting into (5) we obtain,

$$K_i P_m < \sum_{j=1}^{i-1} K_i Q_m + \sum_{j=i+1}^{m} K_i Q_m$$

or

$$\frac{P_m}{Q_m} + 1 < \frac{\sum_j K_j}{K_i} \qquad (6)$$

Looking again at the function Q_m we see that for m = 3, 4, 5 we have

$$Q_3 = \bar{\alpha}\,(\bar{\alpha} - 1)$$

$$Q_4 = -\bar{\alpha}\,(\bar{\alpha} - 1)(\bar{\alpha} - 1)$$

$$Q_5 = \bar{\alpha}\,(\bar{\alpha} - 1)(\bar{\alpha} - 1)(\bar{\alpha} - 1)$$

and in general

$$Q_m = (-1)^{m-1} \bar{\alpha} (\bar{\alpha} - 1)^{m-2}$$

Similarly we can generalize the function P_m. The first term of P_m must be P_{m-1} since there is a one in the upper left hand corner of the matrix. The next terms are the (m-2) remaining submatrices -- identified above as Q_m -- multiplied by the rest of the terms of the second row of the original matrix, all of which are $\bar{\alpha}$. In symbols,

$$P_m = P_{m-1} - (m-2) \bar{\alpha} Q_{m-1}$$

Writing out the entire set of P's, we have

$$P_{m-1} = P_{m-2} - (m-3) \bar{\alpha} Q_{m-2}$$
$$P_{m-2} = P_{m-3} - (m-4) \bar{\alpha} Q_{m-3}$$
$$\vdots$$
$$P_{m-m+3} = P_{m-m+2} - (m-m+1) \bar{\alpha} Q_{m-m+2}$$
$$P_{m-m+2} = P_{m-m+1}$$
$$P_{m-m+1} = -1$$

which combine to give,

$$P_m = \left[\sum_{i=1}^{m-2} (m - i - 1) \bar{\alpha} Q_{m-i} \right] - 1$$

Substituting for Q_{m-i}

$$P_m = \left[\bar{\alpha}^2 \sum_{i=1}^{m-2} (m - i - 1)(1 - \bar{\alpha})^{m-i-2} \right] - 1$$

Substituting P_m and Q_m into (6)

$$1 + \frac{1}{\bar{\alpha}(1-\bar{\alpha})} - \bar{\alpha} \sum_{i=1}^{m-2} \frac{(m-i-1)}{(1-\bar{\alpha})^i} < \frac{\sum_{j=1}^{m} K_j}{K_i} \qquad (7)$$

Letting the left hand side of 7 be symbolized by $F(\bar{\alpha}, m)$, it can be shown that $F(\bar{\alpha}, m) + 1 = F(\bar{\alpha}, m+1)$. Thus, we can graph $F(\bar{\alpha}, m)$ against $\bar{\alpha}$ as is done in figure 6. The interesting part of figure 6 is that for the values of $\bar{\alpha}$ for which we are interested ($\bar{\alpha} < 1$), $F(\bar{\alpha}, m)$ is always greater than m.

Relation (7) may be used to test each species (if its K value is known) to see if it will have a positive or negative equilibrium density. We know from $\bar{\alpha}$ and cov α what the maximum number of species in the community can be, and we call that number m. Knowing $\bar{\alpha}$ and m, we can compute the left hand side of (7) and compare that value with the m different values of $\sum_j K_j/K_i$. If, for the ith species, relation (7) is satisfied, the equilibrium density of the ith species (N_i in equation 3) will be positive. Otherwise the density will be negative, i.e., the species will become extinct. We now wish to examine the behavior of the right hand side of equation (7), under various conditions of the distribution of the K's.

Suppose there exist two communities. Let the variance in K of the first community be zero, (i.e., each $K_i = K$) and the variance of the second community large, e.g., such that the frequency of species having a particular value of K is $1/(K_{max} - K_{min})$ (a uniform distribution). In the first case, zero variance, it is easily seen that [using relation (7)] as long as $F(\bar{\alpha}, m) < m$, all the species will be represented in the community, since $\sum K_j/K_i = m$ when the variance is zero. As soon as $F(\bar{\alpha}, m) > m$, none of the species will be represented. This case of zero variance represents one extreme. The uniform distribution represents the other extreme -- given the existence of fixed K_{max} and K_{min} -- and allows fewer species than

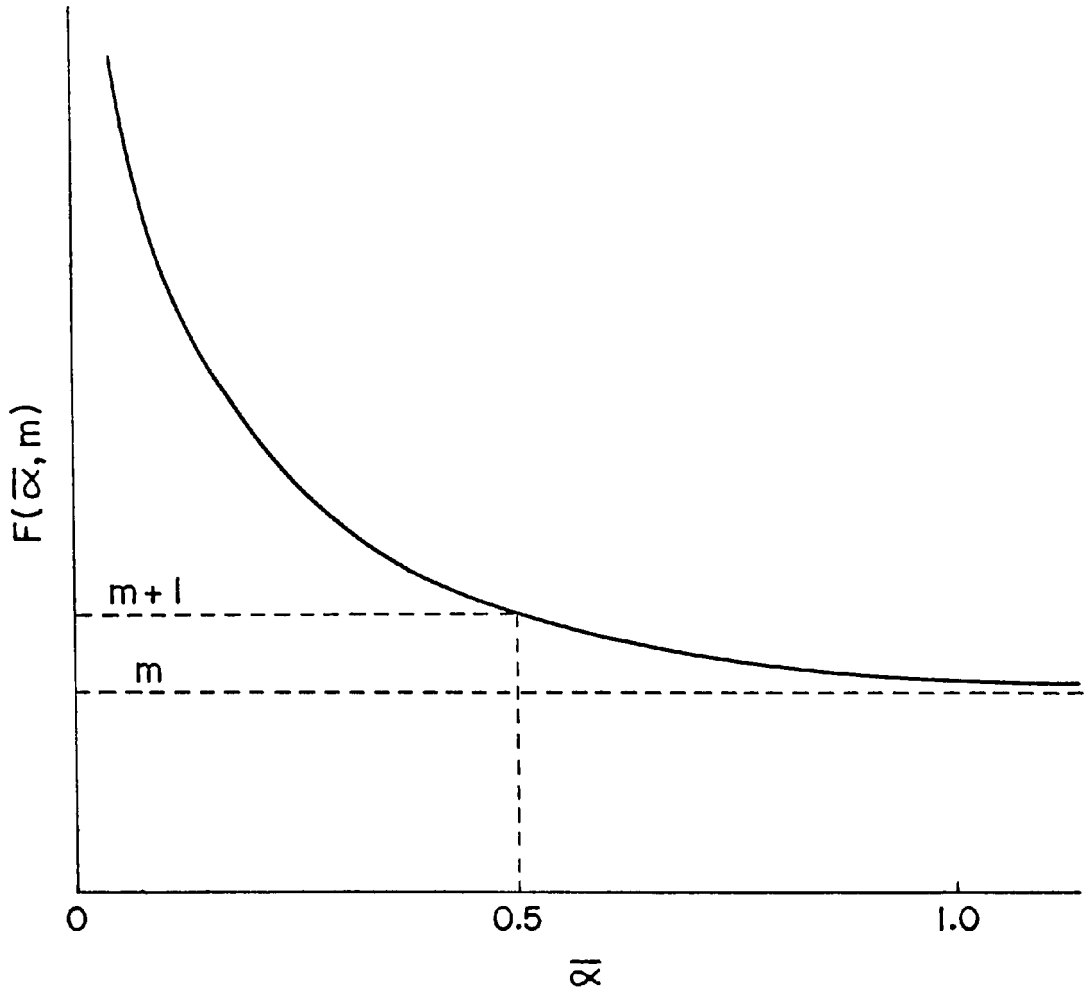


Figure 6. Relationship between $F(\bar{\alpha}, m)$ and $\bar{\alpha}$. See text for explanation.

the zero variance if $F(\bar{\alpha}, m) < m$ but more species of $F(\bar{\alpha}, m) > m$. The relation between the expected per cent of species (per cent of maximum number in equilibrium community of a fixed $\bar{\alpha}$ and cov α), $F(\bar{\alpha}, m)$, and variance in K is shown in figure 7.

Thus, for the cases in which we are interested $F(\bar{\alpha}, m) > m$ and therefore the per cent representation in an equilibrium community should increase as the variance in K increases. This result is based on the assumption that the distribution of K is symmetrical on an arithmetic basis. If K were positively skewed on an arithmetic base, the effect discussed above would be more striking (See figure 7.).

Qualitatively, if two communities have the same $\bar{\alpha}$ and cov α and the distribution of K is of the same form for both, the community with the highest variance in K should have the greater number of species.

Partial analysis of interactive communities: A critical assumption made above is that communities are non-interactive. This assumption is made clear by returning to the graphical models presented earlier in this paper. Consider the competitive effect on one particular species. Holding the average α constant is analogous to holding the amount of overlap contributed by each additional species constant. The mean α is held constant in such a way that each new species overlaps with 25 per cent of the particular species in question. If one species is added, the original species only occupies 75 per cent of its former niche without competitive pressure. If another species is added the species in question only has 50 per cent of its niche free of competition. In general as competitors accumulate in the system, if the average competition coefficient remains constant, the weight of competition eventually gets so strong that other species

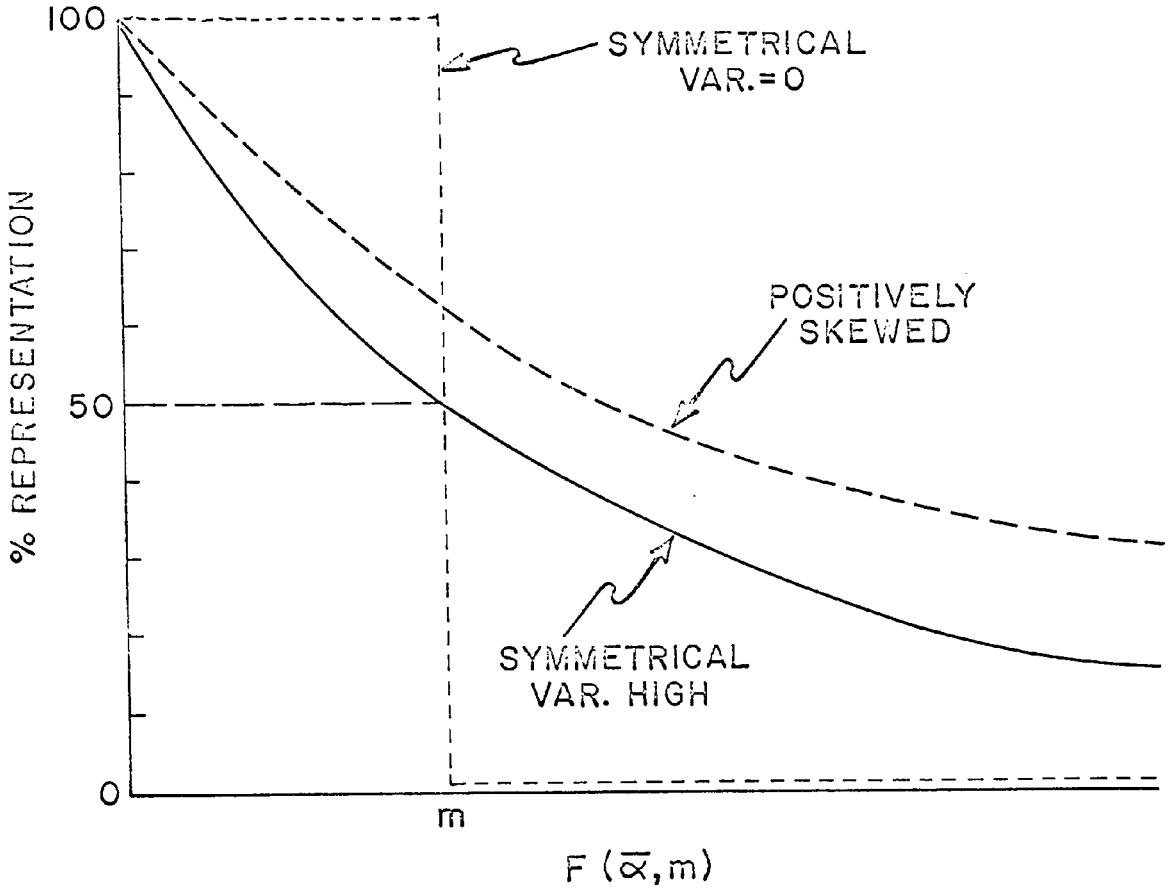


Figure 7. Relationship between % representation and $F(\bar{\alpha},m)$. The relationship is shown for three cases: (1) symmetrical distribution of K and zero variance in K (dotted line), (2) symmetrical distribution of K and high variance (solid line), and (3) positively skewed distribution of K (dotted line).

cannot make their way into the community. By a rough analogy to genetic load, this effect might be termed competitive load. The solution to the problem of genetic load (Li, 1967) suggests that the assumption of non-additivity in communities may be quite important and may make it impossible to compute the expected number of species from the competitive load. The essential point is that if an animal is excluded from part of its niche, it doesn't make much difference which of the other organisms in the community have done the excluding. For instance suppose fish species A occupies the entire length of a stream. Suppose further than experiments are undertaken in which species B and C are added one at a time, to estimate α's. If B and C each have X effect on species A, we would expect that the combination of B and C together would have effect 2X. But suppose that the result of B and C competing with A is that in either case A is eliminated only from the upstream section of the stream. It does not matter to species A which of B or C is eliminating; the fact is, it is being eliminated. Thus, the predicted effect of B and C together on A would be 2X but the observed effect would be X.

The type of higher order interaction discussed above implies $\beta, \gamma, \ldots \omega$ of equation 4 are positive. If the higher order terms were negative, it would imply a coalition formed by two or more species against some other species. If $\beta, \gamma, \ldots \omega$ are positive they will be referred to as non-coalition type higher order interactions; if negative, coalition type higher order interactions. The higher order interaction reported by Hairston, et al. (in press) is an example of a coalition type interaction.

Thus, it is not possible at the present time to predict the general effect of higher order interactions except qualitatively.

However, it is clear that their effects may be highly significant. It, therefore, would be quite important to discover whether or not they commonly occur in nature.

EMPIRICAL TEST

Statement of problem: The motivation for undertaking the experiments reported below, derives from the foregoing discussion of interactive communities. Since several interesting consequences are deducible from the premises of non-interactive communities, it would be desirable to know either the importance of higher order interactions in real situations, or the theoretical effect which higher order interactions would have on the consequences derived from the non-interactive assumptions. As remarked earlier, it is virtually certain that higher order interactions will have an effect on the outcomes of the model, but the nature and extent of this effect are difficult to assess owing to the intractable nature of the model when applied to interactive communities. Thus, the simplest approach is to verify the existence or non-existence of higher order interactions in nature, and this is the approach of this paper.

Induction in biology -- the implied approach suggested in the above discussion -- has often been eased by first studying extremes. In the present case, if the existence of higher order interactions can be demonstrated for a group of species which would be expected on an a priori basis not to exhibit them, it may be safely assumed that such interactions are more or less of universal occurrence. If, on the other hand, that group of species does not exhibit higher order interactions, the broad implications for which the experiment was designed are lost.

Obtaining an extreme example and satisfying the basic postulates of the model have been the two guidelines in choosing experimental

subjects and situations. Different species of free living ciliates, from different localities seem to satisfy both of these guidelines. Ciliates are simple organisms from the population point of view, and in several cases are known to conform to simple population mathematics, making it likely that most of the basic premises of the model are satisfied. Obtaining different species from different localities in a sense minimizes the likelihood that higher order interactions will be part of the system, since the system has not really existed in nature before. This does not rule out higher order interactions resulting by the chance mixture of two species having very similar physiologies.

Therefore, four species of ciliates from four different localities were studied in a laboratory situation. Parameters of population growth were estimated for each species separately. Values of α and β (see equations 1) were estimated for each possible combination of two species. Then all four species were cultured together and compared to the prediction made on the basis of the simple growth parameters and competition coefficients measured earlier.

Methods and materials: Three of the four ciliates, Paramecium bursaria (PB), Paramecium aurelia (PA), and Paramecium caudatum (PC) were obtained from three different localities in the vicinity of Ann Arbor, Michigan. The fourth species, Blepharisma sp. (BL), was obtained from a biological supply house. The Varieties are unknown except for PA which is Variety 3.

Culture techniques are those of Sonneborne (1950), with various modification after Hairston and Kellerman (1965). Cultures were

maintained at 15° C. and all experiments were done at 25° C. All cultures and experiments were kept in darkness -- i.e., PB was without effective symbiotic algae.

Experiments were done in 10 ml. test tubes, filled with 5 ml. of culture. Each day a sample of 0.05 ml. was rapidly removed with a coarse pipette after vigorously shaking the test tube. The tubes were shaken after semi-sterilizing a section of rubber glove in hot distilled water and using this as a covering for the test tube. Verification of the test tube sampling procedure was accomplished by repeated sampling and subsequent replacement of samples in several groups of test tubes. The sampling procedure was extensively experimented with to obtain a reasonably close correspondence between the mean and variance of a set of repeated samples, i.e., to assure a random sampling technique.

Bacterized culture medium was added to each culture to exactly replace the 0.05 ml. which had been removed as a sample. The culture medium had been aged for various lengths of time and was used in an orderly sequence based on this age. This was originally done to introduce a forced environmental oscillation on the experiments. Since absolutely no relationship between food age (food quality) and population growth or competition was observed anywhere in the study, the food source is considered as a constant in this paper.

Population growth: The mathematical model used for the simple population growth experiments was the familiar logistic equation,

$$\frac{dN}{dt} = rN\left(\frac{K - N}{K}\right)$$

where N is number of individuals, K is saturation population density, and r is the intrinsic rate of natural increase. The parameters K, r, and N_o were estimated exactly as in Gause (1934) excepting the case of PC in which several points were discarded as wild points for purposes of estimating the parameters — not in plotting the figures. In all cases the intercept of the equation

$$\log_e \left(\frac{K - N}{N}\right) = a + rt$$

was used to estimate N_o, which was needed to generate the expected curve. Expected curves were obtained from the recurrence relation given by Leslie (1957),

$$N_{t+1} = \frac{\lambda N_t}{(1-bN_t)}$$

where $\lambda = e^r$ and $b = \frac{(\lambda - 1)}{K}$.

Statistical testing of the fit of the data to the model is at best difficult (Smith, 1952). Leslie's (1957) procedure depends on the assumption of independence of observations from one time to the next. It was obvious by inspection that there was a rather high correlation between times within replicates — i.e., that replicate which had the highest value at time t was most likely to be the replicate with the highest value at time t + 1. Because of this statistical difficulty, and the difficulties raised by Smith (1952), the statistical testing of Leslie (1957) was not used.

Figure 8 presents the expected and observed values for population growth of BL. The fit is generally good, except for a systematic deviation of observed from expected. This deviation is biased above the curve at early times, and below the curve at later times. The

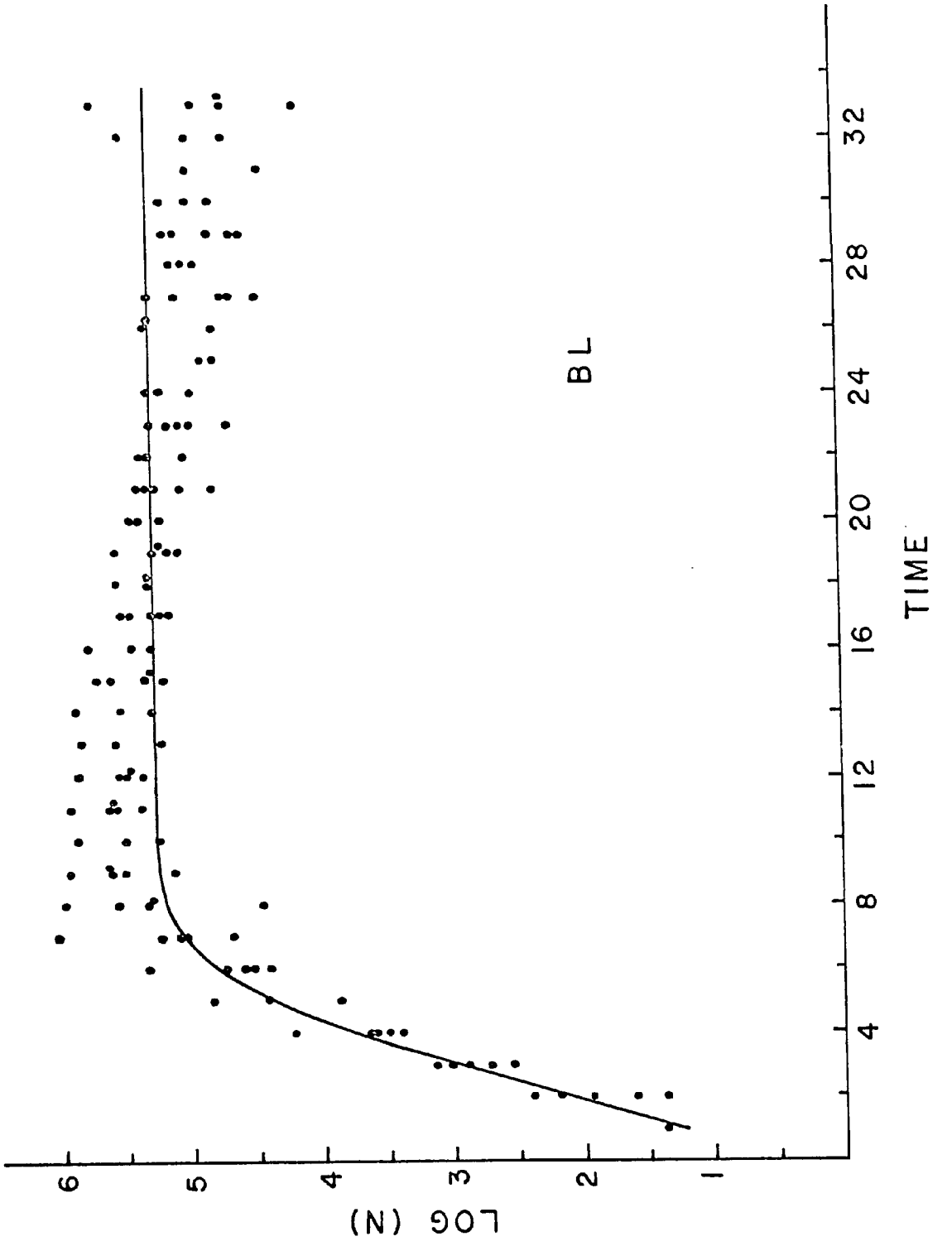


Figure 8. Population growth of Bl.

pattern is reminiscent of that obtained when time lags are added to the logistic equation (Cunningham, 1954). This point will be discussed later.

In figure 9 are shown expected and observed for PB. This species is the most highly variable of the four species in its population growth. The relatively large variance in observed values is somewhat clarified by noting that two of the replicates are suggestive of a very large time lag and three are suggestive of a smaller, if at all existent, time lag. The curve predicted by the logistic (figure 9) seems to be an adequate representation of the basic trend of population growth in this species.

The expected and observed values for PC and PA are shown in figure 10 and 11. The fits are obviously excellent and need no further discussion here.

The parameters for population growth for all four species are summarized in table 1.

Time Lags: It was mentioned earlier that one of the single species population growth experiments was suggestive of a time lag phenomenon. That situation was examined in somewhat more detail in hopes of clarifying the exact effects particular friction components might have on the basic model.

Cunningham (1954) and Wangersky and Cunningham (1956) analyzed the differential difference equation,

$$\frac{dN(t)}{dt} = rN_{(t-\gamma_1)}\left(\frac{K - N_{(t-\gamma_2)}}{K}\right). \qquad (8)$$

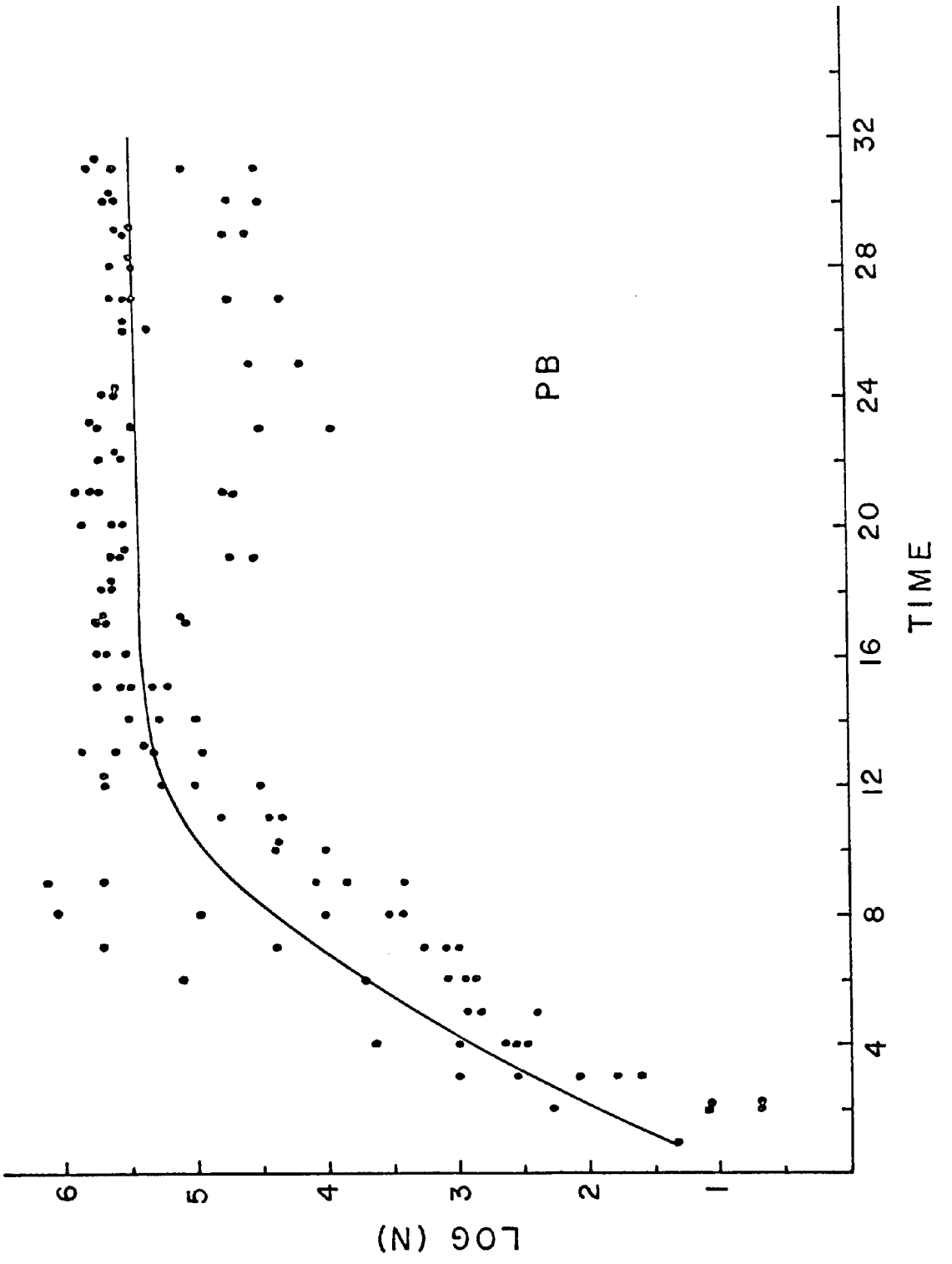


Figure 9. Population growth of PB.

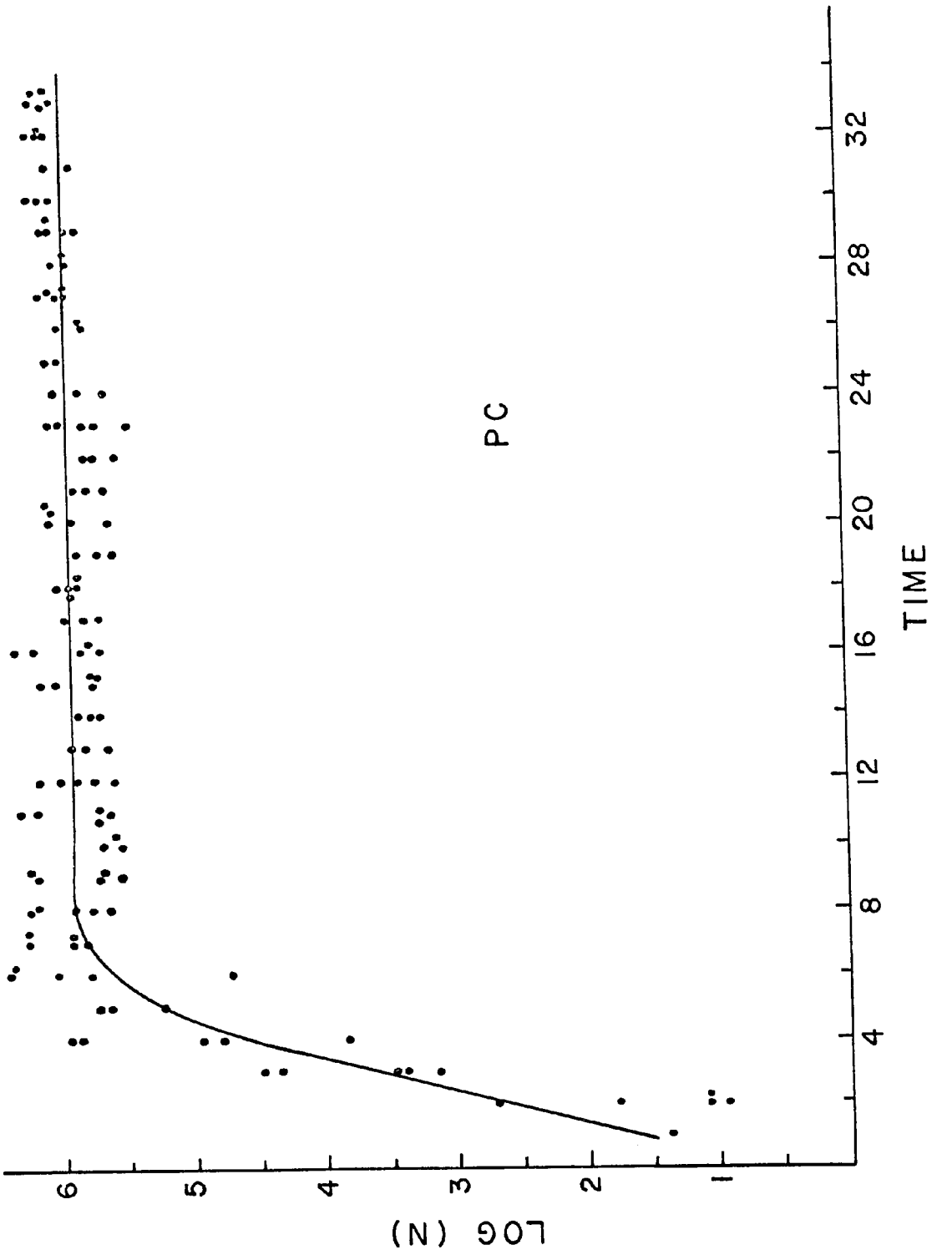


Figure 10. Population growth of PC.

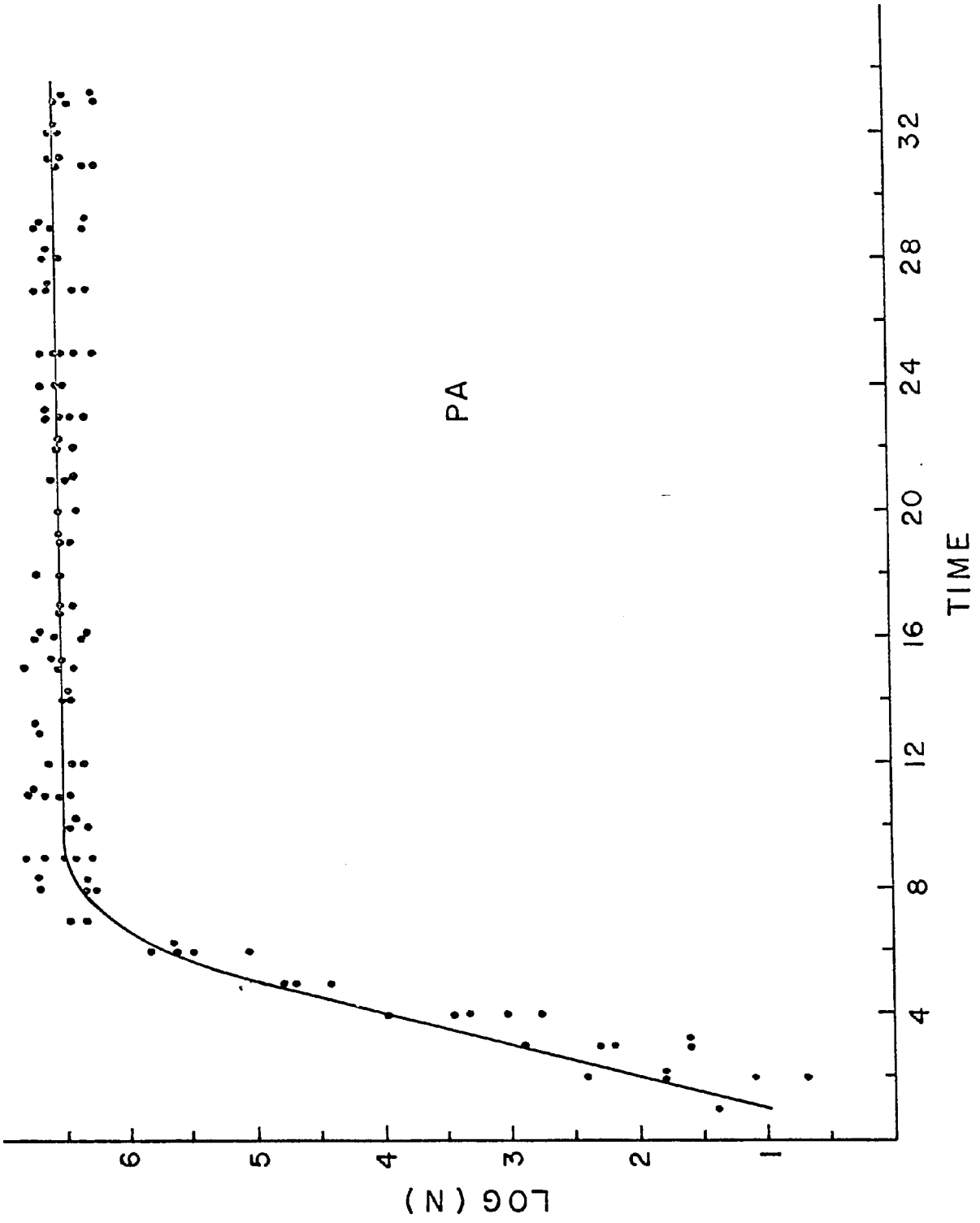


Figure 11. Population growth of PA.

TABLE 1. Parameters of the Logistic Equation

SPECIES	r	K	N_o
PA	1.05	671	2.5
PC	1.07	366	5.0
PB	0.47	230	5.0
Bl	0.91	194	3.0

This is evidently the logistic equation with a time lag of duration τ_1, associated with reproduction, and a lag of τ_2 associated with the response to density pressure. Cunningham and Wangersky's major conclusions are (1) under certain situations, oscillations are generated and when they are, the period of the oscillation is approximately equal to $\sqrt{2}\pi\tau_2$ and (2) the effective rate of growth at very low population densities is equal to $1/(1 + r\tau_1)$. These two conclusions make it possible to estimate, in a very approximate way, τ_1 and τ_2, and the ordinary methods (Gause, 1934) may be somewhat modified to estimate r and K.

Values of the parameters r, K, τ_1, τ_2 were estimated as above and a solution to equation 8 was simulated using simple numerical integration $\Delta t = 1/16$. Then the parameters were systematically varied in an attempt to find a curve that fits the data. It became apparent that equation 8 will not produce an integral curve that even remotely resembles the data in figure 8.

The reasons for the above are apparent. The period of oscillation in the data is in the neighborhood of 30 - 40, indicating a τ_2 of about 8.0. To realize the observed rate of growth in the early times of the experiments the value of r must be around 1, and the value of K between 100 and 200. The other parameter τ_1 does not seem to matter a great deal and may be varied rather freely without changing the outcome. The combination of $\tau_2 = 8$ and $r = 1$ yields oscillations with a period of about 35, but an amplitude approximately 40 to 50 times greater than is suggested by the data. To reduce the amplitude of the oscillation, maintaining the same period, requires that r be much smaller (say about 0.1 or 0.2). However, if r is

made that small the initial rate of growth is exceedingly slow, i.e., the population reaches a peak at about t = 35. Thus, it would seem impossible to reasonably fit the data of figure 8 with equation 8. What would be required is a discontinuity of the sort that when $t < 10$ the population obeys the exponential equation and when $t > 10$ the population obeys equation 8. Such restrictions seem unduly arbitrary and are not pursued further. Indeed, if the apparent oscillatory behavior of BL is due to some sort of time delay, it must be a somewhat more complicated delay than that suggested by equation 8. To introduce a more complicated delay would require either a great deal of additional information about the population dynamics of BL, or some rather stringent and arbitrary assumptions about the population dynamics of BL.

Two-way competition: The mathematical methods used here are even more inexact than those used in single species population growth. A smooth curve was drawn by eye through the observed data points, and estimates of α and β were obtained for each time from two to 32, with the equations given by Gause (1934),

$$\alpha = \frac{1}{N_2}\left[K_1 - \frac{(dN_1/dt)\,K_1}{r_1 N_1} - N_1\right]$$

$$\beta = \frac{1}{N_1}\left[K_2 - \frac{(dN_2/dt)\,K_2}{r_2 N_2} - N_2\right]$$

The K's and r's were obtained from the single species experiments. The N's were taken off of the smooth curve, and the derivatives were computed as,

$$\frac{dN(t)}{dt} = \frac{N(t+1) - N(t-1)}{2}$$

The resultant values of α and β -- 31 values of each for each of the six competition experiments -- were highly variable within experiments. The values were exceptionally extreme at very early times and very late times. Intermediate values were somewhat less variable, but the variation seemed to always form some sort of trend. However α and β are defined as constants so the objective is to obtain those values of α and β which produce the curve which best fits the observed data.

To obtain a reasonable first approximation to α and β I took the average of the intermediate values as described above -- i.e., the average of those values that tended to form a reasonably invariant clump. With these values, integral curves were computed using the predictor corrector method of Hamming (Ralston and Wilf, 1960; see also System/360 Scientific Subroutine Package, 1968). Usually, these first approximations gave curves that rather poorly represented the observed data. A trial and error procedure was then pursued in which α and β were systematically varied and the behavior of the integral curves investigated under this variation. It eventually became apparent that the curves obtained were about the best obtainable under the present model. In all cases the boundary conditions were considered as random variables, and were thus relatively free to vary in the trial and error procedure.

The comments about statistical testing made in the previous section apply equally well here. However, a relative measure of the goodness of fit is needed for a later section, and is introduced here to facilitate easy comparison of the goodness of fit of one experiment

to that of another. The arbitrary criterion used is mean square deviation of logs of observed from log of expected.

The results of the six pairwise competition experiments are presented in figures 12 through 23, in order of decreasing mean square deviation. The aforementioned variability of PB is reflected in figures 13, 15, but appears to be somewhat dampened by the presence of BL (figure 21). Figures 14 and 16 both show some indication of a time lag, but since the population growth data for these two species (PA and PC) alone were not suggestive of any frictional components, one must presume that the presence of a competitor is the factor which initiates the observed systematic deviation. However, the magnitude of the deviation in this case appears to be negligible.

Thus, the six cases of pairwise competition are represented quite well by the basic theory, minor deviations being interpretable as a result of unknown but insignificant frictional components or excessive inherent variability. Since at least the general trend of the data is in agreement with that of the model, these small deviations most likely will not interfere with the basic hypothesis to be tested.

In table 2 is presented the community matrix for this artificial community.

Four-way competition: Having estimates of the intrinsic rate of natural increase and saturation density for each species, and estimates of all interaction coefficients on a pair-wise basis, it is now necessary to substitute into equations (2) -- four-way competition without higher order interactions -- solve the equations,

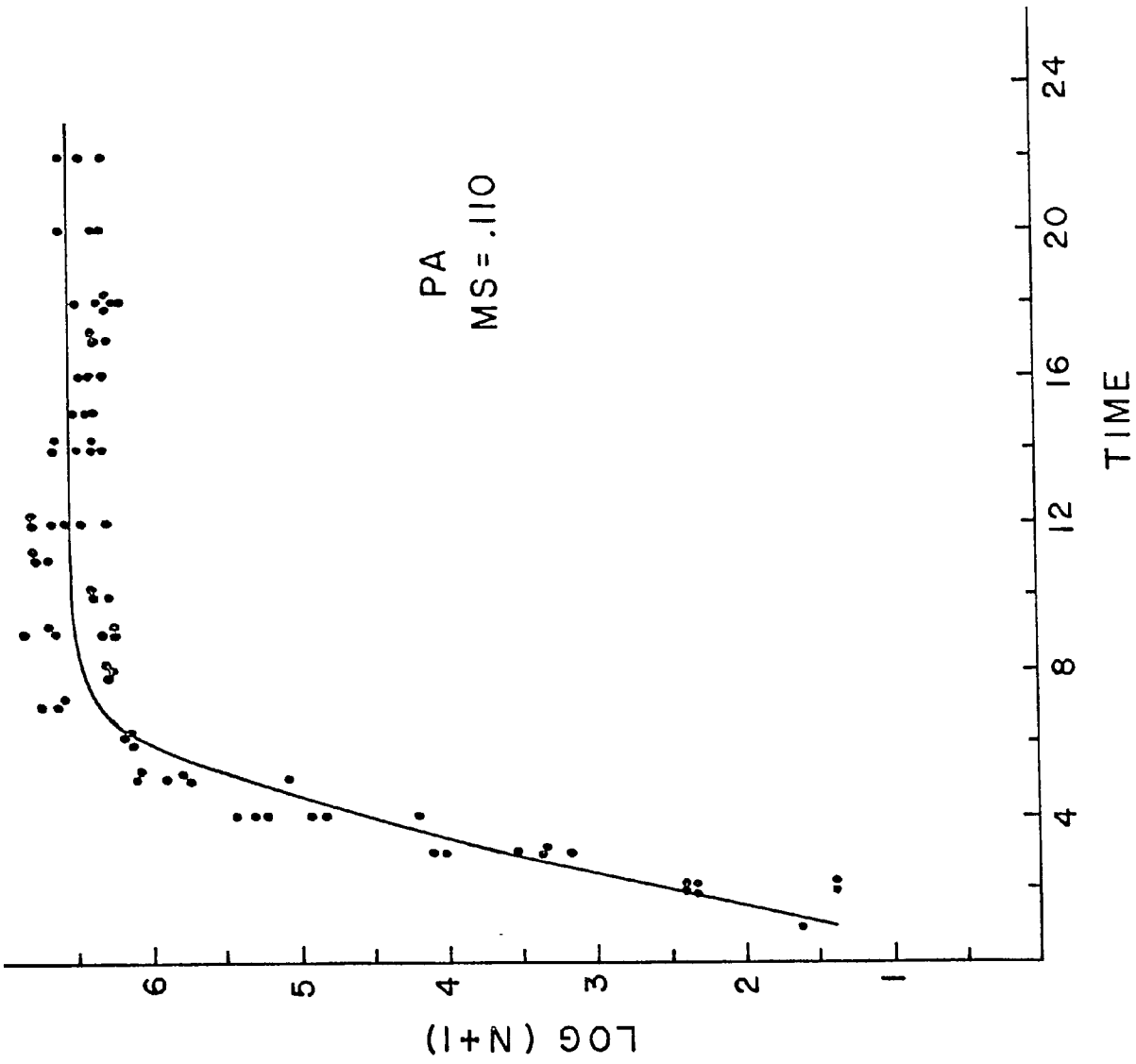


Figure 12. PA in competition with PB.

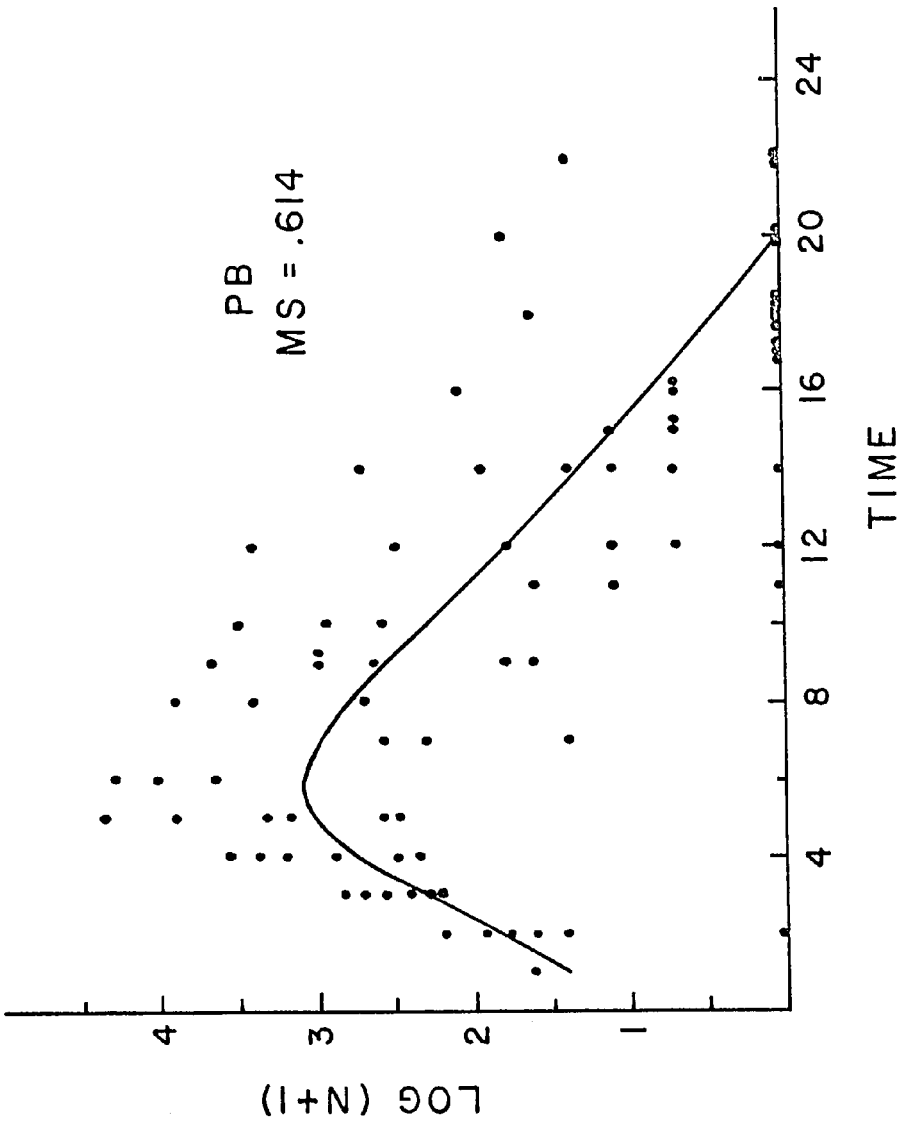


Figure 13. PB in competition with PA.

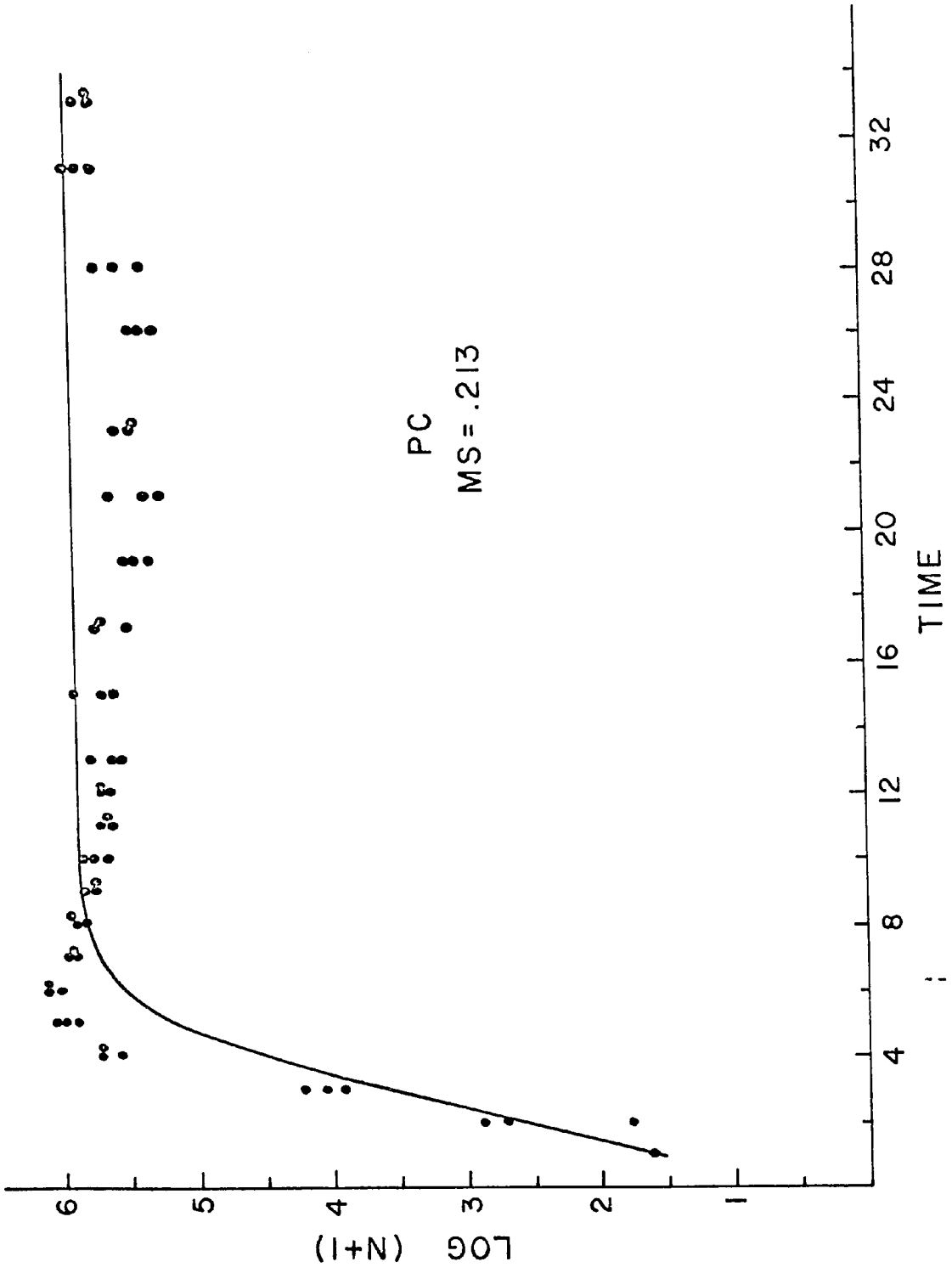


Figure 14. PC in competition with PB.

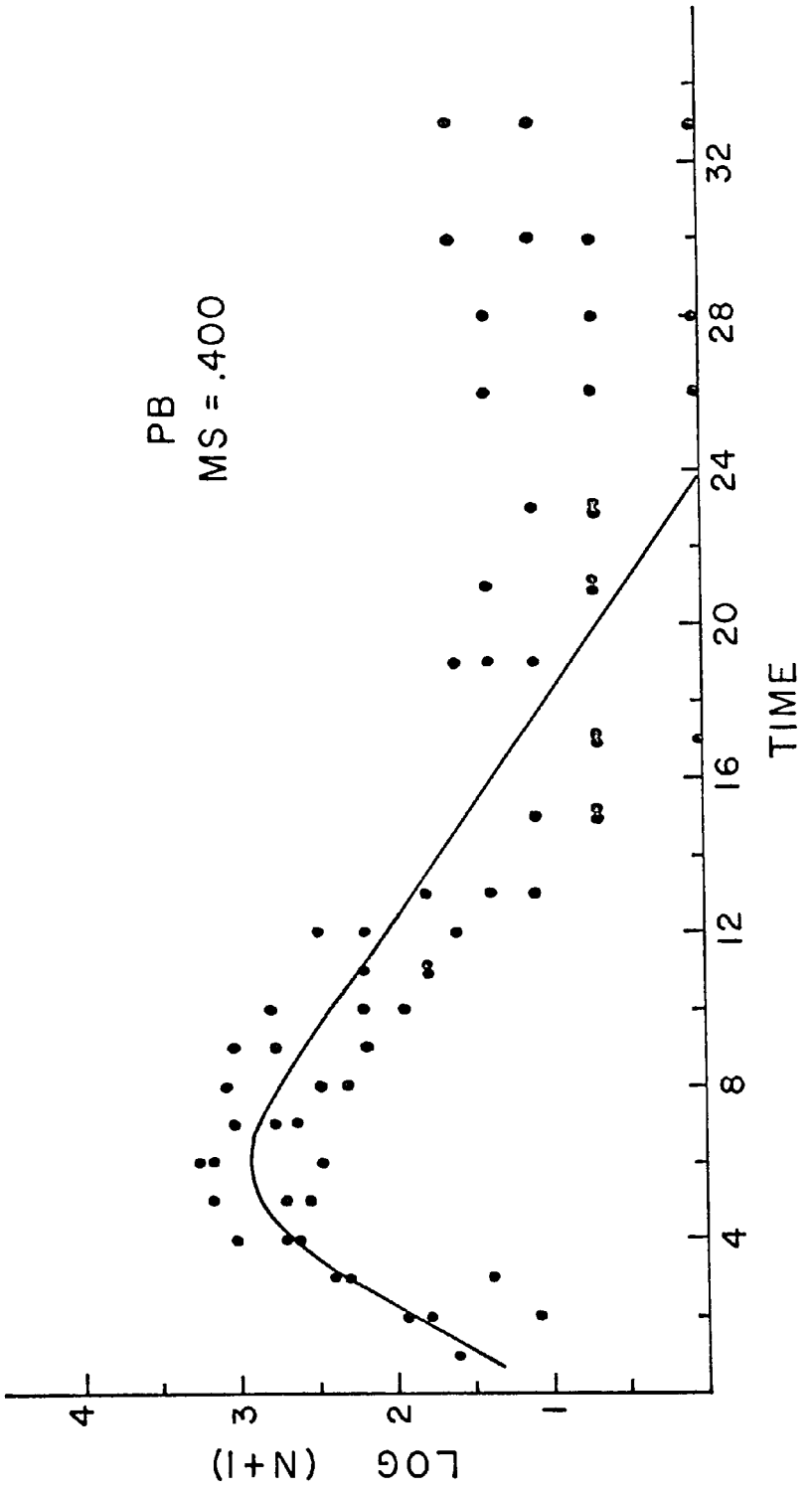


Figure 15. PB in competition with PC.

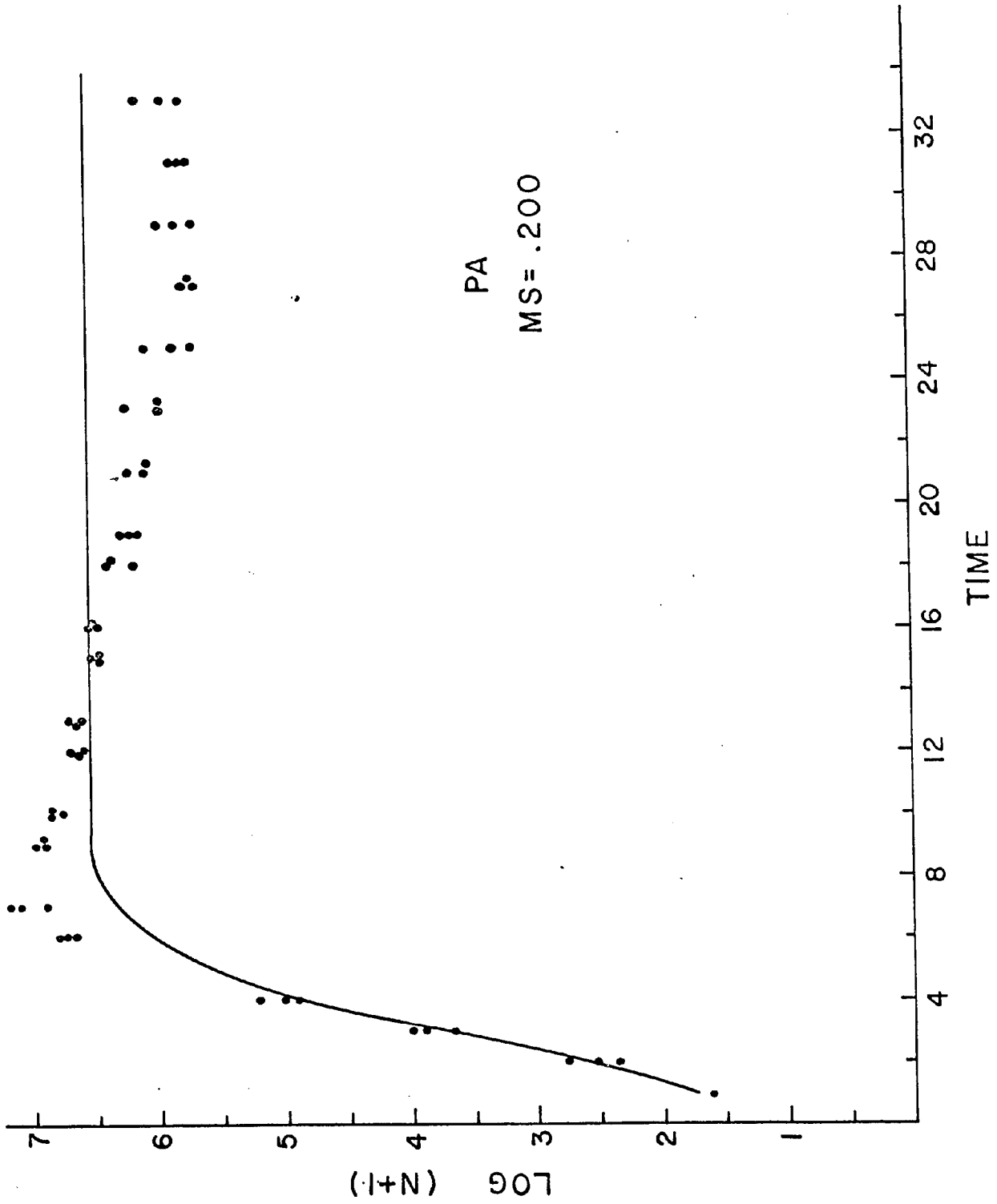


Figure 16. PA in competition with BL.

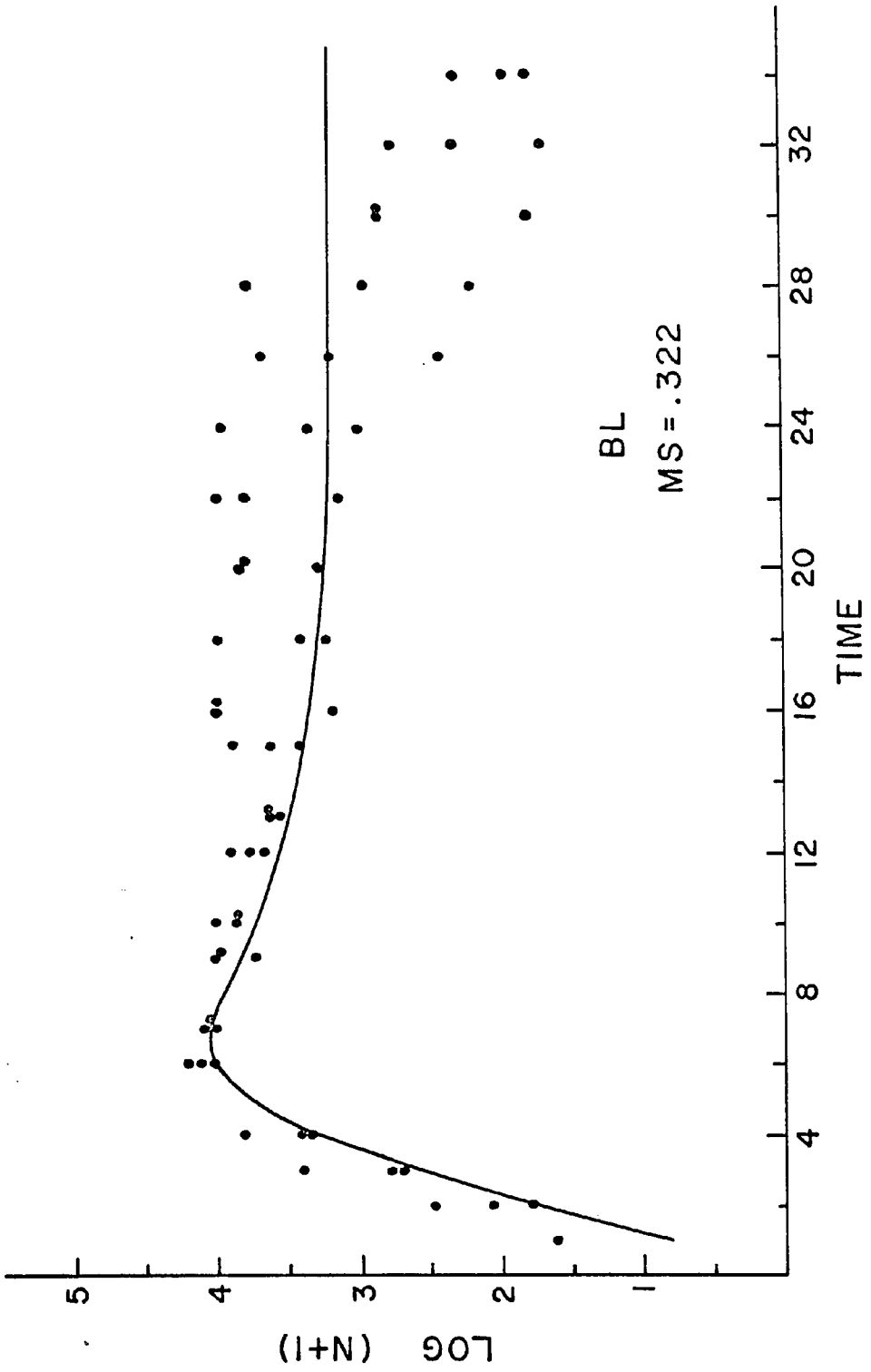


Figure 17. BL in competition with PA.

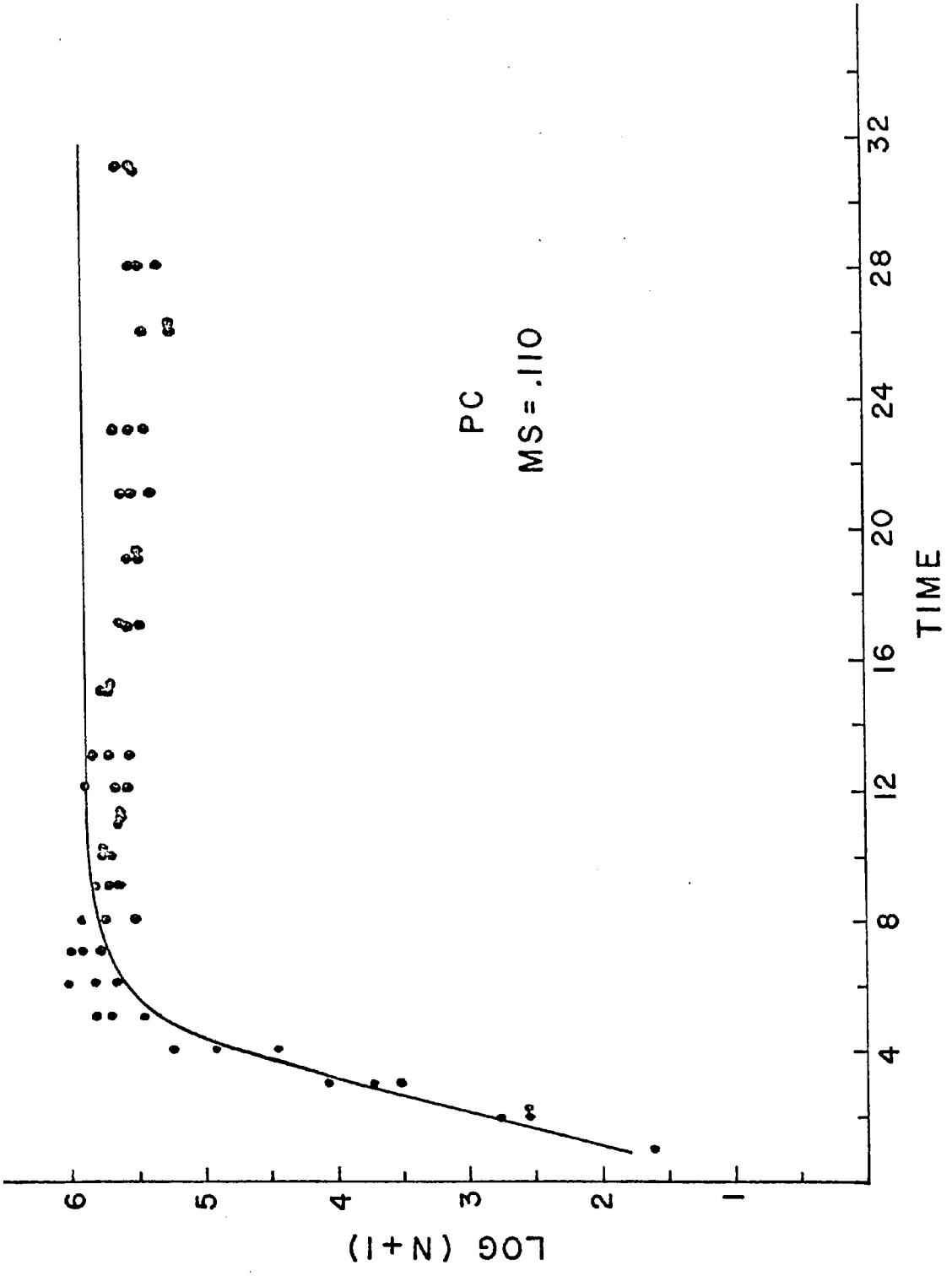


Figure 18. PC in competition with Bl.

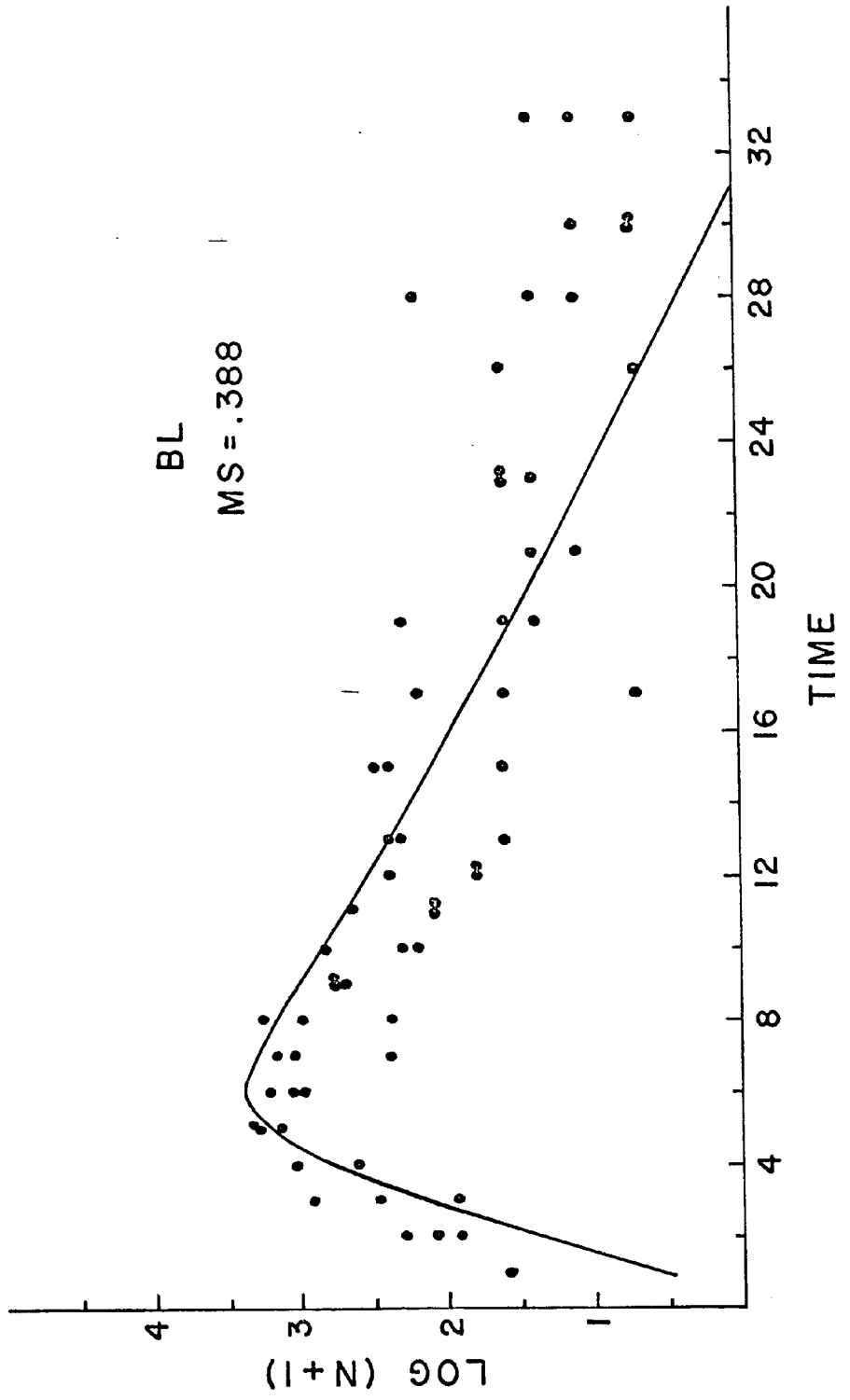


Figure 19. Bl in competition with PC

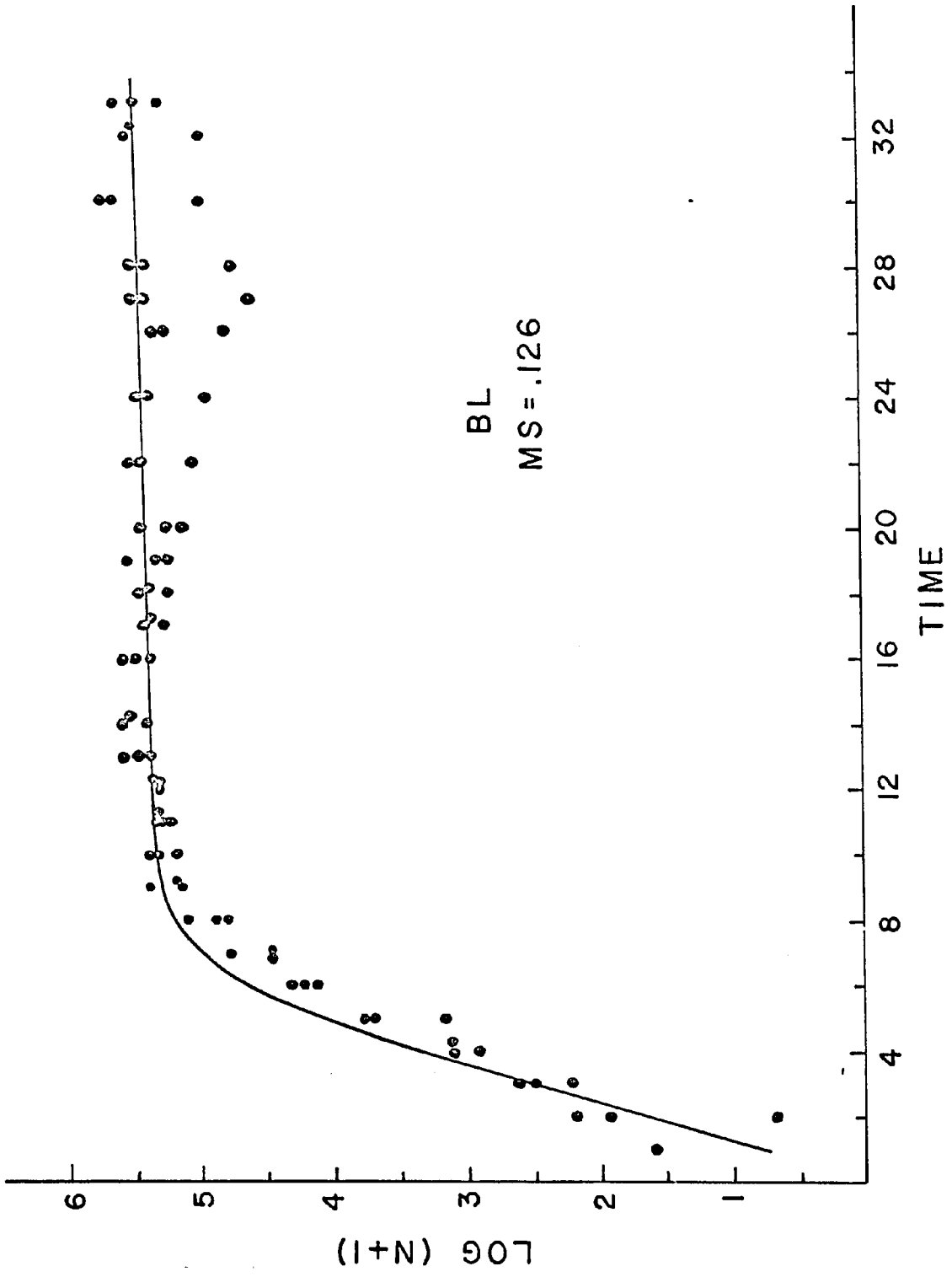


Figure 20. Bl in competition with PB.

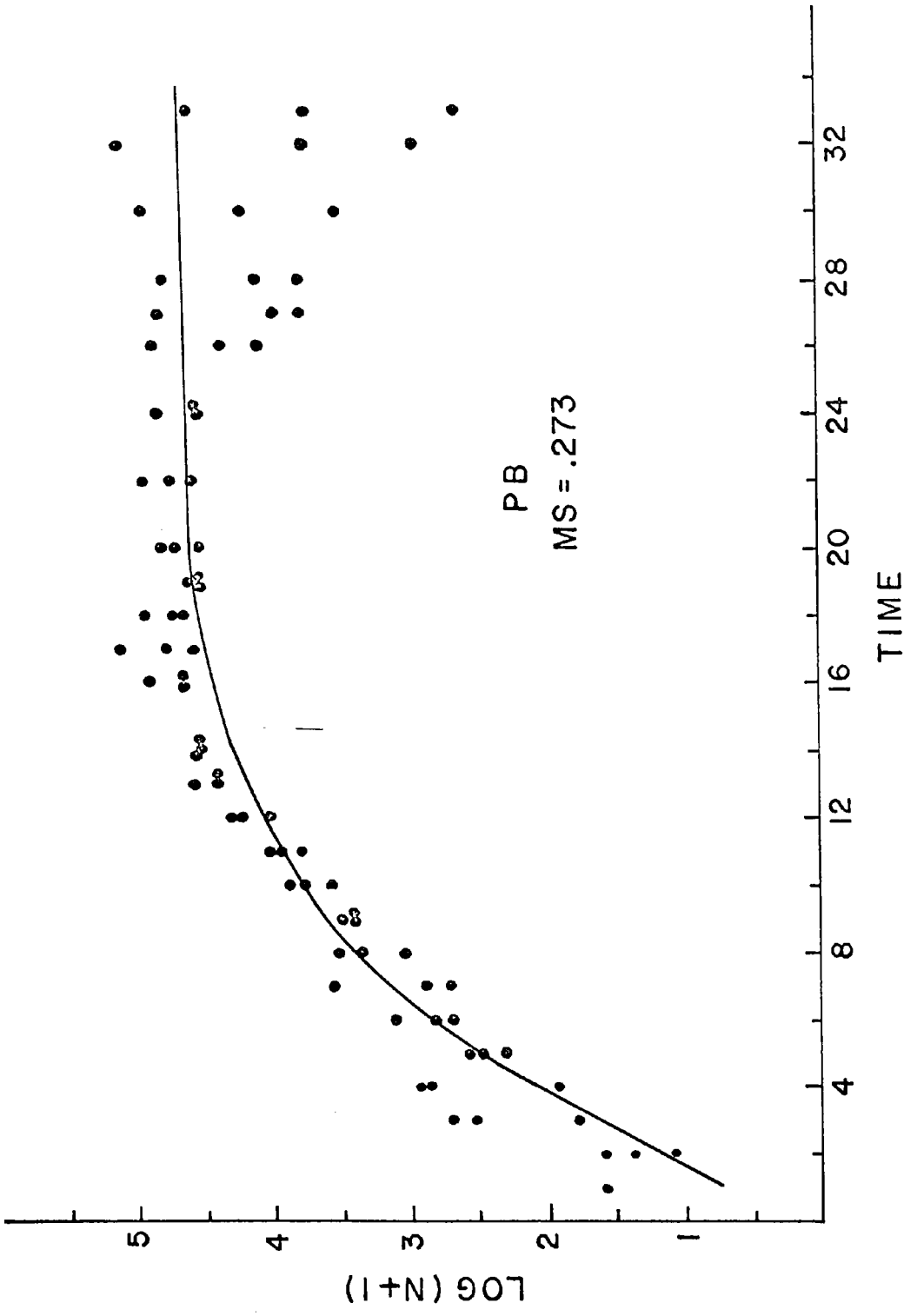


Figure 21. PB in competition with B1.

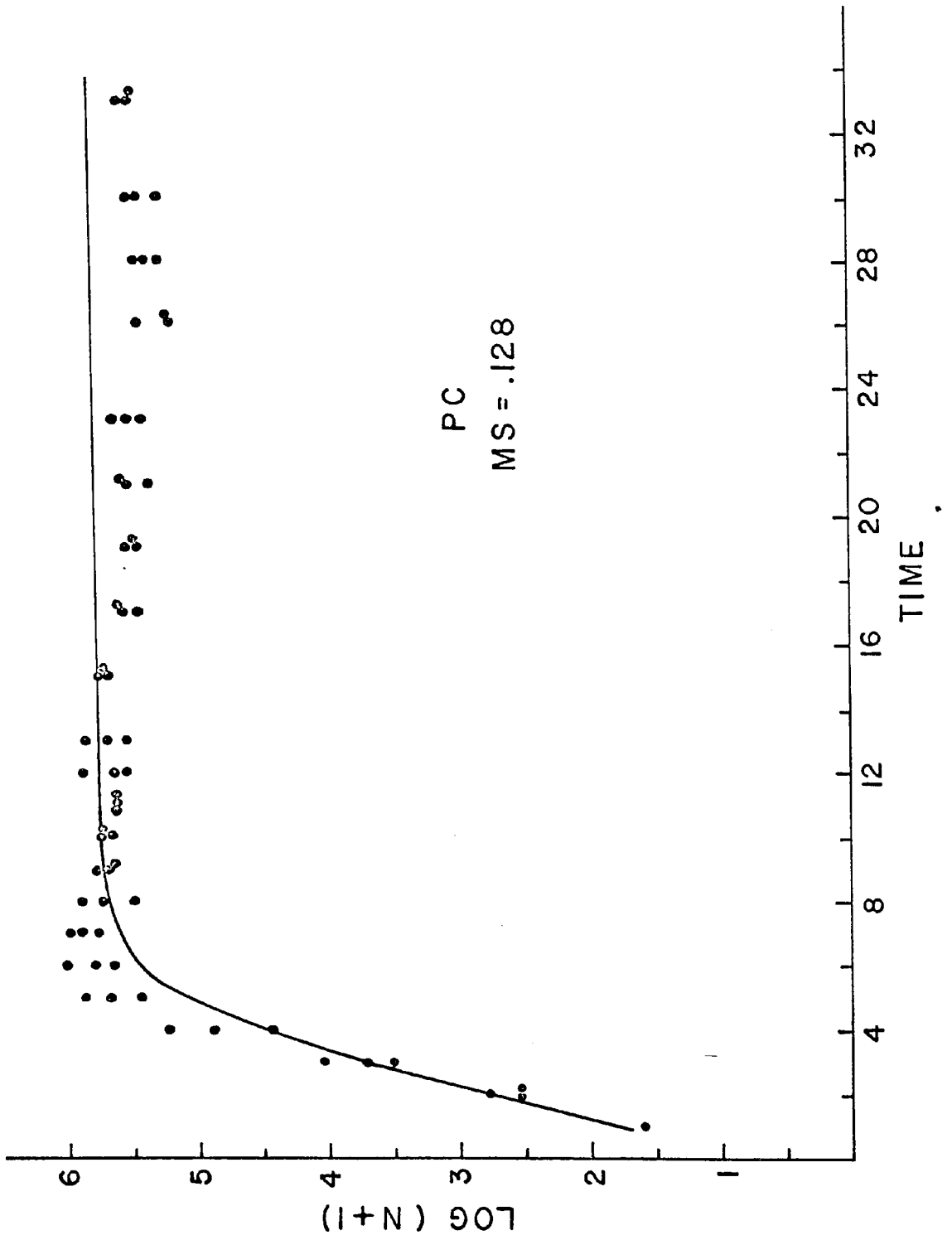


Figure 22. PC in competition with PA.

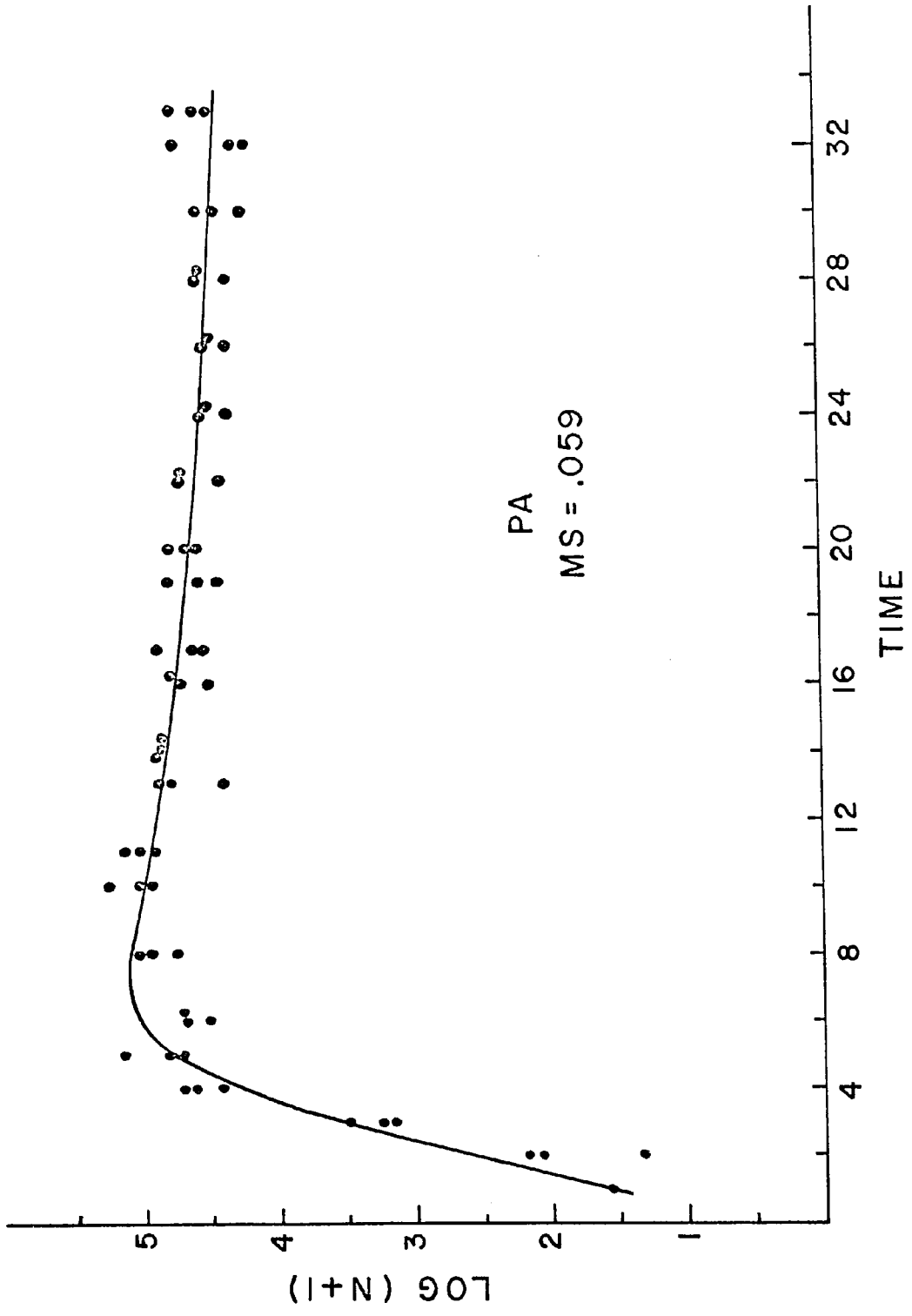


Figure 23. PA in competition with PC.

TABLE 2. Community Matrix for Four Species of Protozoa in Test Tubes. (The α_{ij}th entry refers to the effect of the jth species on the ith species.)

ith Species \ jth Species	PA	PC	PB	Bl
PA	1	1.75	-2.00	-.65
PC	.30	1	.50	.60
PB	.50	.85	1	.50
BL	.25	.60	-.50	1

and see if the solution agrees with the data obtained from the laboratory experiments. It must be emphasized that up to this point all curves in this paper have been fit. That is, the expected curves are based on the data which they are describing, and therefore, cannot deviate too greatly. In the case of four-way competition, however, the expected curves are based on independent estimates of the parameters, estimates which were made from different experiments. As a consequence, a reasonable expectation, if higher order interactions are not important, is that the fit to the four-way situation is, at best, as good as the fits to the pair-wise competitions. Though it cannot be expected that the four-way competition experiments will fit the model as well as the two-way competition, it is not clear exactly how "good" a fit is necessary to judge a model as being valid. Such a judgement, of course, depends on the purposes for which the model is to be used. In the present case it seems that there are three vaguely distinguishable levels of purpose which might be used in helping to judge the validity of this model. First, if only the equilibrium conditions of the model are needed -- say in predicting the maximum number of species in an equilibrium community -- we might only require that the model predict accurately which species will persist and which will go to extinction. Second, the relative numbers of individuals at any particular point in time may be desired -- say, in a theoretical study of the relative abundance of species -- or, more or less equivalently, the general behavior of the populations within the framework of the larger system must be known -- i.e., does species i oscillate, does it tend to be peaked and then drop off fast, and similar general questions. Under this requirement, we

accept the model as valid if the general shape of the curves reflects the general trend of the data. Third, we may wish to make very precise predicitons with the model such as exactly how much pesticide must be applied at time x to produce a y per cent change in species i by time x + a. At this level we require the fit to four-way competition to be almost as good as the fit to the two-way competitions. Certainly these three levels are not discrete, but are merely useful points in a continuum, defined so as to be able to judge the relative validity of the model as applied to a simple community.

In figures 24, 25, 26, and 27 are shown the results of simulating four-way competition with the community matrix of the last section and the r's and K's from the single species population growth experiments. Also shown in these figures are the observed data from the four-way competition experiments.

Under the first criterion of validation -- only the final outcome is desired -- the data are described perfectly by the model. The model predicts that PB will be extinct, BL will be at a very low population density, PA and PC will have higher densities. As can be easily seen from figure 24 - 27, the data correspond exactly to these predictions.

Likewise under the second criterion the model is validated. The general trends are predicted in every case, and the rank order of abundance is as predicted, at virtually all points in time. The general trends of growth, peaking, and decay are predicted fairly accurately. The early peak for PC reflected in the experiments is essentially the same as that species exhibits in two-way competition (See figures 14, 18, and 22.).

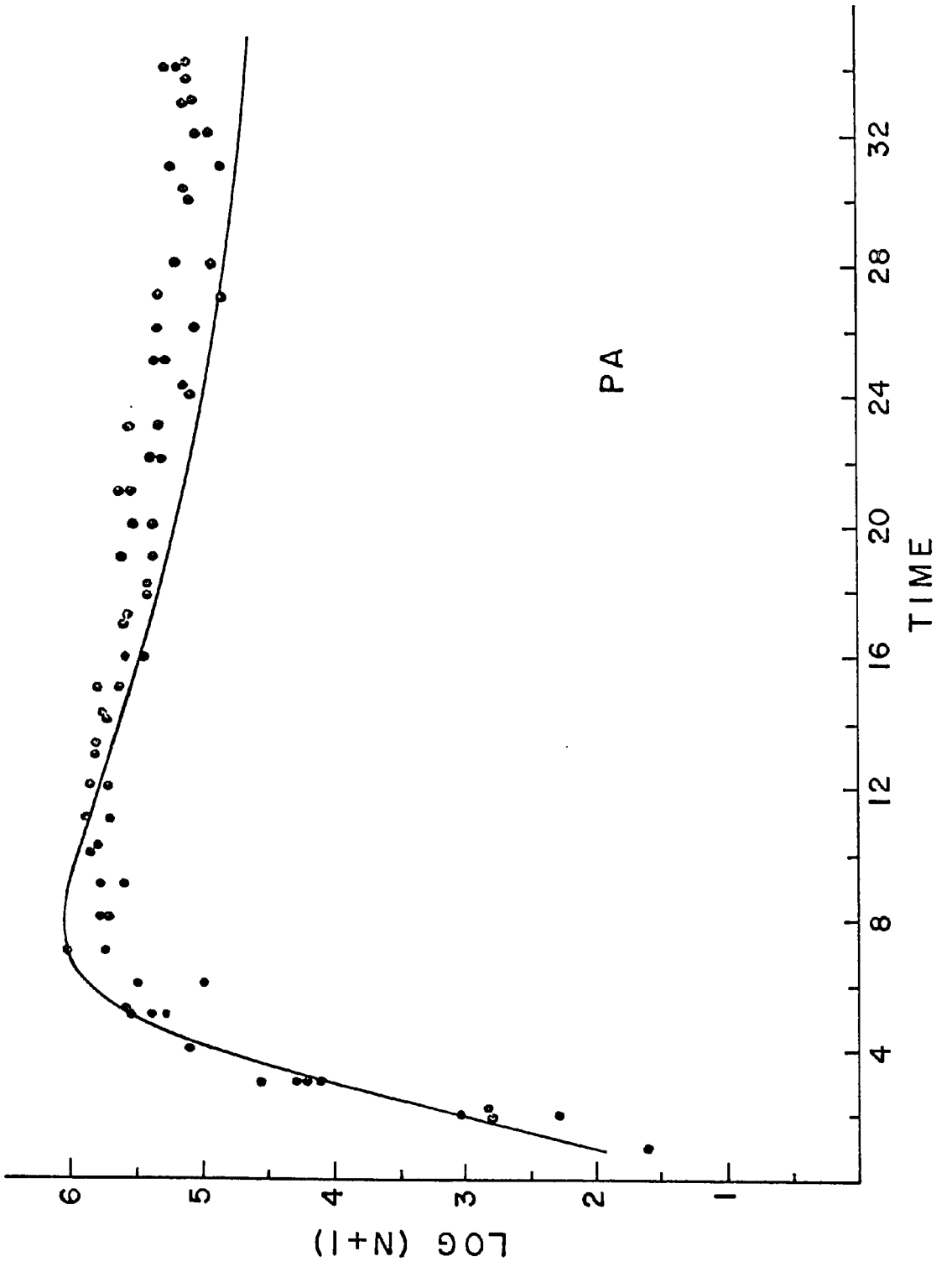


Figure 24. PA in four-way competition.

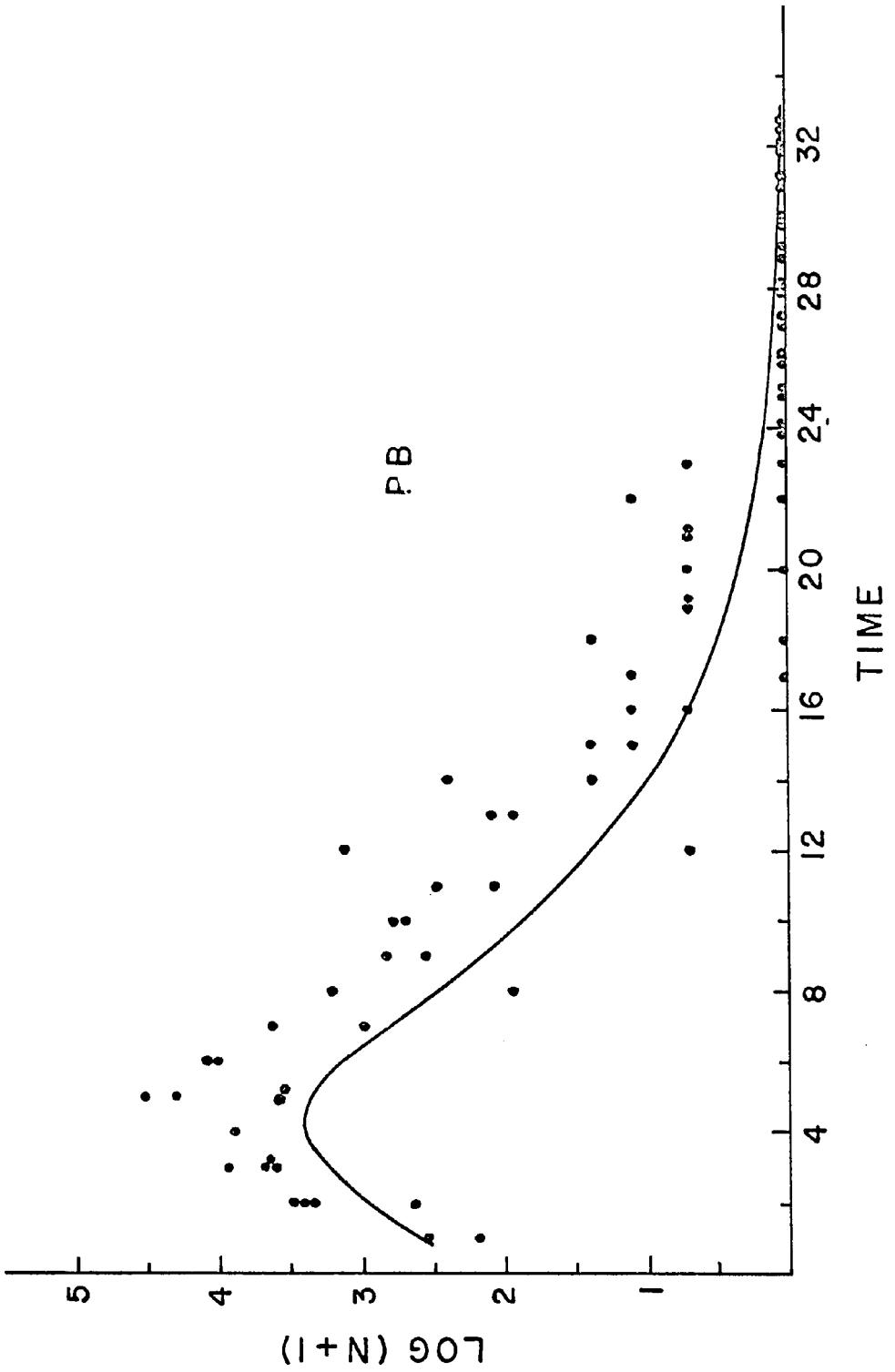


Figure 25. PB in four-way competition.

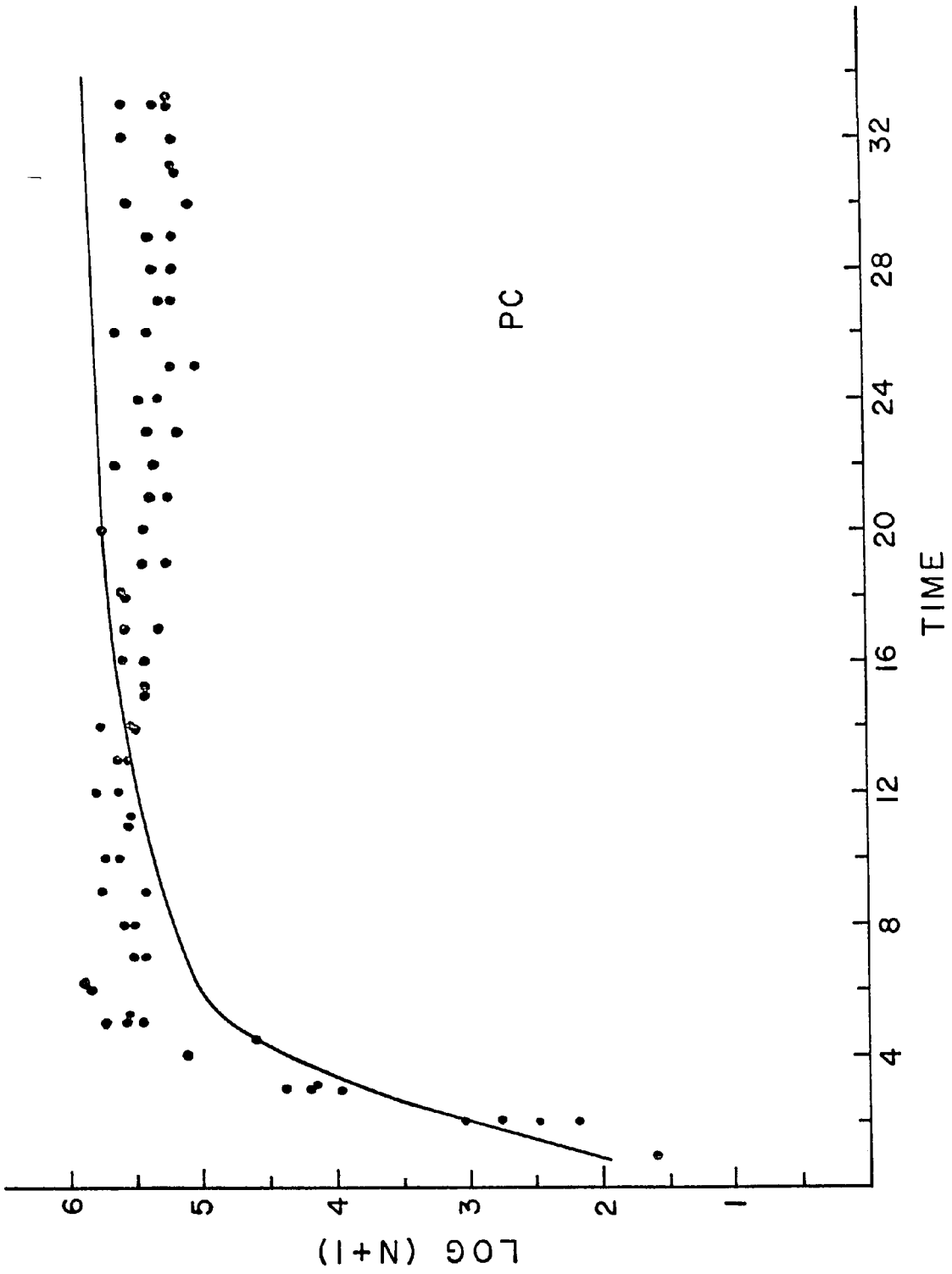


Figure 26. PC in four-way competition.

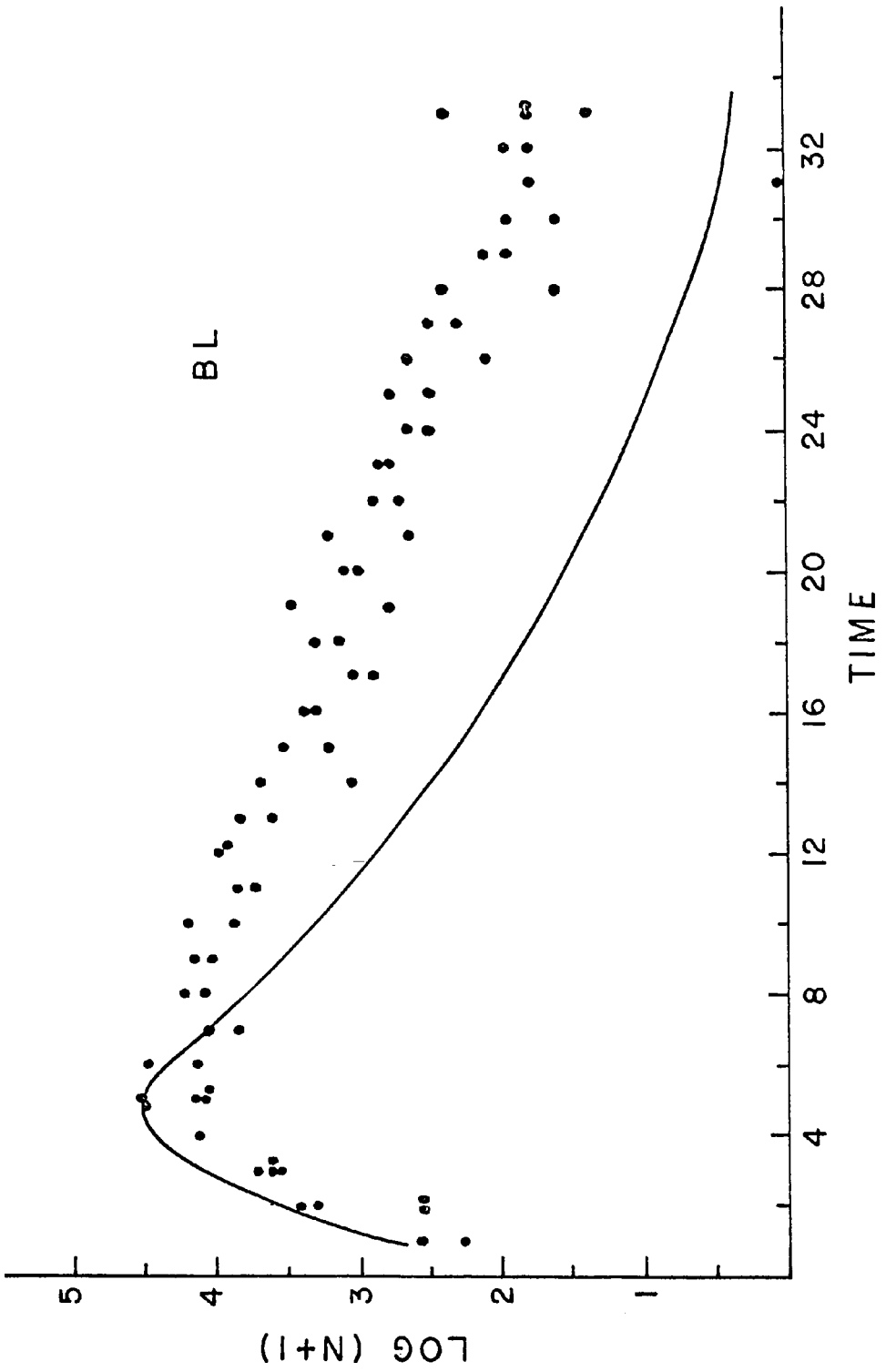


Figure 27. Bl in four-way competition.

Finally, consider the third level of validation. Somewhere in between the second and third level the validation becomes questionable. The third level requires that precise predictions be made. The three species PC, PA, and PB conform quite well, but BL seems to deviate excessively from the expected. However, as discussed previously, it is not sufficient to examine the data and expectation alone, but they must be considered in the light of the pair-wise experiments, since the correspondence between expected and observed can only be as good as that of the basic model. It is for this reason that the mean square deviations were computed earlier (figures 12 through 23). In table 3 are listed the pooled mean squares for each species -- pooled over all two-way competitions in which that species was a part -- and the mean squares for the same species in four-way competition. The first three species show very similar mean squares between two-way and four-way competition, indeed PA and PB are even better predicted in the case of four-way than in the case of two-way competition. The case of BL is somewhat less encouraging. The mean square is rougly five times greater in four-way than in two-way. The fact that the experimental points are always greater than predicted, implies that whatever higher order interaction there may be, they act solely to decrease the competitive effect felt by BL. They are non-coalition type higher order interactions.

However, if one is interested in this model from the standpoint of the community, it is not valid to compare predictions on a specific basis. We should instead be interested in the general performance of the model in predicting community dynamics. To this end the sum of squares pooled over all two-way competition cases was computed as

TABLE 3. Mean Squares for Two-way and Four-way Competition Experiments, and Ratio Between the Two (Taking Largest Mean Square as Numerator). Numbers in Parentheses are Degrees of Freedom.

	SPECIES			
	PA	PC	PB	Bl
Pooled mean square for 2-way competition	.1110(212)	.1486(197)	.4277(230)	.2648(209)
Mean square for 4-way competition	.1040(74)	.2217(74)	.3621(74)	1.2824(74)
Ratio	1.15	1.49	1.18	4.84

0.246 and the same pooled over all four-way cases was 0.487, only a two-fold difference. Thus, the four-way model predicted about half as well as the two-way model, implying that, from the point of view of the community as a whole, the higher order interactions are rather unimportant.

The above discussion is similar to the problem of multiple comparisons tests in statistics. Given a group of means, we wish to test for differences. In setting an error rate we are faced with deciding on the relative importance of pair-wise or experiment-wise rates. That is, is it more important to minimize the probability of making any mistake at all, or the probability that a given pair of means may be judged different when they are truly the same. Similarly in the present context, we are faced with deciding whether we want the model to make predictions about the community as a whole, or about the components of the community. The former criterion provides a single judgement of the model. The latter provides as many judgements as there are components.

Thus, if we are concerned with judging the present model under the third criterion -- absolutely precise predictions -- and if we are interested in the individual components, the non-interactive model is "good" three times and "bad" once. On the other hand, it appears to be simply "good" on the level of the whole community.

Conclusion: The conclusions of these experiments were basically stated in the previous section. However, it might be well at this point to recall statements made earlier about the choice of the experimental system. It was the author's prejudice that higher order interactions are very important in nature. Thus, the experimental

system was chosen so as to maximize the chance of not finding higher order interactions, but with the hope that even then such interactions would be significant. Then, because of the way the experimental system was put together, one could make a fairly powerful statement about the universal occurrence of higher order interactions in nature. Unfortunately, the basic models proved to be excellent predictors (i.e., higher order interactions did not seem important), and one can only cite this study as a single example of the non-significance of higher order interactions.

SUMMARY

(1) A classification of communities is suggested based on average amount and kind of niche overlap as reflected in competitive interactions. The major dichotomy is based on the existence or non-existence of higher order interaction terms in the Gause multi-species competition equations. The major dichotomy is interactive and non-interactive communities. Non-interactive communities may be thought of as forming a continuum between completely open and completely additive based on the number of interactions per species.

(2) Derivations are presented for two approximate measures of relative openness based on the covariance of the community matrix.

(3) The expected number of species in a community is discussed with reference to the distribution of the saturation densities (K's) of the individual populations.

(4) The probable effects of higher order interactions are discussed, and it is concluded that they are important but that it is difficult to predict their exact effects.

(5) An empirical test of the existence of higher order interactions was carried out using four ciliate protozoans, Paramecium caudatum, P. bursaria, P. aurelia, and Blepharisma sp..

(6) All four ciliates were cultured individually and their population histories were described quite well by the simple logistic equation.

(7) Attempts to explain minor deviations of the data from the logistic by use of the one or two time lag logistic failed. It was concluded that a more complicated time lag phenomenon must be operative.

(8) Every possible pair of the four ciliates was cultured and a trial and error procedure was used to estimate α and β of the Gause equations.

In all cases the simple Gause equations seemed to adequately describe the data.

(9) All four ciliates were cultured together and compared to predictions made by use of the competition coefficients estimated from pair-wise competition and population parameters estimated from single species population growth. The correspondence between prediction and data suggest that the higher order interactions have slight or no effect on the dynamics of this artificial community.

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