A MODIFIED LOGISTIC GROWTH EQUATION: EFFECTS OF CADMIUM CHLORIDE ON THE DIATOM, THALASSIOSIRA WEISSFLOGII AND THE DINOFLAGELLATE, AMPHIDINIUM CARTERI IN UNIALGAL AND BIALGAL BATCH CULTURES

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A simple modification to the logistic equation is proposed: it extends the description of microbial population growth in batch cultures from the exponential, through the stationary, into the decline phase. The modified equation described the effects of cadmium chloride on a diatom and a dinoflagellate in unialgal and bialgal cultures by specifying changes in four parameters: the specific rate of growth, an asymptotic maximum population density, the specific rate of decline, and a parameter related to the time at which the population density is reduced to one half of its value at stationary phase.

Key words: Amphidinium carteri, cadmium chloride, logistic growth, Thalassiosira weissflogii

INTRODUCTION

Mathematical models are important to the study of microbial population growth: they serve to generalize the results, and to provide a basis for deducing further properties of the population (Pirt, 1975). Growth of bacteria and microalgae in batch cultures follows a well-known pattern characterized by successive phases: lag, exponential, stationary, and decline. The lag phase can usually be eliminated by starting with a reasonably sized inoculum of exponentially growing cells (Fogg, 1965; Dean and Hinshelwood, 1966; Pirt, 1975). The logistic equation of Verhulst (see Hutchinson, 1978) is widely used to describe the growth of populations; however, it pertains only to the exponential and stationary phases. In the special case where decline of one population arises from competition with another population, the dynamics of growth are often described by a pair of coupled logistic equations modified according to Gause (1934).

This paper presents a different modification to the logistic equation that extends the description of microbial growth from the exponential, through the stationary and into the decline phase. This description does not stipulate the mechanism of decline and is therefore a more general model of growth than that of Gause. The
modified equation was first applied to the growth of a diatom and a dinoflagellate, each in mono-specific culture. Following this, the conditions in each culture were changed by introducing: a chemical inhibitor (cadmium ion), the other species, and finally both the inhibitor and the other species together. The effects of these changes were described by changes in the equation parameters for each species.

THE MODEL

The mathematical derivation of the logistic model for population growth is widely available (e.g. Pielou, 1977; Hutchinson, 1978): it is given here in its integrated form:

\[ B = B_m \left( \frac{1}{1 + e^{\ln(B_n/B_0) - \mu t}} \right) \tag{1} \]

where \( B \) is the total cell volume of the population at time \( t \); \( B_0 \) is the initial value of \( B \); \( \mu \) is the specific growth rate; \( B_m \) is the asymptotic value of \( B \) at large values of \( t \), namely the saturation level of the population.

The basic logistic equation may be extended to include population decline simply by multiplication with a function that describes survivorship in a sigmoidal fashion (cf. Dean and Hinshelwood, 1966; Hutchinson, 1978) as follows:

\[ B = B_m \left( \frac{1}{1 + e^{\ln(B_n/B_0) - \mu t}} \right) \left( \frac{e^{\gamma - \delta t}}{1 + e^{\gamma - \delta t}} \right) \tag{2} \]

Two new parameters are introduced: \( \delta \) is the specific decline rate; and \( \gamma \) is a non-dimensional parameter related to the horizontal scaling of the growth curve. The significance of \( \gamma \) is easily grasped by considering a parameter, \( \tau \), derived from it. Notice that the term appearing in equation 2 but not in 1 is simply the fraction \( f \) of the population remaining at time \( t \) after accounting for cell decline:

\[ f = \frac{e^{\gamma - \delta t}}{1 + e^{\gamma - \delta t}} \tag{3} \]

Define \( \tau \) as the value of \( t \) for which \( f \) is 0.5.

\[ \tau = \frac{\gamma}{\delta} \tag{4} \]

Therefore, \( \tau \) might be considered as the time at which the population has declined to one half of its value at stationary phase. In principle, \( f \) cannot have a value of unity but in practice, the basic logistic equation is effectively recovered by setting \( \delta = 0 \) and \( \gamma \) to a very large number: equation 2 may thus be considered a practical description for the growth of microbial populations in batch culture.
MATERIALS AND METHODS

The diatom *Thalassiosira weissflogii* (Grunow) G. Fryxell and Hasle, comb. nov. (*= Thalassiosira fluviatilis* Hustedt) and the dinoflagellate *Amphidinium carteri* Hulburt were supplied by J.S. Craigie, National Research Council of Canada. Growth experiments were initiated by inoculation of exponentially-growing cells into 50 ml f/2 medium (Guillard and Ryther, 1962) modified slightly as described previously (Li, 1980). Cultures were incubated at 20°C under a 16:8 light:dark cycle. Irradiance at the surface of the flasks was 300 μE·m⁻²·s⁻¹ provided by cool-white fluorescent bulbs. The effect of Cd²⁺ (as CdCl₂·2½H₂O) on growth was tested at initially added concentrations of 1, 10, and 100 μg Cd²⁺·l⁻¹. Three series of experiments were performed on bialgal cultures: each differed in the ratio (R) of diatom to dinoflagellate inoculum size.

Population growth was monitored by measuring total cell volume per ml of culture. Frequency distributions of apparent cell volumes, established from a Coulter counter (Model ZS) and a Coulter Channelizer (Li, 1979), were areally integrated to obtain total cell volumes. The fit of data to equation 2 was by non-linear parameter estimation according to the Gauss–Newton method (Bard, 1974) using a computer.

RESULTS AND DISCUSSION

The utility of equation 2 is illustrated in an experiment which tested the effects of Cd²⁺ on the growth of individual species in bialgal cultures (Fig. 1). Not only did the model provide an adequate fit to the measurements in cases where a phase
of decline was observed, but it also did not impair the fit for cases where no decline was evident. In the latter cases, \( \delta = 0 \) and \( \gamma \) was a very large number.

For the diatom, the mean percentage deviation of observed values from computed values (±SD of this mean) was +2.45 (±2.37)% in the 4 unialgal experiments (\( R = \infty \)) and +1.37 (±0.51)% in the 12 bialgal experiments (\( R = 1.62, 0.83, 0.47 \)). For the dinoflagellate, this mean (±SD) was +1.45 (±1.68)% in the 4 unialgal experiments (\( R = 0.00 \)) and +11.56 (±3.62)% in the 12 bialgal experiments (\( R = 1.62, 0.83, 0.47 \)).

The effects of Cd\(^{2+} \) on \( B_m, \mu, \delta, \) and \( \tau \) for unialgal and bialgal cultures are given in Table I. For unialgal cultures of both species, and for the dinoflagellate in bialgal

<table>
<thead>
<tr>
<th>( R )</th>
<th>( \text{Cd} )</th>
<th>Diatom</th>
<th>( B_m )</th>
<th>( \mu )</th>
<th>( \tau )</th>
<th>( \delta )</th>
<th>Dinoflagellate</th>
<th>( B_m )</th>
<th>( \mu )</th>
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<td>146(6)</td>
<td>1.45(0.13)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>244(6)</td>
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<tr>
<td>1</td>
<td>151(6)</td>
<td>1.33(0.13)</td>
<td>-</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
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<td>131(7)</td>
<td>1.06(0.13)</td>
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<td>-</td>
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<tr>
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<td>0.97(0.15)</td>
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<td>-</td>
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<td>1.62</td>
<td>0</td>
<td>149(3)</td>
<td>1.57(0.10)</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>221(9)</td>
<td>0.21(0.01)</td>
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<td>1.61(0.08)</td>
<td>19.7(6.6)</td>
<td>0.51(0.24)</td>
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<td>17.8(4.4)</td>
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<tr>
<td>0.83</td>
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<td>106(3)</td>
<td>1.68(0.14)</td>
<td>16.6(4.0)</td>
<td>0.84(0.21)</td>
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<td>-</td>
<td>147(5)</td>
<td>0.42(0.01)</td>
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</table>

\( R: \) \( B_0 \) of diatom/\( B_0 \) of dinoflagellate; \( R = \infty \) refers to mono-specific diatom culture; \( R = 0.00 \) refers to mono-specific dinoflagellate culture.

\( \text{Cd:} \) \( \mu \text{g Cd} \cdot \text{l}^{-1} \).

\( B_m: \) \( 10^6 \mu \text{m}^3 \cdot \text{ml}^{-1} \).

\( \mu, \delta: \) day\(^{-1} \).

\( \tau: \) days.

Standard deviations of parameter estimates appear within parentheses.
cultures, no decline phase was observed over the experimental durations.

When the diatom was in unialgal culture, Cd\(^{2+}\) diminished both \(\mu\) and \(B_m\). No such effects were noted for the dinoflagellate in unialgal culture. The results confirm previous findings of differential toxicity of Cd\(^{2+}\) to marine microalgae (Li, 1978a,b, 1980).

The effect of the dinoflagellate on the diatom was quite different from the effect of the latter on the former. Regardless of the Cd\(^{2+}\) concentration or the ratio of inoculum sizes (\(R\)), the diatom generally had slightly higher values of \(\mu\) in bialgal than in unialgal cultures: it appeared as if the dinoflagellate stimulated the early growth of the diatom. However, except in two cases, the diatom was caused to enter the decline phase by the dinoflagellate: the diatom was usually the eventual loser in bialgal competition.

Conversely, regardless of the Cd\(^{2+}\) concentration or \(R\), the dinoflagellate had substantially lower values of \(\mu\) in bialgal than in unialgal cultures: it appeared as if the diatom depressed dinoflagellate growth in the early part of the experiment. However, in almost all cases, the dinoflagellate attained higher values of \(B_m\) in bialgal than in unialgal cultures: the diatom appeared to extend the carrying capacity of the medium for the dinoflagellate.

Perhaps the most interesting aspect of Cd\(^{2+}\)-influenced competition was the role of \(R\). When the diatom was initially dominant (\(R = 1.62\)), the outcome of competition in the absence of Cd\(^{2+}\) was co-existence with the dinoflagellate; Cd\(^{2+}\) caused the diatom to decline – the higher the concentration, the faster (higher \(\delta\)) and the earlier (lower \(\tau\)) was the decline. When the two species were initially approximately equal (\(R = 0.83\)), the situation was much different: Cd\(^{2+}\) provided a refuge for the diatom. This was clearly evident at 100 \(\mu\)g Cd\(^{2+}\) \(\text{L}^{-1}\) where the diatom established a stable population in co-existence with a much reduced stationary population of the dinoflagellate. Finally, when the diatom was initially subdominant (\(R = 0.47\)), no refuge against the dinoflagellate was provided for the diatom by Cd\(^{2+}\) at the tested concentrations.

Other studies, including ones involving microalgae, have already demonstrated (1) differential sensitivities of various species to heavy metals (Davies, 1978), (2) the ability of one species to affect the growth rate and maximum population density of another species (Elbrächter, 1976), (3) the dependence of competition outcome on the initial population densities (Fedorov and Kustenko, 1972) and (4) the influence of pollutants on the course of competition (Mosser et al., 1972; Fisher et al., 1974; Dayton and Lewin, 1975; Kayser, 1977). The virtue of the analysis afforded by equation 2 is the simplicity with which the response of easily recognized growth phases can be objectively quantified. The shortcoming of this approach is that, like the basic logistic equation and other modifications thereof (Wangersky, 1978), it is at best semiempirical. The form of the survivorship function (equation 3) was not chosen on the basis of perceived mechanisms of population dynamics. In fact, the description as given implies that the process of cell decline starts immediately upon
the initiation of the culture. This is perhaps unrealistic. Alternative geometric representations are no doubt possible: they should be evaluated on the same bases of parsimony and interpretability of parameters, goodness of fit, as well as biological implications.

A numerical analysis based on a semiempirical model is useful for organizing data: it is a fully objective method for reducing many observations to a few parameters amenable to interpretation in the context of population dynamics (i.e. specific rates of growth and death, maximum population size and a time-scaling parameter). However, the semiempirical model alone cannot be the basis for an understanding of the growth dynamics in mechanistic terms. Accordingly, this has not been attempted for the data presented in this paper. For a more complete understanding of the system it is necessary to strive towards a mechanistic representation.

Interactions between algal species in batch culture occur in the form of competition for nutrients, both inorganic (Maestrini and Bonin, 1981a) and organic (Bonin and Maestrini, 1981), including vitamins (Bonin et al., 1981a) and in the form of allelopathy (Maestrini and Bonin, 1981b). Furthermore, such interactions are influenced by factors such as light intensity, temperature (Bonin et al., 1981b) and population size (Fedorov and Kustenko, 1972; Elbrächter, 1976; Kayser, 1977) to the extent that not only the degree, but also the outcome, of competition is dependent upon these factors (e.g. Gause and Witt, 1935). The results of this study clearly indicate that Cd\(^{2+}\) is a potentially important factor influencing algal competition. The mechanism by which this influence is exerted is not known. However, the complicated interdependencies of Cd\(^{2+}\) and \(R\) with the parameters \(\mu\), \(B_m\), \(\gamma\) and \(\delta\) of the 2 species suggest that there may be more than one simple mechanism.

Finally, several instances have been reported in studies of unialgal response to heavy metals in which population growth resumed after the period of decline (Davies, 1974; Kayser, 1976; Li, 1980): equation 2 would not be adequate in those cases.

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REFERENCES


