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## Slope of the Monod Equation as an Indicator of Advantage in Nutrient Competition

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**Abstract.** Apparently by analogy with enzyme kinetics, the half-saturation value ( $K$ ) for nutrient uptake or growth has frequently been overemphasized in discussions of competition, and the role of maximum rates ( $R_m$ ) has not been given sufficient emphasis. The ratio  $R_m/K$ , which is the slope of the Monod equation at lowest substrate concentration, offers a simple way of emphasizing both factors. Several examples from the literature are cited to show that this ratio better reflects rates at lowest concentrations, and therefore competitive position in the process being considered, than do  $K$  values alone.

Both nutrient uptake rates and growth rates of microscopic algae have often been found to approximate hyperbolic functions of external nutrient concentrations (8, 18, 21, 23). These relationships are empirically described by the equation:

$$R = \frac{R_m S}{K + S}$$

where  $R$  = rate of nutrient uptake or growth,  $R_m$  = maximum rate of nutrient uptake or growth,  $S$  = substrate concentration, and  $K$  = half-saturation value, or substrate concentration supporting half the maximum rate of nutrient uptake or growth.

When applied to growth rates, this relationship is generally referred to as the Monod equation, based on early work on bacterial growth (19). When applied to nutrient uptake, the term Michaelis-Menten is often used, by analogy with enzyme kinetics (7). Formal identity of this relationship for nutrient uptake or growth with the Michaelis-Menten equation for enzyme kinetics does not necessarily imply a theoretical or functional relationship with enzyme kinetics. The nutrient uptake and growth equations offered in the literature are entirely empirical and are accepted here only because they seem to fit the data adequately. For simplicity, and to differentiate the empirical uptake and growth relationships from the theoretically supported enzyme relationship, the term Monod equation will be used here to cover both uptake and growth situations.

Analogy of  $K$  values for uptake or growth with the  $K_m$  of enzymology appears to have led to some confusion in discussions of competition. In enzymology,  $K_m$  is used as an indicator of the affinity of an enzyme for its substrate, a lower  $K_m$  indicating a higher affinity (3). This concept has wrongly been transposed into ecology to imply that species with low  $K$  values for a particular process will be at an advantage in that process at low nutrient concentrations to species with higher  $K$  values (1, 4, 9, 24). For example, Hanisak and Harlin (11) state that on the basis of uptake kinetics the seaweed *Codium fragile* can be expected to be competitive in N uptake with phytoplankton simply because the  $K$  values are similar. This argument ignores the fact that, because the seaweed's maximum uptake rates (per unit dry weight) are about only 1–5% those generally found in phytoplankton (13), similar  $K$  values imply that uptake rates by the seaweed can be expected to be 1–5% those by phytoplankton at all concentrations. The ability of the seaweed to maintain itself in the face of this competitive disadvantage argues for the role of other advantages pointed out by the authors. Other discussions, although not explicitly denying the importance of maximum rates, have placed much more emphasis on  $K$  values than on maximum rates (14, 17). This, of course, can be done only when maximum rates are the same (22, 23).

To be of more general application, both  $R_m$  and  $K$  values should be included in one index. The ratio  $R_m/K$  increases as  $R_m$  increases and  $K$  decreases; thus a higher ratio indicates a higher rate at lowest nutrient concentrations, and therefore competitive advantage in the process and conditions being considered as competition drives nutrient concentrations down. More importantly, this ratio is the slope of the Monod equation at lowest substrate concentrations. This can be seen by taking the derivative of this equation with respect to the substrate concentration ( $S$ ) and evaluating it as  $S$  approaches zero.

A comparison of some curves of rate against concentration will illustrate these points. The two diatoms *Cyclotella nana* and *Thalassiosira fluviatilis* (clone T. fluv.) show similar  $K$  values for urea uptake, but markedly different maximum rates and as a result different rates of uptake at low concentrations (Fig. 1; Table 1). *Thalassiosira fluviatilis* (clone Actin) has a higher  $K$  value than *C. nana* but also a higher maximum rate, resulting in similar rates at low concentrations. The ratio  $R_m/K$  reflects rates at low concentrations much better than do  $K$  values alone (Table 1).

**Table 1.** Comparison of kinetic parameters for urea uptake by 3 diatom clones (18)

Alga	$K^a$	$R_m^b$	$R_m/K$	$R_L^b$
<i>Cyclotella nana</i>	0.42	0.0076	0.018	0.0040
<i>Thalassiosira fluviatilis</i>				
clone Actin.	1.66	0.024	0.014	0.0060
clone T. fluv.	0.45	0.030	0.067	0.016

<sup>a</sup>  $K$ , half-saturation value in  $\mu\text{g-at urea-N/L}$ .

<sup>b</sup> Rate terms ( $R_m$  = maximum rate of urea uptake,  $R_L$  = rate of urea uptake at the lowest concentration where measurements made,  $0.5 \mu\text{g-at urea-N/L}$ ) in  $\text{h}^{-1}$ .

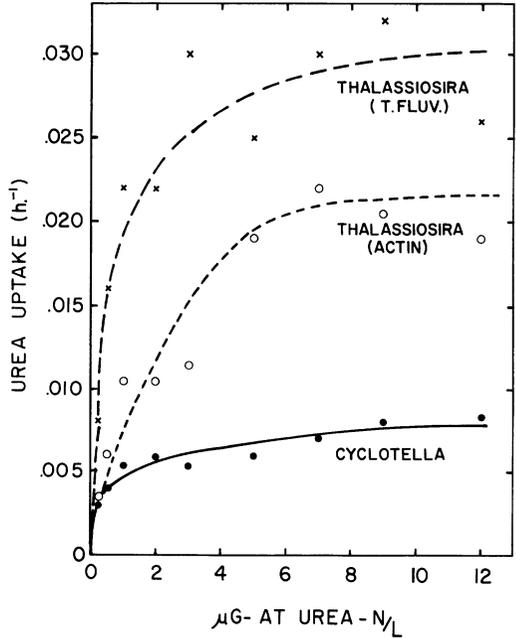


Fig. 1. Urea uptake as a function of urea concentration by *Cyclotella nana* (●), *Thalassiosira fluviatilis* (Actin) (○), and *Thalassiosira fluviatilis* (T. fluv.) (×). Redrawn from McCarthy (18).

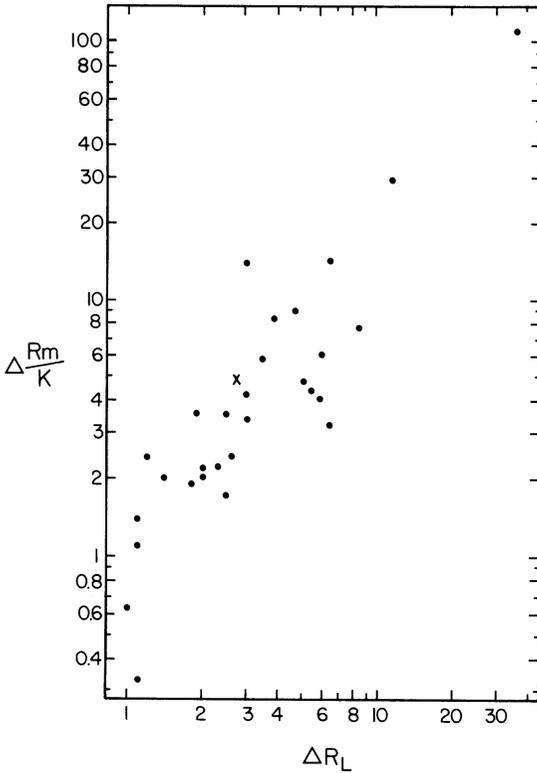
The ratio  $R_m/K$  is useful in two types of comparisons. One is in comparisons between different strains or species of microorganisms during uptake or growth under the same conditions. Here the higher  $R_m/K$  ratio indicates the strain at competitive advantage in the process and conditions studied. The second involves a single strain and comparison of rates of a particular process under different conditions. In these situations, the higher  $R_m/K$  ratio indicates the condition which would tend to improve the competitive position of the alga in the process being considered. In each of a number of these varied situations, differences in the  $R_m/K$  ratio are reasonable indicators of the differences in rates at low concentrations (Fig. 2). The ratio a little more than doubles with a doubling of  $R_L$ , the rate at the lowest concentration used in each study. The scatter in Fig. 2 is perhaps greater than would be expected. This is probably due largely to the great difficulty in accurately measuring rates at lowest concentrations as well as to errors associated with the kinetic parameters. Half-saturation values, of course, showed little relationship with  $R_L$ .

In order to relate kinetic parameters for growth and uptake, Droop (5, 6) derived the relationship:

$$K_s = \frac{\mu_m k_Q k_s}{u_m}$$

where  $K_s$  = half-saturation value for growth,  $\mu_m$  = maximum growth rate in units of time<sup>-1</sup>,  $k_Q$  = minimum cell quota in  $\mu g$  nutrient/unit biomass,  $k_s$  = half-saturation value for uptake, and  $u_m$  = maximum rate of nutrient uptake in units of  $\mu g$  nutrient/unit biomass/time. This can be rearranged to:

$$\frac{\mu_m}{K_s} = \frac{u_m}{k_s k_Q} \quad \text{or} \quad \frac{\mu_m}{K_s} = \frac{U_m}{k_s}$$



**Fig. 2.** The relationship between difference in rate at low concentration ( $\Delta R_L$ ) and difference in slope of the Monod equation ( $\Delta R_m/K$ ) in several comparisons. For each data point, two situations are compared.  $\Delta R_L$  is the ratio between the rates of the process being studied at the lowest substrate concentration used in the study. The rate in the situation giving the lower rate at lowest concentration is used in the denominator.  $\Delta R_m/K$  is the corresponding ratio of the index  $R_m/K$  in the same two situations. For example, when comparing urea uptake by the two clones of *Thalassiosira fluviatilis* (Table 1),  $\Delta R_L$  is the ratio of the rate at  $0.5 \mu\text{g}$ —at urea N/L shown by clone T. fluv. to that shown by clone Actin;  $\Delta R_m/K$  is the corresponding ratio for  $R_m/K$ . This comparison is shown above as ( $\times$ ). The other situations ( $\bullet$ ) include both comparisons between different clones under one set of conditions (urea uptake by 6 clones of marine diatoms, 18; Si-limited growth rates of two clones of *Thalassiosira pseudonana*, 10; Si-limited growth rates of two strains of *Asterionella formosa*, 17; P- and Si-limited growth and uptake rates of *Asterionella formosa* and *Cyclotella meneghiniana*, 23; and uptake of acetate, glycollate, and lactate by *Ankistrodesmus falcatus*, *Chlorella sp.*, and *Chlamydomonas segnis*, 1); and comparisons of one clone under different conditions (phosphate uptake by *Chorella pyrenoidosa* when P-deficient and not P-deficient, 16; phosphate uptake by *Anabaena variabilis* at high and low Mg concentrations, 12; cell surface alkaline phosphatase activity of *Anabaena variabilis* at high and low Ca concentrations, 12; and phosphate uptake by *Corynebacterium bovis* at several stages of P deficiency, 2).

where  $U_m = u_m/k_Q$ , that is, the maximum rate of uptake by cells with minimum nutrient content in units of  $\text{time}^{-1}$ . This implies that  $K_s$  (for growth) can be expected to be less than  $k_s$  (for uptake) in the same proportion that  $U_m$  exceeds  $\mu_m$ , a suggestion in line with some recent observations (23). More importantly, if the ratio  $U_m/k_s$  is found in uptake studies using cells with minimum practical cell

quota, it should provide an estimate of the  $\mu_m/K_s$  ratio for growth. This is really only an extension of the application of the above relationship to derive  $K_s$  (for growth) from the other parameters (5, 21). This approach is not in conflict with the suggestion that uptake parameters alone cannot predict outcome of competition in growth (23) because  $U_m/k_s$  includes both uptake parameters and the minimum cell quota, which appear to be the principal factors involved in growth competition.

The object of this discussion has been primarily to point out the usefulness of  $R_m/K$  over  $K$  alone in simple competition arguments. When a species has a higher  $K$  and  $R_m$  than another, a crossover point can exist in the two plots of  $R$  against substrate concentration, with one species being at advantage at high and the other at low concentration (15). However, as competition for the limiting nutrient becomes intense, the species with the highest initial slope of rate against concentration is at advantage. When the consideration of competition is limited to a single process such as nutrient uptake or growth, we are really concerned with some index of rates at lowest concentrations. The best reflection of this would be measurement of the initial slope of the curve of rate as a function of concentration or of rates at some standard low concentration. However, these rates are most difficult to measure, making the  $R_m/K$  ratio, the calculated initial slope of the Monod equation, the next best candidate. But it should be emphasized that this ratio applies to competitive position only for the process and conditions under consideration. Since the kinetic parameters are measured on single species cultures, it also assumes this competition is not affected by a phenomenon coming into play only when two or more species are present together, such as a metabolite of one being inhibitory to the other. Furthermore, the outcome of competition in terms of species succession is dependent on such factors as efficiency of nutrient utilization and the size of loss terms (20, 22) as well as nutrient-limited uptake and growth rates.

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