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Phosphorus-dependent growth kinetics of 11 species of freshwater algae

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Abstract

Mixed-species batch cultures were used to measure kinetics of phosphorus-dependent growth for 11 species of freshwater algae. Results were fitted to the Monod model, and significant interspecific differences were found. Indices of competitive ability calculated from the Monod parameters suggest that *Synedra radians*, *Synedra rumpens*, *Nitzschia acicularis*, and *Chlamydomonas* sp. are good competitors for P, and that *Nitzschia palea* and several nonsiliceous algae are poor competitors for P. These indices of competitive ability are largely consistent with competitive outcomes in a companion experiment with these species and with other studies. No relation was found between maximal growth rate and the effect that fluctuations in P supply had on a species' performance in the competition experiment. Growth parameters and competitive indices were not significantly correlated with cell volume, surface area, or surface: volume ratio.

In the equilibrium theory of resource competition, the function relating population growth rate of an algal species to the concentration of a dissolved nutrient is a critical determinant of that species' ability to compete for that nutrient (Tilman 1977; Tilman et al. 1982). The Monod (1950) equation is often used to represent the saturation kinetics typical of nutrient-limited algal growth:

$$\mu = \frac{\mu_{\max} R}{(K_{\mu} + R)} \quad (1)$$

where growth rate (μ) reaches an asymptotic value (μ_{\max}) when nutrient concentration (R) is saturating, and μ is half-maximal when R is equal to the half-saturation constant (K_{μ}). This model has been fitted to algal growth by many researchers, studying a wide variety of taxa and nutrients (e.g. Fuhs et al. 1972; Guillard et al. 1973; Paasche 1973a,b; Goldman et al. 1974; Klaveness and Guillard 1975). The nutrient concen-

tration (R^*) required by an algal population at equilibrium is

$$R^* = \frac{DK_{\mu}}{(\mu_{\max} - D)} \quad (2)$$

where $D < \mu_{\max}$ is the per capita loss rate (Tilman et al. 1982). If several algal species are competing for a nutrient, and if their mortality rates are known, then the outcome of competition can be predicted by calculating R^* for each species: the species with the lowest R^* will win the competition. It has also been suggested that the initial slope of the Monod function (μ_{\max}/K_{μ}) be used as a competitive index (Healey 1980; Mechling and Kilham 1982).

This theory has been verified in simple communities of algae assembled from unialgal stock cultures, competing in laboratory microcosms near equilibrium (Tilman 1977, 1981; Holm and Armstrong 1981; Tilman et al. 1981; Tilman and Sterner 1984). Kilham (1986) and Sommer (1986) allowed natural algal communities to compete for nutrients in laboratory cultures, and then isolated species dominant at equilibrium, and found that competitive outcomes were consistent with measured values of R^* .

Experiments with algal competition under nonequilibrium conditions suggest that some predictions of the equilibrium theory are not met. Nonsteady nutrient supply can allow more species to coexist than could do so at equilibrium (Sommer 1984, 1985;

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Grover 1989), delay the exclusion of competitively inferior species (Grover 1988), and alter competitive dominance between species (Turpin and Harrison 1979). In theory, nonequilibrium competition can allow a species with a high R^* to outcompete or coexist with a species with a low R^* , provided that the species with the higher R^* also has the higher μ_{\max} (Hsu 1980; Butler et al. 1985). Sommer (1985) presented evidence that nonsteady nutrient supply enhances the competitive performance of species with high μ_{\max} . The existence of a correlation between μ_{\max} and cell volume (Williams 1964; Eppley and Sloan 1966; Sommer 1981) raises the possibility that cell size may be a useful predictor of competitive performance under nonequilibrium conditions.

Here I report the kinetics of P-limited growth in a group of algae that was isolated from an experimental study of nonequilibrium competition for P and Si (Grover 1989). The results of that experiment suggested that these algae differ in their ability to compete for P. I examined growth kinetics measured in batch cultures to see if estimates of R^* were consistent with the competitive outcomes of the previous experiment. I also examined the hypothesis that μ_{\max} was an important competitive parameter under nonequilibrium conditions by comparing μ_{\max} between species whose competitive performance was enhanced by nonsteady state supply in the previous experiment and those whose performance was not enhanced. I report minimal cell quotas (Q_{\min}) for P and examine correlations of all measured parameters with cell size.

Methods

The algae studied here were isolated from semicontinuous cultures used in a study of competition for P and Si and represent organisms that were common in those cultures (Grover 1989); the original source is Square Lake (Washington County, Minnesota). Stock cultures were maintained in the same medium as used in the competition experiment, with Si and P concentrations of 137 and 5.0 $\mu\text{mol liter}^{-1}$. Stock cultures were not all axenic, but all were unialgal and free of protozoan and fungal contaminants;

sterile technique was used throughout. Cell sizes for all species are from Grover (1989) except for *Fragilaria capucina*, which underwent a pronounced increase in cell size following isolation and was remeasured by the same methods. Mean cell volume was 859 μm^3 (SD 409 μm^3), mean cell surface area was 829 μm^2 (SD 213 μm^2), and mean surface: volume ratio was 1.103 μm^{-1} (SD 1.103 μm^{-1}).

P-dependent growth kinetics were measured with the short-term batch culture method (Kilham 1978). Several species were grown together in the same cultures (Kilham 1986). Very low densities of algae were inoculated to minimize any intraspecific and interspecific density-dependent interactions, such as nutrient competition or allelopathy. Cultures were run in an incubator at $12^\circ\text{C} \pm 0.5^\circ$, with a photon supply rate of $\sim 60 \mu\text{mol m}^{-2} \text{s}^{-1}$ on a 14:10 L/D cycle. Siliceous algae were grown together in one set of experimental cultures and nonsiliceous algae in another. Experimental cultures were grown in 1-liter Pyrex Erlenmeyer flasks that had been autoclaved several times with $\text{K}_2\text{S}_2\text{O}_8$ in distilled deionized water and rinsed with distilled deionized water. Into these flasks a basal growth medium without added P was dispensed, and varying levels of P were added from a fresh stock solution of Na_2HPO_4 that had been calibrated against an external standard solution. The experimental cultures with siliceous algae had 137 $\mu\text{mol liter}^{-1}$ added Si (as $\text{Na}_2\text{SiO}_3 \cdot 9\text{H}_2\text{O}$); those with nonsiliceous algae had no added Si. Flasks and media were autoclaved before inoculation.

Before inoculating the experimental cultures, algae were grown to stationary phase in P-limited single-species batch cultures ($P = 0.24 \mu\text{mol liter}^{-1}$). Soluble reactive P (SRP, Strickland and Parsons 1972) was measured in duplicate during stationary phase and found to be $< 0.03 \mu\text{mol liter}^{-1}$ in all these cultures. Cell quota of P (considered to be an estimate of the minimal cell quota for P, Q_{\min}) was calculated as particulate P divided by cell density. Volume-specific Q_{\min} was calculated as Q_{\min} divided by cell volume. Dilute suspensions of preconditioned algae were prepared with sterile growth medium without added P and inoculated into ex-

perimental cultures at densities of 0.5–1.0 cells ml⁻¹. Experimental cultures were grown for 7 d, with 100-ml samples removed on days 3, 4, 6, and 7 and preserved with M3 (Meyer 1971). These 100-ml samples were then settled for at least 48 h in graduated cylinders, after which the upper 90 ml was removed by aspiration. The remaining 10 ml was sedimented in chambers and counted by the method of Utermöhl (1931) with a Zeiss inverted microscope. At the end of the experiment, SRP was measured and compared to the assigned level; cultures in which there was >30% depletion of P were eliminated from data analysis. Cultures that were retained in the analysis despite measurable P depletion all had assigned P concentrations >0.3 μmol liter⁻¹. These levels are at least 6× the measured K_{μ} of any species in these experiments, so that depletion could have had only a negligible impact on growth rates. Distilled deionized water and reagent grade chemicals were used throughout, and all labware was acid-rinsed (HCl) and rinsed with distilled deionized water. Autoclaving was used to sterilize growth media and culture vessels. Cultures were swirled at least twice daily.

For each experimental culture, the natural logarithms of sample counts from days 3, 4, 6, and 7 for each species were regressed against time to estimate the growth rate (μ). Nonlinear regression was then used to fit the Monod model for substrate-dependent growth to the growth rates of each species, with assigned nutrient concentrations for each mixed culture used as the independent variable. A version of the Levenberg-Marquardt algorithm was used to minimize the sum-of-squares for error (SSE) for each regression (STSC, Inc. 1985).

Intrinsic and parameter-effected nonlinearities (Ratkowsky 1983) of the solution loci from each regression were calculated according to formulae for the Monod equation (Johansen 1984). Nonlinearities were very small for all regressions and within the limits suggested by Ratkowsky (1983) for the application of asymptotic statistics concerning confidence limits and parameter differences. The estimated biases of fitted parameters were calculated according to Box's formulae (Ratkowsky 1983). Upper and

lower 95% confidence limits for μ_{\max} and K_{μ} were calculated by a maximum-likelihood method based on probability contours of SSE (Ratkowsky 1983), using a correction factor to improve the accuracy of the nominal type I error rate, α (Johansen 1984). To test for interspecific differences in μ_{\max} and K_{μ} , I used the nonlinear analog of ANCOVA (Ratkowsky 1983). The SSE values from each individual species' regression were pooled to estimate the SSE of a full model having an individual μ_{\max} and K_{μ} for each species. Three reduced models were fitted: one with a common μ_{\max} and K_{μ} for all species, one with a common μ_{\max} but individual K_{μ} , and one with a common K_{μ} but individual μ_{\max} . The significance of differences in fitted parameters between species was then assessed by an *F*-test on the SSE of full and reduced models.

Results

Mallomonas sp. failed to grow in the mixed-species cultures used to measure phosphorus-dependent growth. Counts of two colonial species, *F. capucina* and *Oscillatoria* sp., were highly variable, and the resulting data did not warrant further analysis. Thus data were available for 11 species to fit the Monod model to phosphorus-dependent growth (Fig. 1, Table 1). Confidence limits for μ_{\max} were nearly symmetrical and estimated biases were <5% for all species and <1% for all but two species. Confidence limits for K_{μ} were wide and asymmetrical, and estimated biases were very high, ranging from -20 to -80% for most species, and up to -190 and -440% for *Sphaerocystis schroeteri* and *Synedra radians* respectively. For these two species, the data hint of inhibited growth at high concentrations of P (Fig. 1).

There were significant differences between species in both μ_{\max} and K_{μ} . Interspecific differences in μ_{\max} were significant whether individual values of μ_{\max} for each species were entered in the regression model before ($F_{10,163} = 7.40$, $P < 0.001$) or after ($F_{10,154} = 7.73$, $P < 0.001$) individual values of K_{μ} had been entered. Interspecific differences in K_{μ} were significant whether individual values of K_{μ} for each species were entered in the regression model before

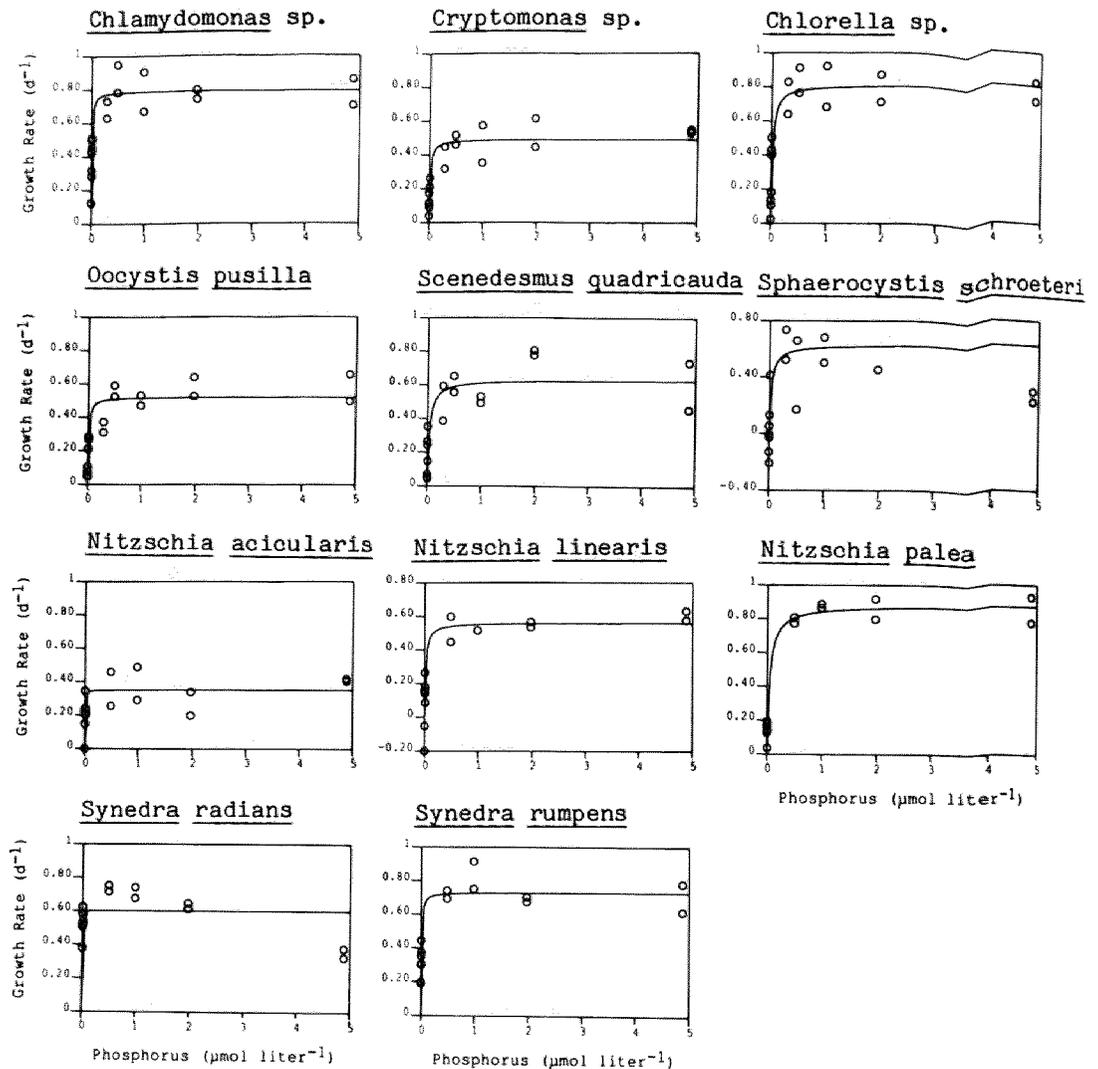


Fig. 1. Phosphorus-dependent algal growth kinetics. Curves were fitted by nonlinear regression (Table 1).

($F_{10,163} = 2.96$, $P = 0.002$) or after ($F_{10,154} = 3.41$, $P < 0.001$) individual values of μ_{\max} had been entered. There was a negative but nonsignificant relationship between μ_{\max} and the ln of cell volume ($r = -0.52$, $P = 0.084$), and a negative but nonsignificant relationship between the ln of μ_{\max} and the ln of cell volume ($r = 0.50$, $P = 0.12$). From the pre-conditioning cultures, Q_{\min} was calculated for 14 species (Table 2). The ln of Q_{\min} was significantly correlated with both the ln of cell volume ($r = 0.79$, $P < 0.001$) and the ln of cell surface area ($r = 0.71$, $P < 0.005$). There were positive but nonsignificant relationships between the ln of volume-spe-

cific Q_{\min} and three quantities: the ln of K_{μ} ($r = 0.57$, $P = 0.066$), the ln of R^* ($r = 0.51$, $P = 0.090$), and the ln of μ_{\max}/K_{μ} ($r = 0.55$, $P = 0.077$).

Discussion

The estimates of μ_{\max} are more reliable than those of K_{μ} , which may be substantially underestimated for many species. This situation probably results from difficulties inherent in measuring algal growth kinetics. For many species and most nutrients, K_{μ} is of low magnitude compared to nutrient concentrations that can reliably be prepared and measured. For some species, K_{μ} is so low

Table 1. Results of nonlinear regressions fitting the Monod model to phosphorus-dependent growth kinetics.

	μ_{max}			K_{μ}			<i>n</i>	SSE
	Estimate (d ⁻¹)	95% C.L.		Estimate ($\mu\text{mol liter}^{-1}$)	95% C.L.			
		Lower	Upper		Lower	Upper		
<i>Chlamydomonas</i> sp.	0.79	0.61	0.96	0.0071	0.00097	0.038	17	0.550
<i>Chlorella</i> sp.	0.81	0.62	1.05	0.022	0.0047	0.23	17	0.588
<i>Cryptomonas</i> sp.	0.49	0.39	0.58	0.014	0.0043	0.096	17	0.122
<i>Oocystis pusilla</i>	0.52	0.43	0.61	0.012	0.0037	0.067	17	0.132
<i>Scenedesmus quadricauda</i>	0.63	0.47	0.93	0.035	0.0043	0.50	17	0.374
<i>Sphaerocystis Schroeteri</i>	0.48	0.28	0.71	0.025	0.0011	0.34	16	0.589
<i>Nitzschia acicularis</i>	0.35	0.24	0.46	0.0023	0	0.019	15	0.171
<i>Nitzschia linearis</i>	0.56	0.45	0.68	0.019	0.0051	0.22	14	0.122
<i>Nitzschia palea</i>	0.88	0.77	1.03	0.047	0.016	0.22	15	0.128
<i>Synedra radians</i>	0.60	0.39	0.85	0.00014	0	0.012	15	0.862
<i>Synedra rumpens</i>	0.73	0.59	0.88	0.0069	0.0014	0.026	15	0.263

that measurable algal growth occurs even when a nutrient is present only as a contaminant (i.e. in a medium without added nutrient). Because of these problems, most measurements of K_{μ} have wide confidence intervals, and most fits of the Monod model to algal growth kinetics have considerable residual variance. Alternatively, the Monod model may be inappropriate for growth kinetics of algae. The steady state derivation of the Monod model from the variable-internal stores model (Droop 1973; Burmaster 1979) requires that the relationship between cell quota and nutrient uptake be linear (Morel 1987). If the relation between uptake and cell quota is nonlinear (McCarthy 1981), then the steady state relation between dissolved nutrient and algal growth

will not be an exact Monod function. Because it would be difficult to distinguish between alternative models on the basis of measured algal growth kinetics alone, alternatives should be posed on the basis of physiological mechanisms.

Synedra radians has a K_{μ} at least five times lower than that of other species. Significant interspecific differences in K_{μ} may have resulted entirely from the inclusion of *S. radians*, for which the regression model is poor. When *S. radians* is deleted from the analysis, interspecific differences in K_{μ} become marginal, both before ($F_{9,149} = 1.811$, $P = 0.070$) and after ($F_{9,140} = 1.788$, $P = 0.075$) individual values of μ_{max} are entered for each species in the regression model. To insist on the use of $\alpha = 0.05$ risks making

Table 2. Minimal cell quotas (Q_{min}) and indices of competitive ability for phosphorus based on the fitted parameters of the Monod growth model. R^* (Eq. 2) is calculated at a hypothetical mortality rate of 0.25 d⁻¹.

	Q_{min} (fmol cell ⁻¹)	Volume-specific Q_{min} (fmol μm^{-3})	Indices of competitive ability for P	
			R^* ($\mu\text{mol liter}^{-1}$)	μ_{max}/K_{μ} (liter μmol^{-1} d ⁻¹)
<i>Chlamydomonas</i> sp.	3.5	0.078	0.0033	111
<i>Chlorella</i> sp.	0.26	0.043	0.010	36
<i>Cryptomonas</i> sp.	12.0	0.015	0.014	34
<i>Oscillatoria</i> sp.	0.39	0.021		
<i>Oocystis pusilla</i>	8.0	0.082	0.011	44
<i>Scenedesmus quadricauda</i>	4.0	0.043	0.023	18
<i>Sphaerocystis Schroeteri</i>	3.7	0.017	0.027	19
<i>Fragilaria capucina</i>	12.0	0.014		
<i>Mallomonas</i> sp.	8.6	0.014		
<i>Nitzschia acicularis</i>	3.1	0.0086	0.0059	148
<i>Nitzschia linearis</i>	49.0	0.056	0.015	29
<i>Nitzschia palea</i>	3.9	0.018	0.019	19
<i>Synedra radians</i>	1.7	0.0046	0.000096	4,440
<i>Synedra rumpens</i>	1.8	0.0051	0.0036	108

a type 2 error, i.e. failing to conclude that interspecific differences in K_{μ} exist when in fact they do. As discussed below, the values of K_{μ} and the resulting values of R^* are largely consistent with results of an algal competition experiment, suggesting that the interspecific differences in K_{μ} are real.

In the competition experiment from which these species were isolated (Grover 1989), a ranking of competitive ability for P was suggested with *Nitzschia acicularis* and *S. radians* being best, followed by *Synedra rumpens*, then *Nitzschia linearis*, and with *Nitzschia palea* and all nonsiliceous algae being worst. Growth kinetics are largely consistent with this ranking. On the basis of R^* (Table 2), *S. radians* and *S. rumpens* are better competitors for P than *N. acicularis*, but these three species are collectively superior to most other algae. *Nitzschia linearis* is a poorer competitor for P than *N. acicularis* but a better one than *N. palea*, as expected. The nonsiliceous algae are relatively poor competitors for P, although some of them are apparently about as good as *N. linearis*. Most surprising is the good competitive ability of *Chlamydomonas* sp. for P. This finding is inconsistent with the results of the competition experiment from which this clone was isolated, with other competition experiments in which green algae were present (Sommer 1983, 1985; Tilman and Kiesling 1984; Kilham 1986; Tilman et al. 1986), and with published kinetics of P-dependent growth for other green algae (Senft et al. 1981; Kilham 1986).

Algal competition experiments suggest that some *Synedra* spp.—*acus* (Smith and Kalff 1983; Sommer 1983, 1985), *filiformis* (Tilman 1981; Kilham 1986; Tilman et al. 1986), and *radians* (Grover 1989)—are good competitors for P. The high ability of *S. filiformis* to compete for P results primarily from its low K_{μ} ($0.003 \mu\text{mol liter}^{-1}$, Tilman 1981), and the clone of *S. radians* in this study has an even lower K_{μ} . Carney et al. (1988) reported a clone of *S. radians* with a K_{μ} of $0.024 \mu\text{mol liter}^{-1}$, however, making it a poor competitor for P. There may be greater variability of growth kinetics within the genus *Synedra* than is currently indicated by laboratory studies of competition. Benndorf (1973) reported kinetics of P-de-

pendent growth for *N. acicularis*: values of μ_{max} (1.3 d^{-1}) and K_{μ} ($0.48 \mu\text{mol liter}^{-1}$) exceed those reported here and are inconsistent with the proposition that *N. acicularis* is a good competitor for P (Sommer 1985; Grover 1989).

Theory (Hsu 1980; Butler et al. 1985) and experiment (Sommer 1985) suggest that the competitive ability of species with a high μ_{max} is enhanced when nutrient supply varies in time. In the competition experiment from which these species were isolated (Grover 1989), *N. acicularis*, *Oocystis pusilla*, and *S. schroeteri* showed enhanced competitive ability in cultures that had higher variability in P supply, but these species have relatively low μ_{max} . Although *N. palea* has a high μ_{max} , its competitive ability was unaffected by variability in P supply. *Chlamydomonas* sp., with a high μ_{max} , showed decreased competitive ability in cultures that had higher variability in P supply. These results provide no support for the hypothesis that a high μ_{max} enhances competitive ability under nonequilibrium conditions. Grazing may have confounded some responses to variability in P supply, however, in the competition study (Grover 1989).

Q_{min} and cell volume were related in the form

$$Q_{\text{min}} = aV^b$$

where V is cell volume. Shuter (1978) found such a correlation for a variety of microorganisms. Given the uncertainties involved, the value of a found here (0.0907) agrees well with Shuter's estimates for all microorganisms (0.124) and for eucaryotes alone (0.0590). The value of b found here (0.714) agrees better with Shuter's estimate for eucaryotes alone (0.690) than for all microorganisms (0.554). Negative correlations between μ_{max} and cell volume have been reported (Williams 1964; Eppley and Sloan 1966; Sommer 1981), but the relation found in this study was marginal ($0.10 > P > 0.05$). Banse (1982) concluded that the dependence of μ_{max} on cell volume is weak at best, especially among diatoms, which were heavily represented in this study. No significant correlations of K_{μ} or indices of competitive ability with cell volume, surface

area, or surface: volume ratio were found. This finding suggests that the competitive ability of algae is poorly predicted by cell size (Sommer and Kilham 1985). The correlation between volume-specific Q_{\min} and K_{μ} , although not statistically significant, suggests that a low K_{μ} , and therefore increased competitive ability, may result from highly efficient use of limiting nutrients in biomass.

Both R^* and μ_{\max}/K_{μ} gave similar information concerning competitive ability, and they were highly correlated ($r = -0.99$, $P < 0.0001$, after \ln transformation). When algal loss rates are known, R^* is the preferred index of competitive ability because it properly emphasizes the important effect that these rates have on competitive ability (Kalf and Knoechel 1978; Tilman et al. 1982). This study and its companion (Grover 1989) provide considerable support for the use of resource competition theory in studies of algal community structure. In these laboratory experiments, estimates of R^* provided qualitatively accurate predictions of competitive performance, despite the nonequilibrium nature of competitive dynamics, grazing, and methodological difficulties in estimating R^* . Recent experiments show a correspondence between estimates of R^* and the distributions of field populations of algae (Sommer 1986; Carney et al. 1988); thus it may be hoped that resource competition theory will prove useful in understanding natural algal communities.

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