

## COMMENT

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### Phytoplankton natural community competition experiments: A reinterpretation

Smith and Kalff (1982, 1983) recently published two articles on phosphorus competition among freshwater phytoplankton whose main conclusions were that among competing phytoplankton there is no partitioning of the gradient of phosphorus availability and that competition for phosphorus occurs to the advantage of small algae. We acknowledge the value of the experiments presented in those papers, but feel that the conclusions are not fully supported by their own data or by recently published observations based on similar experimental techniques (Tilman et al. 1982; Sommer 1983; Tilman et al. in prep.).

Using natural community competition experiments, Smith and Kalff (1983) concluded that there was no partitioning of a gradient of phosphorus availability among competing phytoplankton species. They derived this conclusion from the fact that in parallel chemostat competition experiments at different dilution rates the same alga, *Synedra acus*, usually was the most successful competitor. Partitioning (sensu Smith and Kalff 1983) means that one species is a better competitor at high supply rates of a resource and another species at low supply rates. We feel that their experiments actually demonstrate three different possibilities. We have abstracted data from their tables 1, 2, and 3 into a single table (Table 1) containing information only on the species that coexisted at the ends of the experiments.

Table 1A shows the results for their experiment 4. *Synedra acus* dominated in all cases over the range of dilution rates from 0.21 to 0.93 d<sup>-1</sup>. This would be the expected result if phosphorus were the only potentially limiting nutrient and if *S. acus* were the superior competitor for phosphorus. This means that *S. acus* can sequester

enough phosphorus (through a combination of processes, including uptake and storage) to maintain growth rate equal to dilution rate and can reduce the phosphorus concentration to a level below that needed by other species to maintain their growth rates equal to the dilution rate. Those are the conditions necessary for competitive exclusion with no resource partitioning, and Table 1A seems to represent just such a set of cases. *Synedra* has also been reported to be the most successful genus in phosphorus competition by Tilman (1981: *Synedra filiformis*), Sommer (1983: *S. acus*), and Kilham (1984: *Synedra* sp.).

The results reported for Smith and Kalff's (1983) experiment 2 (Table 1B) showed that at least one other species, *Dinobryon bavaricum*, coexisted at steady state with *S. acus* over a range of dilution rates from 0.055 to 0.43 d<sup>-1</sup>. This would be the expected result only if each species were limited by a different resource (Petersen 1975; Taylor and Williams 1975; Tilman 1977, 1981, 1982; Holm and Armstrong 1981; Tilman et al. 1982; Sommer 1983). Unfortunately, a chemical analysis of the experimental medium (filtered water from Lake Memphremagog) was not given in the paper, only a rough estimate of the P:N:Si ratios for data published elsewhere. Cattaneo and Kalff (1980) gave silicate analyses only from a shallow macrophyte bed in a bay of the lake (2.2-3.1 mg SiO<sub>2</sub> liter<sup>-1</sup>). It seems very likely to us that the Si concentration of the open water of the lake may be less than this, and such low levels are within the range of potential Si limitation of *Synedra* species (Tilman 1981; Tilman et al. 1981; Kilham 1984). At the very low dilution rates (0.055 and 0.06 d<sup>-1</sup>), a very large *Synedra ulna* also coexisted with *S. acus* and *D. bavaricum*. This coexistence looked fairly stable (fig. 2,

Table 1. Data abstracted from Smith and Kalff (1983) tables 1, 2, and 3. The species that maintained growth rates equal to dilution rates are shown, along with their volume ( $\mu\text{m}^3$ ).

Exp.	Table	Species	Volume	Growth rate at dilution rate					
A.				0.22	0.21	0.32	0.34	0.76	0.93
4	2	<i>Synedra acus</i>	163	0.22	0.21	0.32	0.34	0.76	0.93
B.				0.055	0.06	0.22	0.30	0.43	
2	3	<i>Synedra acus</i>	158	0.055	0.06	0.22	0.30	0.43	
2	3	<i>Synedra ulna</i>	5,100	0.055	0.06				
2	3	<i>Dinobryon bavaricum</i>	60	0.055	0.06	0.22	0.30	0.43	
2	3	<i>Rhizosolenia eriensis</i> (S)	108				0.30		
2	3	<i>Stephanodiscus hantzschii</i>	150	0.055					
2	3	<i>Diatoma tenue elongatum</i>	960		0.07				
C.				0.06	0.06	0.20	0.30	0.43	
3	1	<i>Synedra acus</i>	69	0.06	0.06	0.20	0.30	0.43	
3	1	<i>Dinobryon bavaricum</i>	80	0.06	0.06				
3	1	<i>Monoraphidium setiforme</i>	36				0.30	0.43	
3	1	<i>Oscillatoria limnetica</i>	275			0.20	0.30		

$D = 0.06 \text{ d}^{-1}$ : Smith and Kalff 1983) and could be explained by *S. ulna* having similar requirements to *S. acus* at these low dilution rates, as in the case for *Asterionella formosa* and *Fragilaria crotonensis* reported by Tilman (1981). The coexistences of *Rhizosolenia eriensis* (S) at  $0.30 \text{ d}^{-1}$ , *Stephanodiscus hantzschii* at  $0.055 \text{ d}^{-1}$ , and *Diatoma tenue v. elongatum* at  $0.07 \text{ d}^{-1}$  are not indicated in their fig. 2 nor are they mentioned in the text, so it is possible that they are misprints in their original table 3.

The pattern of dominance and coexistence of species in Smith and Kalff's (1983) experiment 3 (Table 1C) is consistent with a hypothesis of phosphorus partitioning along a dilution rate gradient. If *S. acus* is silicate-limited (for the reasons proposed earlier), then it looks as if *D. bavaricum* is the best phosphorus competitor at low dilution rates ( $0.06 \text{ d}^{-1}$ ), *Oscillatoria limnetica* at intermediate dilution rates ( $0.20$  and  $0.30 \text{ d}^{-1}$ ), and *Monoraphidium setiforme* at high dilution rates ( $0.30$  and  $0.43 \text{ d}^{-1}$ ). Unfortunately, the relative proportions of the coexisting species were not illustrated for this experiment, but from the data presented we cannot eliminate the possibility of phosphorus partitioning. The rank order *Dinobryon*–*Oscillatoria*–*Monoraphidium* is by no means a surprise and lies within the experience of species replacements in the course of increasing phosphorus supply rates

during lake eutrophication (Hornström 1981; Rosen 1981).

According to Smith and Kalff, the absence of partitioning of the P gradient is a consequence of the size dependence of growth rate and nutrient kinetics. We agree that there is a general trend of decreasing maximum growth rates with increasing cell sizes where algae vary in size over at least three orders of magnitude (Banse 1976; Sommer 1981, 1983). Flagellates appear to be an exception to this trend. Their population growth rates are independent of cell size over several orders of magnitude, and medium and large size flagellates have much higher growth rates than coccoid species of comparable size (Sommer 1981, 1983; Tilzer 1972).

Smith and Kalff (1982) found no significant differences in the half-saturation constant for uptake ( $k_m$ ) among eight species investigated. However, saturated uptake rates ( $V_{\text{max}}$ ) on a per cell basis increased with cell size. As a consequence, the initial slope of the uptake curve ( $V_{\text{max}}/k_m$ ) was also positively correlated to cell size. But in the range of cell sizes from  $50$  to  $1,000 \mu\text{m}^3$  (the range of the coexisting species in the competition experiments; Table 1) there was no relationship between the initial slope and the cell volume (fig. 3: Smith and Kalff 1982). Cell quota ( $Q$ ) on a per cell basis also increased with cell size. They found a positive

relationship between  $V_{\max}$  and  $Q$  for their data and compared this relationship to published values for freshwater algae. However, the positive relationship of the literature values depended totally on a single datum, the point for *Euglena gracilis* (the cited source for the  $V_{\max}$  value did not contain the uptake data for *E. gracilis*; Chisholm et al. 1975). Without that point, there is no relationship between  $V_{\max}$  and  $Q$  from the literature data from freshwater, and the initial relationship of slope vs.  $Q$  is also not significant. On a per cell volume basis,  $V_{\max}$ , the initial slope, and  $Q$  all decrease with increasing cell size.

Smith and Kalff (1982, 1983) argued that taxonomic effects on these relationships are probably not important. However, they used uptake data for only diatoms and blue-green algae in generating their conclusions. In their 1983 paper the important species in the case where resource partitioning could not be ruled out were a green alga (*Monoraphidium*) and a chrysophyte (*Dinobryon*), neither of which were included in the uptake experiments. We feel that this is rather a weak basis for their conclusion that size effects exceed the importance of taxonomic differences. Also, we think it is not appropriate to use colony volume for the estimate of cell size for filamentous algae such as *Fragilaria crotonensis*, *Anabaena planctonica*, *Aphanizomenon flos-aquae* (unless it occurs in bundles), and *Oscillatoria tenuis*. The equivalent spherical volume has a much lower surface area available for uptake than does a filament of equal volume. It was only these colonial forms which imparted significance to the uptake and growth relationships with cell size, so it is circular reasoning to then say that "they fall on the same continuum of uptake and growth rates" as unicells (Smith and Kalff 1983, p. 460).

Smith and Kalff (1983) concluded that at all levels of phosphorus availability competition favors small algae. Thus the rank order of size must be equivalent with the rank order of competitive ability for phosphorus. This argument is open to criticism from several sides. First, every planktologist knows of the existence of small coccoid algae of 1–3- $\mu\text{m}$  diameter, commonly called  $\mu$ algae. They may be greens (cf. *Chlorella*)

or blue-greens (cf. *Synechococcus*) and are found in nearly every lake. Their absence in Lake Memphremagog would be a great surprise. Why did they fail to become dominant in the mixed culture experiments? Second, whenever natural phytoplankton communities have been subjected to strong phosphorus limitation, diatoms become the dominant species, usually *Synedra* species (Smith and Kalff 1983; Sommer 1983; Tilman et al. in prep.). Using Monod growth parameters, Tilman et al. (1982) have shown that the smallest diatoms studied to date (*Stephanodiscus minutus* and *Cyclotella meneghiniana*) are very inferior to larger araphid species (*Synedra filiformis*, *A. formosa*, and *F. crotonensis*) in phosphorus competitive ability. Kilham (1984) has confirmed this for the two-species interaction of *Synedra* sp. and *S. minutus*, and Tilman (1977) demonstrated it for *A. formosa* and *C. meneghiniana*. Also, there is evidence for a tradeoff in competitive ability for silicon and phosphorus for these species (Tilman et al. 1982), so it would not be possible to use a size-based kinetic argument for both silicon and phosphorus.

The experiments of Sommer (1983) support both previous arguments. He performed a series of multispecies experiments in chemostats which differed from the experiments of Smith and Kalff (1983) in one respect: the inoculum was mixed 1:1 with nutrient solution at the start of the experiment in order to enable unlimited growth of algae during the initial phase. Thus, starting concentrations of  $\text{PO}_4^{3-}\text{-P}$  were between 60 and 75  $\mu\text{g liter}^{-1}$ . It took several days until P was depleted in the supernatant and until the equilibrium biomass was reached (usually somewhat later). During this initial phase most algae achieved growth rates close to  $\mu_{\max}$  values reported in the literature. For coccoid algae there was the expected inverse relationship between size and  $\mu_{\max}$ , but, remarkably, the large colonial flagellate *Pandorina* achieved a  $\mu_{\max}$  nearly identical with the smaller *Scenedesmus opoliensis* (*Pandorina*: 18,000  $\mu\text{m}^3$ ,  $\mu_{\max}$  1.64  $\text{d}^{-1}$ ; *Scenedesmus*: 500  $\mu\text{m}^3$ ,  $\mu_{\max}$  1.68  $\text{d}^{-1}$ ). If it were true, as Smith and Kalff assert, that  $k_m$  varies only insignificantly among co-occurring phytoplankton, it should have been expect-

ed that the algae with the highest growth rates during the initial phase also would have been the final winners of competition under limited conditions (dilution rate =  $0.3 \text{ d}^{-1}$ ; Si:P ratio variable). In that case it should have been *Chlorella* sp. ( $4 \mu\text{m}^3$ ,  $\mu_{\text{max}} 2.19 \text{ d}^{-1}$ ). This was clearly not the case. All the small chlorococcalean algae, all small centric diatoms, and all green flagellates that had been the most successful algae during the initial phase were excluded from the final equilibrium phase of the experiments. Among the final winners of competition (controlled by the Si:P ratio) were three algae of medium size with medium  $\mu_{\text{max}}$  values (*S. acus*:  $1,400 \mu\text{m}^3$ ,  $\mu_{\text{max}} 1.11 \text{ d}^{-1}$ ; *A. formosa*:  $700 \mu\text{m}^3$ ,  $\mu_{\text{max}} 1.34 \text{ d}^{-1}$ ; *Mougeotia thylespora*:  $2,000 \mu\text{m}^3$ ,  $\mu_{\text{max}} 1.22 \text{ d}^{-1}$ ) and only one nanoplanktonic alga with a high maximum growth rate, *Koliella spiculiformis* ( $30 \mu\text{m}^3$ ,  $\mu_{\text{max}} 2.02 \text{ d}^{-1}$ ). Under Si-sufficient conditions, *Synedra* was always the most successful competitor.

This experimental design was later modified by discontinuous addition of phosphorus (Sommer 1984). Phosphorus was added in discrete, weekly pulses, thus offering the algae a short period of nonlimiting ambient concentrations, resulting in a repeated, weekly gradient of phosphorus availability. If there is a specialization between algae requiring high phosphorus levels and algae superior at low levels of phosphorus this should lead to a periodic shift in selective advantage, reducing competitive exclusion and permitting the coexistence of more species than in classical steady state experiments (Stewart and Levin 1973; Tilman et al. 1982). As expected, some of the small Chlorococcales and *Pandorina morum*, that had been outcompeted in the previous steady state experiments, could maintain themselves in an oscillating environment.

The three points addressed by Smith and Kalf (1983) seem to us to have different answers from those presented. 1. Competition for phosphorus favors small cells over a range of competitive intensities. If this were the case, then  $\mu$ algae would dominate under P-limiting conditions. They did not do so in Smith and Kalf's experiments nor did they in other natural community ex-

periments (Sommer 1983; Tilman et al. in prep.). 2. The variable internal stores model is applicable to competition in communities of phytoplankton. We view this as an unnecessary complication when considering steady state experiments. The Monod growth parameters, which incorporate the processes involved in turning external substrates into growth (Kilham 1978), are proven predictors of the outcome of competitive interactions for phytoplankton (Tilman et al. 1982) under steady state conditions. There is as yet insufficient evidence to support a relationship between size and the Monod half-saturation constants for growth or  $R^*$  values. 3. Co-occurring freshwater phytoplankton species do not partition gradients in the availability of limiting phosphorus. In fact, Smith and Kalf's experiments showed three results: in one case *Synedra* (not the smallest species) outcompeted all other species for phosphorus over a range of dilution rates; in another case, *Synedra* (probably Si-limited) coexisted with *Dinobryon* (the next best phosphorus competitor) over a range of dilution rates; and in another case it was not possible to eliminate the possibility that three species did partition phosphorus over a range of dilution rates (with *Synedra* probably Si-limited). It seems obvious from the available information that Chlorococcales, Volvocales, and some small centric diatoms have high maximum growth rates but low competitive abilities for phosphorus. On the other hand, araphid diatoms and chrysophytes are successful competitors at low phosphorus levels. Generalizations about cryptophytes are difficult because they have been handicapped by mechanical stress in experimental designs to date. Thus we feel that taxonomic considerations are important in determining competitive abilities and may override the effects of size on kinetic parameters.

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## Phosphorus competition among phytoplankton: A reply

In two recent articles (Smith and Kalff 1982, 1983) we concluded that observed growth and phosphorus uptake kinetics failed to provide evidence that co-occurring phytoplankton species could partition gradients in the intensity of phosphorus limitation under conditions of uniform and

nearly steady state limitation. We also reported that both phosphorus uptake and realized growth were to the advantage of smaller-sized species. Sommer and Kilham (1985) argue that we were mistaken on both counts, citing both selected aspects of our data and their own, largely new, data. While