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## TEMPERATURE EFFECTS ON SILICON LIMITED GROWTH OF THE LAKE MICHIGAN DIATOM *STEPHANODISCUS MINUTUS* (BACILLARIOPHYCEAE)<sup>1</sup>

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### ABSTRACT

The effect of temperature on the silicon limited growth and nutrient kinetics of *Stephanodiscus minutus* Grun. was examined using batch and semicontinuous culture methods. Short-term batch culture methods gave maximum growth rates which were essentially constant over the temperature range of 10° to 20° C ( $\mu_m = 0.71-0.80$  d<sup>-1</sup>). The half-saturation constant for growth ( $K_s$ ) was significantly lowest at 10° C ( $K_s = 0.51$   $\mu$ M Si; 0.22-0.41), and higher at both 15° C ( $K_s = 1.03$   $\mu$ M Si; 0.68-1.47) and 20° C ( $K_s = 0.88$   $\mu$ M Si; 0.60-1.22). Two methods were used to evaluate the semicontinuous experiments. The Droop relationship showed that the minimum cell quota was about  $1.50 \times 10^{-7}$   $\mu$ mol Si cell<sup>-1</sup>, but there was much overlap in the results at all three temperatures. The Monod growth relationship for the semicontinuous experiments gave estimates of  $K_s$  which were lowest at 15° C ( $K_s = 0.12$   $\mu$ M Si), and higher at 10° C ( $K_s = 0.68$   $\mu$ M Si) and 20° C ( $K_s = 1.24$   $\mu$ M Si), although 95% confidence intervals overlapped. The maximum growth rate estimates for the semicontinuous experiments were similar at 10° and 15°, and higher at 20° C, but the number of points used in making the calculations makes the results less reliable

than those from batch cultures. Generally, there were no consistent significant differences in the silicon limited growth of *S. minutus* over the temperature range studied. Our values of  $K_s$  for *S. minutus* are the lowest recorded for a freshwater diatom, and are consistent with the distribution of this species in nature. Generally, this species becomes abundant in areas with high phosphorus loading and very low silicon levels (low Si:P loading rates). *Stephanodiscus* species are also fossil indicators of eutrophication in north temperate lakes.

*Key index words:* diatoms; nutrient kinetics; nutrient limitation; silicon; *Stephanodiscus*; temperature

The effect of temperature on nutrient utilization by freshwater algae has received little attention. The purpose of this study was to investigate the effect of temperature on the silicon limited growth and nutrient kinetics of *Stephanodiscus minutus* Grun. [= *S. astraea* var. *minutula* (Kutz.) Grun.]. This planktonic diatom is widely distributed in both nearshore and offshore regions of Lake Michigan (Stoermer and Yang 1969) and appears to be favored by nutrient enrichment and low temperature (Bradbury and Megard 1972, Stoermer and Ladewski 1976,

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TABLE 1. Half-saturation constants,  $K_s$ , of various marine and freshwater algal species at different temperatures.

Species	Limiting nutrient	Experiment	°C	$K_s$ , $\mu\text{M}$	Reference
<i>Skeletonema costatum</i>	Nitrate	Uptake	8	0.0	Eppley et al. 1969
			18	0.5	
			28	1.0	
<i>Dunaliella</i> sp.	Nitrate	Batch growth	15	0.28	Thomas & Dodson 1974
			25	0.95	
<i>Gymnodinium splendens</i>	Nitrate	Batch growth	18	1.02	Thomas & Dodson 1974
			25	6.55	
<i>Thalassiosira nordenskiöldii</i>	Silicate	Batch growth	3	0.09	Paasche 1975
			10	0.02	
<i>Oscillatoria agardhii</i>	Phosphate	Chemostat growth	15-16	0.032	Ahlgren 1978
			20-21	0.006	
			25-26	0.035	
<i>Asterionella formosa</i>	Silicate	Batch growth	4	2.0	Tilman et al. 1981
			8	1.9	
			12.5	2.1	
			20	4.0	
			24	11.0	
<i>Synedra ulna</i>	Silicate	Batch growth	8	5.7	Tilman et al. 1981
			12.5	4.5	
			20	6.11	
			24	4.9	

Stoermer and Yang 1970). Increased phosphorus loading has created a silicon demand by diatoms (Kilham 1971, Schelske and Stoermer 1971). In areas of the lake with increased phosphorus loading, the most common diatoms should be those best able to compete for silicon. Our hypothesis is that *S. minutus* is a superior competitor for silicon and that this ability is relatively more important to the distribution of this species than is temperature.

It is clear that resources are important in species interactions in freshwater phytoplankton communities (Kilham and Tilman 1979, Kilham and Kilham 1982). Many models developed to describe phytoplankton population dynamics have assumed that the rate of growth of each species of phytoplankton is determined primarily by the availability of nutrients (Dugdale 1967, O'Brien 1974, Paasche 1973, Petersen 1975, Tilman 1977, 1980). The use of these models has up to now allowed no consideration of the interdependency of environmental factors which affect nutrient uptake and growth of phytoplankton. One of the most obvious factors which may affect nutrient kinetics in temperate lakes is temperature.

The effect of temperature on the nutrient kinetics of selected species of marine and freshwater algae has been examined by several workers (Table 1). Half-saturation constants have been shown to increase with increasing temperatures (Eppley et al. 1969, Thomas and Dodson 1974), to decrease with increasing temperature (Paasche 1975), to have a U-shaped response along a temperature gradient (Ahlgren 1978), and to be independent of temperature (Tilman et al. 1981).

Within defined limits, maximum division rates of

phytoplankton increase with increasing temperature (Eppley 1972, Goldman and Carpenter 1974). The effect temperature has on nutrient utilization will have a large influence on the chemical composition of algal species (Goldman and Ryther 1976, Goldman 1977, Rhee 1980, Rhee and Gotham 1981). Two different experimental and theoretical approaches have been used to evaluate the relationship between external nutrient concentration and growth, the Monod (1950) model, and the variable internal stores (Droop 1974) model (see Kilham 1978 or Rhee 1980 for discussion of these models).

The present paper reports the silicon limited growth and nutrient kinetic information of *S. minutus* at temperatures of 10°, 15° and 20° C. Data generated by short-term batch culture growth experiments were applied to the Monod model, and data generated by semicontinuous culture experiments were applied to the variable internal stores model and the Monod model.

#### METHODS

Using a sterile pipet technique (Guillard 1973a) a single clone of *Stephanodisus minutus* (LM STEPH S-1 JM), was isolated by J. Mechling in October 1977 from a nearshore water sample taken in southern Lake Michigan near the Donald C. Cook Power Plant. A freshwater medium (WC; Guillard 1975) with added boron and with no addition of ammonia or buffers, was used for all cultures. Maintenance cultures were grown in a culture box at 20° C and 55  $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  illumination provided by cool-white fluorescent bulbs on a 14:10 h LD cycle. Experiments were performed in culture boxes at 10°, 15° and 20° C, and 100  $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  illumination on a 14:10 h LD cycle.

Populations were counted with a Sedgwick-Rafter chamber using the calibrated Whipple-disk method (Guillard 1973b). Samples were preserved with Lugol's acetate solution immediately after being taken.

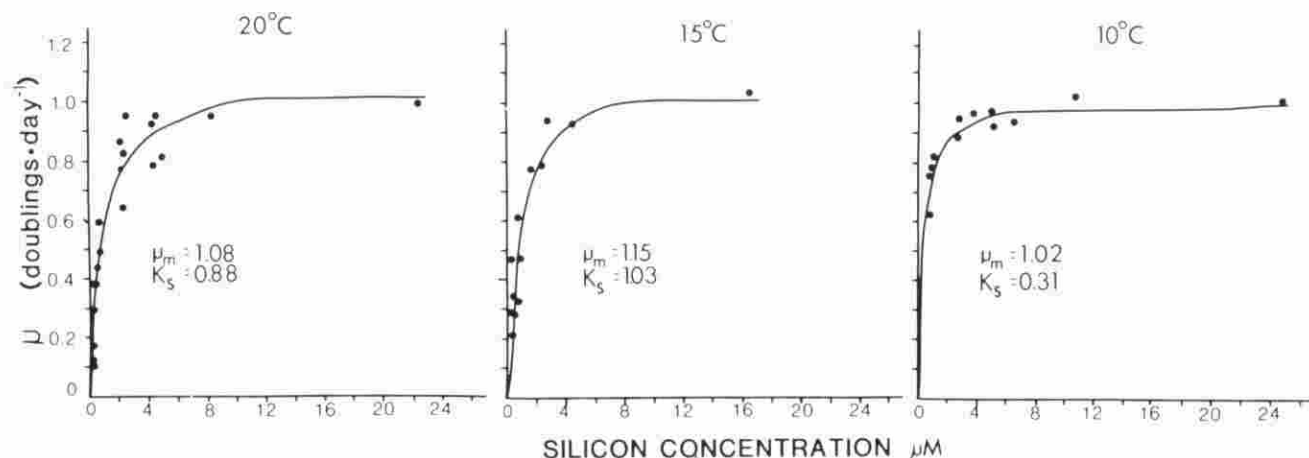


FIG. 1. Growth rates of *Stephanodiscus minutus* as a function of silicon concentrations at three temperatures in short-term batch cultures (line is the fitted Monod curve).

Silicon was measured with a modified silicomolybdate method (Strickland and Parsons 1972) with all samples filtered through 0.45  $\mu\text{m}$  filters presoaked in distilled water. The sample size was reduced to 10 mL and readings were made using a 50 mm path length cuvette in a Bausch and Lomb Spectronic 100, which allows accurate silicon determinations to ca. 0.01  $\mu\text{M}$  Si. Calibration standards used were 1  $\mu\text{M}$  and 10  $\mu\text{M}$  sodium silicofluoride solutions.

A Fortran IV program (Bliss and James 1966) obtained from the Yale University Computing Center was used to calculate the half-saturation constants and maximal rates of growth. The kinetic constants were determined by an iterative nonlinear regression of the Michaelis-Menten equation (Hanson et al. 1967).

**Batch culture growth experiments.** Short-term batch culture growth experiments were used to evaluate the relationship between external nutrient concentration and growth rate of *S. minutus*. To condition the diatoms prior to each experiment, exponentially growing diatom cultures were inoculated into flasks containing sterile WC medium with ca. 5  $\mu\text{M}$  Si and allowed to grow at the experimental temperature for about five days, until

the ambient silicon concentration was less than 0.5  $\mu\text{M}$  Si. Polycarbonate 250 mL flasks containing 150 mL of WC medium minus silicon were used for the silicon limited batch growth experiments. A stock solution of  $\text{Na}_2\text{Si}_3\cdot 9\text{H}_2\text{O}$  containing 0.5 mM Si was used for adding various amounts of silicon to each experimental flask, with initial concentrations of ca. 0.2 to 45.0  $\mu\text{M}$  Si. The flasks were then autoclaved. Cells from the preconditioned cultures were inoculated into each flask to an initial density of ca. 100 cells  $\text{mL}^{-1}$ . Each experiment was continued for 5 days. Samples for counting were taken daily at the same time during the light cycle. Silicon measurements were made at the beginning and end of each experiment. Calculations were made according to Kilham (1978).

**Semicontinuous culture experiments.** Semicontinuous culture experiments were used to evaluate the relationship between internal cell quota of a nutrient and the approximate steady state growth rate. For each experiment, six polycarbonate 250 mL flasks of sterile medium were inoculated with exponentially growing diatom cultures so there were ca. 2000 cells  $\text{mL}^{-1}$ . The influent silicon concentrations were 11.3  $\mu\text{M}$  Si at 10° and 15° C, and 12.3  $\mu\text{M}$  Si at 20° C, with 50  $\mu\text{M}$  phosphate in all cases. Each flask was run at a different dilution rate, from 0.1 to 0.6  $\text{d}^{-1}$ . Dilution was done manually once a day by removing a portion of the well mixed culture suspension and replacing it with an equal volume of sterile medium from the influent reservoir. Dilution rates were expressed as the volume removed per day relative to the total culture volume. Cell counts and nutrient analyses were performed periodically. Experiments were ended after steady state nutrient concentrations and cell numbers had been observed for a week, usually after ca. 20 days. Calculations of cell quota (Q) were made using the following relation: (influent nutrient concentration minus reactor nutrient concentration/number of cells at steady state). The calculations were made following Kilham (1978).

TABLE 2. Physiological constants for *Stephanodiscus minutus* under silicon limitation. The 95% confidence intervals are in parentheses.

Batch growth temperature °C	$K_s$ ( $\mu\text{M}$ )	$\mu_m$ (doublings $\cdot \text{d}^{-1}$ )	$\mu_m$ ( $\text{d}^{-1}$ )	$\mu_m/K_s$
10	0.31 (0.22–0.41)	1.02 (0.98–1.07)	0.71	2.29
15	1.03 (0.68–1.47)	1.15 (0.99–1.31)	0.80	0.78
20	0.88 (0.60–1.22)	1.08 (0.97–1.19)	0.75	0.85

Semicontinuous culture temperature °C	$k_d$ ( $\mu\text{mol cell}^{-1}$ )	$D_m$ ( $\text{d}^{-1}$ )	$K_s$ ( $\mu\text{M}$ )	$\mu_m$ ( $\text{d}^{-1}$ )	$\mu_m/K_s$
10	$2.01 \times 10^{-7}$ (0.34–3.71)	0.92 (0.91–0.93)	0.68 (0.12–1.39)	0.86 (0.67–1.04)	1.26
15	$1.05 \times 10^{-7}$ (0.35–1.93)	1.00 (0.88–1.11)	0.12 (0.05–0.21)	0.85 (0.69–1.02)	7.08
20	$1.69 \times 10^{-7}$ N.S.	1.59 N.S.	1.24 (0.20–5.94)	1.29 (0.42–2.16)	1.04

TABLE 3. Cell quotas,  $Q$  ( $\times 10^{-7}$   $\mu\text{mol Si cell}^{-1}$ ), for *Stephanodiscus minutus* at various growth rates,  $\mu$  ( $\text{d}^{-1}$ ), from semicontinuous cultures under silicon limitation at three temperatures.

$\mu$	$Q$ , 20° C	$Q$ , 15° C	$Q$ , 10° C
0.11	2.53	1.90	2.02
0.22	2.10	1.72	1.93
0.36	2.34	1.16	1.80
0.51	2.48	1.49	—
0.69	1.99	1.54	14.8
0.92	3.21	13.3	438

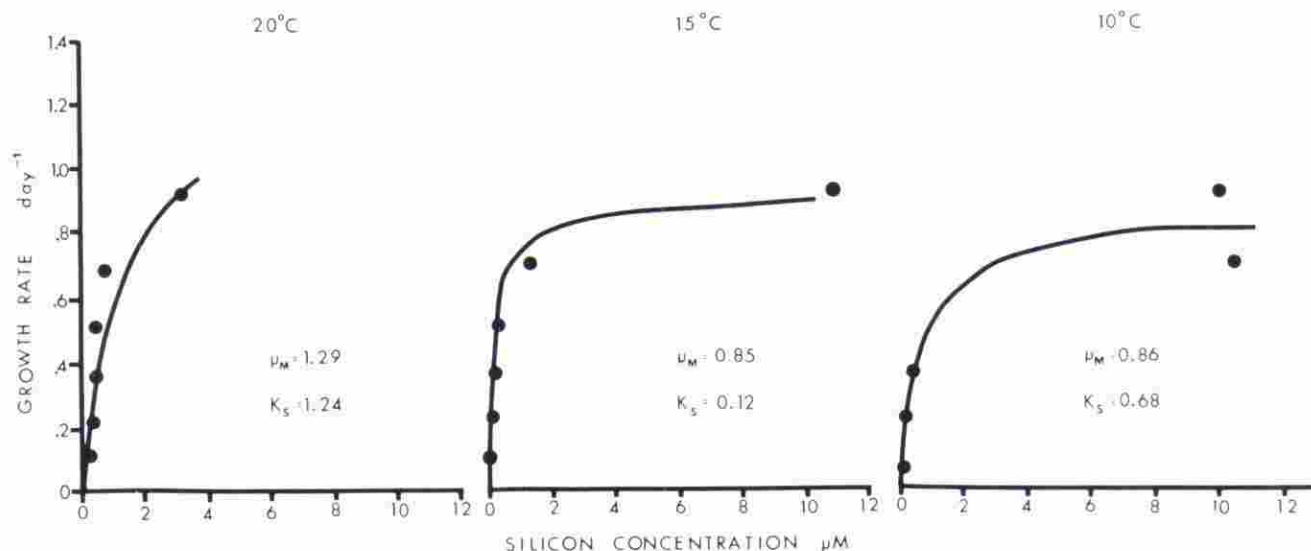


FIG. 2. Steady state growth rates as a function of silicon concentration for *S. minutus* at three temperatures in semicontinuous culture (line is the fitted Monod curve).

#### RESULTS

Table 2 gives the physiological constants for silicon limited growth of *S. minutus* at three temperatures. The results of the batch growth experiments are illustrated in Fig. 1, which gives the growth rate in relation to the initial silicon concentrations at 10°, 15° and 20° C. *Stephanodiscus minutus* had similar maximum growth rates (mean  $\mu_m = 1.08$  doublings  $d^{-1}$ ) over the temperature range studied. The half-saturation constant was lowest at 10° C ( $K_s = 0.31$   $\mu M$  Si; 0.22–0.41) but significantly higher at 15° C ( $K_s = 1.03$   $\mu M$  Si; 0.68–1.47), and 20° C ( $K_s = 0.88$   $\mu M$  Si; 0.60–1.22).

The physiological constants calculated from the semicontinuous culture experiments are also given in Table 2. The relationship between cell quota ( $Q$ ) and growth rate ( $D$ ) for cells grown under silicon limitation at 10°, 15° and 20° C was calculated according to Droop's (1974) equation. Droop's equation did not fit the data at 20° C. Minimum cell quota ( $k_Q$ ) is roughly estimated to be about  $1.5 \times 10^{-7}$   $\mu mol$  Si  $cell^{-1}$  for all three temperatures. It can be seen from Table 3 that there was very little variation in cell quotas at growth rates below 0.6  $d^{-1}$  from one temperature to another.

In all of the semicontinuous cultures there was measurable residual silicon remaining in the flasks at steady state, so it was possible to calculate the Monod relationship between growth rate and external silicon concentration (Fig. 2, Table 2). A nonlinear regression was used for calculating the fitted curves. The half-saturation constant ( $K_s$ ) was lowest at 15° C ( $K_s = 0.12$   $\mu M$  Si; 0.05–0.21), with higher values at 10° C ( $K_s = 0.68$   $\mu M$  Si; 0.12–1.39) and 20° C ( $K_s = 1.24$   $\mu M$  Si; 0.20–5.94). Maximum growth rates were insignificantly different at all three temperatures.

#### DISCUSSION

In both the semicontinuous and batch experiments the estimated maximum growth rates of *S. minutus* were essentially constant over the temperature range studied. Goldman and Carpenter (1974) and Eppley (1972) have both used the Arrhenius equation to quantitatively describe the relationship between maximum growth rate and temperature for phytoplankton. As Goldman and Carpenter (1974) pointed out, the general relationship may not hold for all species of algae, or over all temperature ranges. Rhee and Gotham (1981) found a linear relationship between maximum growth rates and increasing temperature in the 'suboptimal' temperature range for *Scenedesmus* sp. and *Asterionella formosa*. Tilman et al. (1981) found a similar (though apparently nonlinear) increase in maximum growth rate with increasing temperature in the 'suboptimal' range, with a constant maximum growth rate in the 'optimal' temperature range for two diatom species, *A. formosa* and *Synedra ulna*. In our experiments, the temperature range from 10° to 20° C is apparently within the 'optimal' range for *S. minutus* (Fig. 3). It is our opinion that the maximum growth rates determined for the batch growth experiments are more trustworthy because they are directly measured values, while those obtained for the semicontinuous experiments are determined by curve-fitting (see Goldman and McCarthy 1978).

The relationships between the half-saturation constants or the minimum cell quotas and temperature are also not simple. In the semicontinuous experiments, there is a minimum in both  $K_s$  and  $k_Q$  values at 15° C as compared to 10° and 20° C. Goldman (1977) found similar U-shaped curves for two marine species for particulate nitrogen per cell at a fixed steady state growth rate over a 15 degree tem-

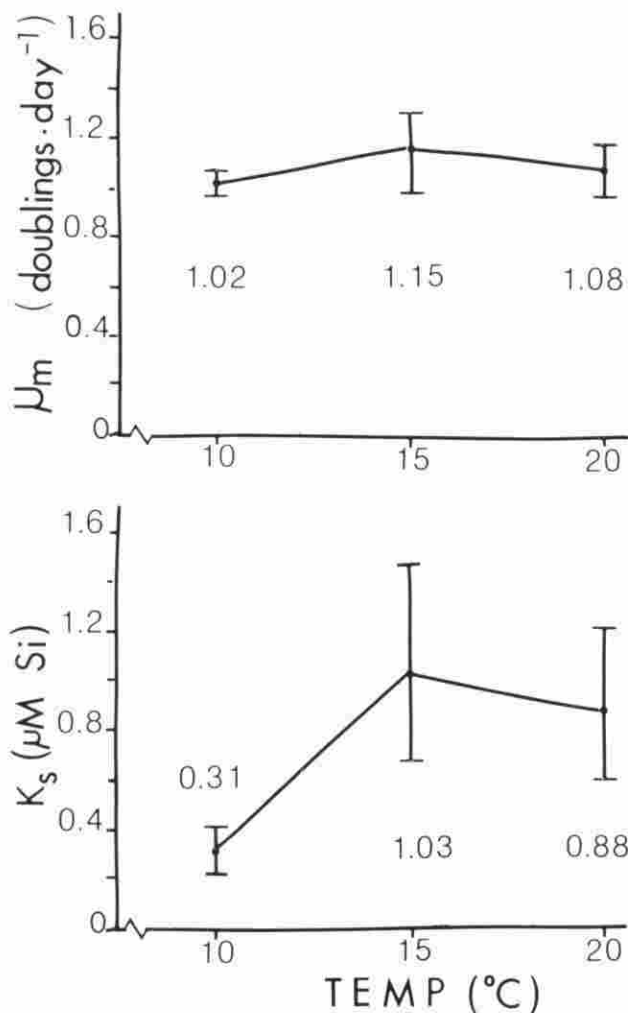


FIG. 3. Comparisons of maximum growth rates and half-saturation constants at three temperatures for *S. minutus* in short-term batch cultures. The 95% confidence intervals for each point are given.

perature range. He argued that this is evidence for uncoupling of cell division and nutrient uptake, and further that this is a species-dependent phenomenon. Ahlgren (1978) also found a U-shaped relationship in  $K_s$  values for phosphate limited *Oscillatoria agardhii* over a 10 degree temperature range. Tilman et al. (1981) found a constant  $K_s$  value for silicate-limited *A. formosa* from 4° to 12.5° C (with higher values at 20° and 24° C) and for *Synedra ulna* from 8° to 24° C. Rhee and Gotham (1981) found that the  $k_d$  values decreased with increasing temperature (from 11° to 20° C) for both phosphate and nitrate limited *Scenedesmus*. The U-shaped relationship in  $K_s$  we observed in the semicontinuous experiments was quite different from the results of the batch growth experiments, with the values in the batch experiments for  $K_s$  being lowest at 10° C (Fig. 3). The reasons for these discrepancies are not clear, but do illustrate that caution must be used when comparing values obtained by different methods. It

TABLE 4. Estimated relative competitive advantage (Healey 1980) under silicon limitation at 20° C for several species of freshwater diatoms using the Monod parameters:  $\mu_m(d^{-1})/K_s(\mu\text{M Si})$ .

Species	$\mu_m/K_s$	Reference
<i>Stephanodiscus minutus</i> (semicontinuous)	1.04	This study
(batch)	0.85	This study
<i>Cyclotella meneghiniana</i>	0.64	Tilman & Kilham 1976
<i>Diatoma elongatum</i>	0.56	Kilham et al. 1977
<i>Fragilaria crotonensis</i>	0.41	Tilman 1981
<i>Asterionella formosa</i>	0.40	Kilham 1975
	0.39	Kilham 1975
	0.35	Tilman 1981
	0.28	Holm & Armstrong 1981
	0.19	Tilman & Kilham 1976
	0.19	Tilman et al. 1981
<i>Synedra ulna</i>	0.12	Tilman et al. 1981
<i>Synedra filiformis</i>	0.06	Tilman 1981
<i>Tabellaria flocculosa</i>	0.04	Tilman 1981

is clear that the relationship between temperature and either  $K_s$  or  $k_d$  is complex and species dependent.

Healey (1980) suggested using the slope of the Monod equation ( $\mu_m/K_s$ ) to estimate the relative competitive abilities of different species for a limiting resource. Table 4 shows the calculated  $\mu_m/K_s$  values for several species of freshwater diatoms. It can clearly be seen that *S. minutus* is hypothesized to be the superior competitor for silicon using these criteria. Competition experiments performed between various species on this list (Tilman 1977, 1981, Tilman et al. 1981) confirm the relative rankings of competitive ability for some of the species.

Kilham (1971) hypothesized that silicon was an important limiting nutrient in aquatic systems, and that the abilities of particular species to utilize this nutrient for growth was an important factor in determining species composition in the planktonic diatom communities. He showed from data in the literature that the occurrence of *Stephanodiscus astraea* as a dominant species was correlated with lower silicon concentrations than for three other diatom species. (*Stephanodiscus minutus* is often identified as *S. astraea* by other workers, the taxonomy of this group being in confusion at present.) Our results show that *S. minutus* is superior under silicon limited growth to *A. formosa* (Table 4), and thus support Kilham's contention. Indeed, at all three temperatures, the  $K_s$  values for *S. minutus* are the lowest yet recorded for a freshwater diatom under silicon limitation.

Tilman (1977, 1980) developed a model of the population dynamics of phytoplankton based on resource competition. Knowledge of the physiological characteristics of nutrient utilization for growth of each species for each potentially limiting nutrient is necessary for the simplest form of the model. The

model assumes there is a particular ratio of relative nutrient supply of the most potentially limiting nutrients at which a species will switch from being limited by one nutrient to being limited by another, assuming all others are in excess (Rhee 1978). This switching point is thought to be the optimum for growth, and is species specific. Kilham and Kilham (1978) hypothesized that *S. minutus* has a low Si:P ratio for optimum growth. The results of the natural community enrichment experiments of Schelske et al. (1974) show that as the phosphorus supply rate increased relative to silicon, causing a lower Si:P ratio, the populations of *S. minutus* increased. No increase in *S. minutus* was found at the highest Si:P ratios.

Bradbury and Megard (1972) examined a sediment core from Shagawa Lake in northeastern Minnesota to determine the impact of eutrophication on historical changes in diatom populations. *Stephanodiscus minutus* and other diatoms favored by enrichment became abundant in the lake after the time of European settlement in the lake basin, indicating that Shagawa Lake responded rapidly to increased nutrient levels caused by disturbance of the landscape and domestic waste disposal into the lake. Kilham and Kilham (1982) interpreted these results to indicate that increased phosphorus loading relative to silicon caused a decreasing trend in the Si:P ratio, allowing species such as *S. minutus* to outcompete other diatom species which have higher Si:P optima for growth.

Stoermer and Ladewski (1976) reported the temperature of maximum occurrence of *S. minutus* in Lake Michigan to be near 3° C. The results of our laboratory study indicate that *S. minutus* has similar maximum growth rates over the temperature range of 10–20° C. The observation that the temperature optima for growth of natural populations are often lower than those measured in the laboratory (Braarud 1961, Smayda 1969, Eppley 1977, Guillard and Kilham 1977) may be explained by the interactions of nutrient competition and temperature on the growth rates of particular species (Rhee and Gotham 1981, Tilman et al. 1981). In the case of the data cited by Stoermer and Ladewski (1976), it is possible that what is actually being observed is a correlation between temperature and relative supply rates of nutrients (especially Si and P), rather than a cause and effect relationship between temperature and optimal growth of *S. minutus*. In Lake Michigan, the mixing of the water column in the winter and spring results in much lower Si:P ratios than are found at other times of the year. Thus, it is impossible to separate temperature and nutrient effects for particular species in such a correlation analysis. Danforth and Ginsburg (1980) observed maximum populations of *Stephanodiscus* spp. during spring mixing in nearshore Lake Michigan waters near Chicago. Holland and Claffin (1975) found that *Stephanodiscus* spp. were dominant in mid-summer in southern

Green Bay, Wisconsin. This area of the bay has very low Si:P ratios (Rousar and Beeton 1973), but high temperatures in the summer. These data and other distributional data on *Stephanodiscus* cited in Kilham (1971) are more consistent with a hypothesis based on *S. minutus* having an optimum growth potential at low Si:P ratios, than with a hypothesis based solely on temperature optima for growth. Eppley (1972) pointed out that the maximum growth potential which is set by temperature is seldom realized because of other limiting factors, notably nutrient levels.

It is obvious that we need a great deal more information about the complex interactions of species dependence, nutrient dependence, and temperature dependence on nutrient limited growth in algae before we can hope to establish any general relationship useful for environmental models. Goldman (1977) correctly pointed out that for temperature such reliably predictive relationships do not yet exist.

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