Is There Really Insufficient Support for Tilman's R^* Concept? A Comment on Miller et al.

J. Bastow Wilson,[1,*] Elly Spijkerman,[2,†] and Jef Huisman[3,‡]

1. Botany Department, University of Otago, P.O. Box 56, Dunedin, New Zealand;
2. Department of Ecology and Ecosystem Modelling, University of Potsdam, Am Neuen Palais 10, D-14469 Potsdam, Germany;
3. Aquatic Microbiology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Nieuwe Achtergracht 127, 1018 WS, Amsterdam, The Netherlands

Submitted April 9, 2006; Accepted September 22, 2006; Electronically published April 5, 2007

Keywords: bacteria, competition experiment, phytoplankton, resource competition, resource-ratio hypothesis, zooplankton.

In the April 2005 issue of the *American Naturalist* (165: 439–448), Thomas E. Miller and colleagues (2005) reviewed the literature from the past 20 years to determine to what extent David Tilman's (1982) resource-ratio theory had been supported. Miller et al. tested seven predictions from the theory. We are particularly interested in their prediction 1: "The species that can survive at the lowest levels of a limiting resource will be the best competitor for that resource" (p. 441). This R^* concept is the most well-known aspect of Tilman's theory, one that lends itself to testing with clear refutation or support.

The R^* concept is simple (Armstrong and McGehee 1980; Tilman 1982). As a monoculture population of a species (or genotype) increases, it will reduce the resource concentration, R, in its environment and thus decrease its own population growth. Eventually, it will reduce R to a level at which the population can no longer grow, and it can therefore reduce R no further. This level of R is called R^*, which is a species-specific parameter. As a mixture of species grows, R will decrease likewise. When R falls below the R^* of a particular species, that species will disappear from the community because it will not be able to maintain its population. Eventually, only one species will remain: the species that has the lowest R^*.

The R^* concept has been referred to many times, but there was no recent meta-analysis to see how often it applies. Miller et al. have done an enthusiastic job of collecting an impressive number of 1,333 papers citing Tilman (1980, 1982), and we thank them for that. They found 13 papers that they thought enabled a test of prediction 1 (i.e., R^*), and these are listed in the appendix of their article. They concluded that although eight papers supported prediction 1, five did not. A balance of 8 : 5 suggests that, all in all, there is insufficient support for the R^* concept. However, being familiar with some of the latter five papers, we were puzzled about Miller et al.'s evaluations and, hence, doubtful of the 8 : 5 outcome. We therefore carefully reexamined all 13 papers.

In principle, R^* values can be determined using two methods. The R^* can be measured directly, as the resource concentration R in a steady state monoculture of a species. Alternatively, R^* can be calculated from the growth kinetics of a species. It is unclear how Miller et al. determined R^* values for articles that did not report these values. We calculated R^* values for such articles from the tabulated growth kinetics of the species using the Monod model (e.g., Tilman 1982):

$$R^* = \frac{mK}{\mu_{\max} - m}, \tag{1}$$

where m is the specific loss rate of the species concerned, K is its half-saturation constant for growth, and $\mu_{\max}$ is its maximum specific growth rate. Many competition experiments with microorganisms are carried out in chemostats. In these flow-through systems, the specific loss rates of the species are determined by the dilution rate, D, of the chemostat (i.e., $m = D$).

Miller et al.'s NO-P1 Studies

We first review, chronologically, the articles that Miller et al. marked "NO-P1," meaning that, by their evaluation,

* E-mail: bastow@bastow.ac.nz.

† E-mail: spijker@rz.uni-potsdam.de.

‡ Corresponding author; e-mail: jef.huisman@science.uva.nl.

Am. Nat. 2007. Vol. 169, pp. 700–706.

the species that was winning in competition was not the species having the lowest R^*.

1. Tilman and Sterner 1984

In Tilman and Sterner's study (1984), diatom *Fragilaria crotonensis* had an R^* for Si that was half that of *Tabellaria fenestrata*, and under Si-limited conditions, it could invade a population of the latter with a trajectory leading toward dominance, whereas *Tabellaria* could not invade a population of *Fragilaria*. This matches the R^* prediction. In conditions where P was limiting, *Fragilaria* was competitively dominant, but in monoculture and in mixture, the two species reduced P to below the level of detection, so prediction 1 cannot be tested. Conclusion: YES-P1 (in the one case where it can be tested).

2. Tilman and Wedin 1991

Tilman and Wedin's study (1991) is the only terrestrial experiment in the set. The R^* for N was estimated by analyzing soil, initially low in N, in which monocultures of three grass species had been growing for just over 2 years. The authors admitted that this is not an ideal estimate of R^*, but the values do look convincingly different between species. In each of the three species pairs, the species with the lower R^* reduced the other species close to extinction. Conclusion: YES-P1.

3. Hu and Zhang 1993

Hu and Zhang (1993) ran 18 competition experiments between the diatom *Cyclotella* sp. and the blue-green alga (= cyanobacterium) *Anabaena flos-aquae* under various nutrient limitations. Although R^* values are not given, kinetic data are provided in their table 1, allowing the calculation of R^*. When N was deficient, *Anabaena* won in competition as a result of its nearly 10-fold lower R^* for N (their fig. 1). Under P-limited conditions, *Cyclotella* was competitively superior as a result of its twofold lower R^* for P (their fig. 2). In the case of Si, prediction 1 cannot be tested because cyanobacteria do not compete for Si. Conclusion: YES-P1 (in the cases where it can be tested).

4. Spijkerman and Coesel 1996

In the study of Spijkerman and Coesel (1996), the green alga *Cosmarium* grew faster than *Staurastrum* at low P levels, but this was reversed at high P levels as the growth curves of *Cosmarium* and *Staurastrum* intersected. The R^* values of the species can be estimated graphically (from fig. 3 in Spijkerman and Coesel 1996) or calculated from equation (1) using the growth kinetics presented in their article. This shows that at low dilution rates, the R^* for P for *Cosmarium* was considerably lower than that for *Staurastrum*, whereas the opposite was true at high dilution rates (table 1). Thus, theory predicts that in this study, the winner of competition should depend on the dilution rate. The competition experiments of Spijkerman and Coesel (1996) support the predictions based on R^*. Conclusion: YES-P1.

5. Huisman et al. 1999

Applied to light, R^* theory predicts that the species with the lowest "critical light intensity" will be the superior competitor for light. There is an issue here of how to measure the critical light intensity. Huisman et al. (1999) did it two ways. First they measured the critical light intensity as the light intensity penetrating through an algal monoculture once it reached steady state. Second, they fitted a population model through the complete data set of the algal monoculture to calculate its critical light intensity. The two methods gave slightly different values. Huisman et al. (1999) preferred the model-fitting method because it was based on more points and it accounted for photoacclimation and the light absorption spectra of the species. The outcomes of competition between all possible pairs of four algal species were correctly predicted. Conclusion: YES-P1.

Miller et al.'s YES-P1 Studies

Now we come to the eight articles that Miller et al. (2005) mark YES-P1, meaning that the winner in competition was the species with the lower R^*, as predicted by Tilman's theory.

1. Tilman 1981

Under P limitation, Tilman (1981) calculated R^* from growth-P curves that were almost flat, so that the R^* values were difficult to determine very precisely. Under Si limitation, the R^* values could be calculated with higher accuracy. The R^* values for Si of *Asterionella formosa* and *Fragilaria crotonensis* were statistically indistinguishable, and these two species remained in competitive balance during the 30 days of the experiment. However, this matches prediction 1 because species with similar R^* values are predicted to be neutral competitors. For the other species pairs, competitive exclusion was not always fully completed within the time span of 30 days, but the trends were clear at the end of each experiment. In total, the R^* values gave correct predictions of the competitive outcome in all 12 experiments (6 species pairs × 2 limiting resources). Conclusion: YES-P1.

Table 1: R^* values (nmol P L^{-1}) for *Cosmarium abbreviatum* and *Staurastrum pingue* at three dilution rates

Dilution rate (h^{-1})	*Cosmarium*	*Staurastrum*
.003	2.6	6.2
.007	7.4	11
.020	113	41

Source: Data from Spijkerman and Coesel (1996).

Note: R^* values are calculated from equation (1). Estimated growth parameters for *Cosmarium* and *Staurastrum*, respectively: $\mu_{max} = .023\ h^{-1}$ and $.042\ h^{-1}$, K = 17 nmol P L^{-1} and 42 nmol P L^{-1}. The calculation takes into account that *Staurastrum* has a threshold resource concentration of 3 nmol P L^{-1}, below which its specific growth rate = 0.

2. Kilham 1986

In Kilham's (1986) study, the algal cultures contained mixtures of species (including some zooplankton), and consequently, a test of R^* is not possible at the species level. When diatoms were compared as a whole with an unnamed green unicell (assumed to be one species), the green alga had a higher R^* for P. Under P limitation, the competition results were in accordance with prediction 1. Under Si limitation, prediction 1 cannot be tested because green algae do not compete for Si. Conclusion: YES-P1 (in the one case where it can be tested, and at a high level of taxonomic aggregation).

*3. Sommer 1986*a

Sommer's (1986*a*) experiments were with five diatom species from the Antarctic, and his table 2 provides kinetic data for the dominant competitors on the basis of which R^* can be calculated. Under N limitation, the predicted dominance of *Corethron criophilum* at dilution rates of 0.1 day^{-1} and 0.25 day^{-1} and of *Nitzschia kerguelensis* at a dilution rate of 0.5 day^{-1} was confirmed by the competition experiments. Under Si limitation, the R^* values of *Nitzschia cylindrus* and *Thalassiosira subtilis* were very close, at dilution rates of 0.1 day^{-1} and 0.25 day^{-1}, and, as predicted, the competition experiments revealed codominance of *N. cylindrus* and *Thalassiosira* at these low dilution rates. In contrast, *N. cylindrus* clearly had the lowest R^* value, at a dilution rate of 0.5 day^{-1}, and it dominated in competition at this high dilution rate. Conclusion: YES-P1.

*4. Sommer 1986*b

Sommer (1986*b*) studied how the dilution rate affects competition for P among a phytoplankton mixture sampled from a lake. Sommer's table 1 allows the calculation of R^* values. The half-saturation constant for P of *Synedra acus* was below the detection limit. This makes it problematic to calculate R^* of *Synedra* with high accuracy, but it is certain that *Synedra* must have a very low R^* for P at low dilution rates, whereas *Achnanthes minutissima* had the lowest R^* for P at high dilution rates. Indeed, as predicted, *Achnanthes* became dominant at the highest dilution rate, while *Synedra* became dominant at all lower dilution rates. In the next series of experiments, without Si, different species of green algae became dominant depending on the dilution rate, again with the dominant species correctly predicted by R^*. Conclusion: YES-P1.

5. Rothhaupt 1988

Rothhaupt (1988) applied the theory to two rotifers of the *Brachionus* genus competing for two algal species. With *Chlamydomonas sphaeroides* as food, *Brachionus calyciflorus* had a lower R^* and ousted its competitor. In contrast, with *Monoraphidium minutum* as food, *Brachionus rubens* had a lower R^*, and it won when *Monoraphidium* comprised more than 75% of the food. Thus, YES-P1.

6. van Donk and Kilham 1990

Van Donk and Kilham (1990) studied how temperature affects competition among three diatoms. The results generally confirmed predictions based on R^*, but not always. In several experiments where *Asterionella formosa* was predicted to win, it was displaced by *Fragilaria crotonensis*. These results were explained by the small difference between the R^* values of *Asterionella* and *Fragilaria* and because *Fragilaria* showed considerable wall growth. As a result, *Fragilaria* could have gained a competitive advantage because its losses by dilution were lower than those of its competitor. This gives an overall score of YES = 4 and NO = 2. Conclusion: a tendency toward P1-YES, but it is not fully convincing, possibly due to experimental limitations (i.e., wall growth).

*7. Grover 1991*b

Grover (1991*b*) investigated competition for P in a variable environment. He found that a competition model based on the Droop equation predicted the competition experiments well. In each competition experiment, the species with the lowest R^* won. However, Grover's (1991*b*) experiments were all conducted in a variable environment, where competition theory predicts that prediction 1 does not necessarily apply (Armstrong and McGehee 1980; Tilman 1982). Conclusion: the P1 test is not applicable.

Table 2: Laboratory competition studies with bacteria, phytoplankton, and zooplankton that allow rigorous tests of the R^* prediction

Competitor	Resource	Consistent with R^* prediction	Reference
Bacilli, yeast	Glucose	Yes	Megee et al. 1971
Clostridia	Glutamate	No	Laanbroek et al. 1979
Proteobacteria	Glucose	Yes	Jost et al. 1973
Proteobacteria	Glutamate	Yes	Bell et al. 1990
Proteobacteria	Lactate	Yes	Harder and Veldkamp 1971
Proteobacteria	Lactate	Yes	Matin and Veldkamp 1978
Proteobacteria	Tryptophan	Yes	Hansen and Hubbell 1980
Proteobacteria	Glycerol, lactate	Yes	Jannasch 1967
Proteobacteria	Iron, phosphorus	Yes	Kuenen et al. 1977
Proteobacteria, diatoms	Phosphorus	Yes	Pengerud et al. 1987
Proteobacteria, green algae	Phosphorus	Yes	Codeço and Grover 2001
Cyanobacteria	Light	Yes	Zevenboom et al. 1981
Cyanobacteria	Light	Yes	Litchman 2003
Cyanobacteria	Phosphorus	Yes	De Nobel et al. 1997
Cyanobacteria	Phosphorus	Yes	Ducobu et al. 1998
Cyanobacteria, diatoms	Phosphorus	Yes	Holm and Armstrong 1981
Cyanobacteria, diatoms	Nitrogen, phosphorus	Yes	Hu and Zhang 1993
Cyanobacteria, green algae	Light	Yes	Mur et al. 1977
Cyanobacteria, green algae	Light	Yes	Huisman et al. 1999
Cyanobacteria, green algae	Phosphorus	Undetermined	Olsen et al. 1989
Cyanobacteria, green algae	Light, phosphorus	Yes	Passarge et al. 2006
Diatoms	Ammonium	Yes	Mickelson et al. 1979
Diatoms	Silicon	Yes	Tilman et al. 1981
Diatoms	Silicon	Yes	Tilman and Sterner 1984
Diatoms	Nitrate, silicon	Yes	Sommer 1986*a*
Diatoms	Phosphorus, silicon	Yes	Tilman 1977
Diatoms	Phosphorus, silicon	Yes	Tilman 1981
Diatoms	Phosphorus, silicon	Yes	Kilham 1984
Diatoms	Phosphorus, silicon	Yes	Kilham 1986
Diatoms	Phosphorus, silicon	Largely yes[a]	van Donk and Kilham 1990
Diatoms, green algae	Phosphorus	Yes	Sommer 1986*b*
Green algae	Inorganic carbon	Yes	Goldman et al. 1974
Green algae	Phosphorus	Yes	Grover 1991*a*
Green algae	Phosphorus	Yes	Spijkerman and Coesel 1996
Mixotrophic and heterotrophic flagellates	Bacterial mixture	Yes	Rothhaupt 1996
Cladocerans	Green algae	Yes	Kreutzer and Lampert 1999
Rotifers	Green algae	Yes	Rothhaupt 1988
Rotifers	Green algae	Yes	Boraas et al. 1990
Rotifers	Green algae	Yes	Ciros-Perez et al. 2001
Rotifers	Cryptomonads	Yes	Kirk 2002
Cladocerans, rotifers	Green algae	Yes	Gilbert 1985
Cladocerans, rotifers	Cryptomonads	Largely yes[a]	MacIsaac and Gilbert 1989
Cladocerans, copepods	Cryptomonads	Yes	Schulze et al. 1995

[a] In these two studies, most experiments were consistent with the R^* prediction, but some were not, probably because of wall growth (van Donk and Kilham 1990) or subtle complexities in zooplankton physiology (MacIsaac and Gilbert 1989).

8. Kirk 2002

In Kirk (2002), R^* correctly predicted the outcome of these experiments of three rotifers competing for an alga. Conclusion: YES-P1.

Conclusion

In conclusion, after a careful reading of all 13 papers, we do not arrive at an overall balance of 8 YES : 5 NO, as Miller et al. (2005) concluded, but rather 12 YES : 0 NO (and one not applicable). Moreover, there are many more competition studies with bacteria, phytoplankton, and zooplankton in which R^* values of the competing species are explicitly given or can be calculated from the growth kinetics (reviewed by Grover 1997). Several of these competition studies do not cite Tilman's works (Tilman 1980, 1982) and therefore were not included in the analysis of Miller et al. (2005). In total, we found 43 competition studies in the microbial and aquatic literature that allow rigorous tests of the R^* prediction (table 2). One of these studies (Laanbroek et al. 1979) was inconsistent with the R^* prediction, but the authors were not primarily concerned with testing the R^* rule and did not comment on this discrepancy. Grover (1997) argues that possibly the competition experiments in Laanbroek et al. (1979) were not limited by glutamate because the unusually high values of R^* calculated from this study suggest limitation by some other factor. In the study of Olsen et al. (1989), the R^* values of the two competing species were so close that it was impossible to tell which species had the lowest value. Accordingly, this study was labeled as "undetermined." All other 41 studies were consistent with the R^* prediction (table 2). Hence, our evaluation shows that there is strong support for the R^* concept, particularly from controlled experiments with bacteria, phytoplankton, and zooplankton.

There is no intrinsic reason that R^* should always predict the outcome of competition between two species. Although the logic is clear, the model is simplistic for higher plants growing in soil (Huston and DeAngelis 1994; Craine 2005). In laboratory experiments with bacteria or plankton, other interactions between species may also be operative (e.g., commensalism, allelopathic interactions). Furthermore, temporal variability and incomplete mixing may promote coexistence (Hassell et al. 1994; Flöder and Sommer 1999; Huisman and Weissing 1999; Descamps-Julien and Gonzalez 2005) or may shift the competitive balance in favor of other species (Sommer 1985; Litchman 2003; Huisman et al. 2004). Finally, technical limitations (e.g., wall growth, concentrations below detection limit) may sometimes prevent successful prediction on the basis of R^*. Miller et al. (2005) concluded that more research was needed to test the resource-ratio theory, and we fully agree. For instance, laboratory experiments have so far not been able to find stable coexistence on the transition from competition for nutrients to competition for light (Passarge et al. 2006). Furthermore, since most rigorous tests of the R^* prediction have been with bacteria and plankton in well-mixed chemostats, it remains to be seen to what extent the R^* prediction can be generalized across more complex habitats and organisms.

However, we are surprised that Miller et al. (2005) concluded that prediction 1 had been insufficiently tested to draw any conclusions. Our reexamination of the literature indicates that, at least in competition experiments with bacteria, phytoplankton, and zooplankton, R^* is almost always a good guide to competitive outcome.

Acknowledgments

We thank J. P. Grover, T. E. Miller, and the anonymous reviewers for their helpful comments. E.S. acknowledges financial support by the German Research Foundation (DFG, SP695/2). J.H. was supported by the Earth and Life Sciences Foundation (ALW), which is subsidized by the Netherlands Organization for Scientific Research (NWO).

Literature Cited

Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. American Naturalist 115:151–170.

Bell, C. R., N. E. Cummings, M. L. Canfield, and L. W. Moore. 1990. Competition of octopine-catabolizing *Pseudomonas* spp. and octopine-type *Agrobacterium tumefaciens* for octopine in chemostats. Applied and Environmental Microbiology 56:2840–2846.

Boraas, M. E., D. B. Seale, and J. B. Horton. 1990. Resource competition between two rotifer species (*Brachionus rubens* and *Brachionus calyciflorus*): an experimental test of a mechanistic model. Journal of Plankton Research 12:77–87.

Ciros-Perez, J., M. J. Carmona, and M. Serra. 2001. Resource competition between sympatric sibling rotifer species. Limnology and Oceanography 46:1511–1523.

Codeço, C. T., and J. P. Grover. 2001. Competition along a spatial gradient of resource supply: a microbial experimental model. American Naturalist 157:300–315.

Craine, J. M. 2005. Reconciling plant strategy theories of Grime and Tilman. Journal of Ecology 93:1041–1052.

De Nobel, W. T., J. Huisman, J. L. Snoep, and L. R. Mur. 1997. Competition for phosphorus between the nitrogen-fixing cyanobacteria *Anabaena* and *Aphanizomenon*. FEMS Microbiology Ecology 24:259–267.

Descamps-Julien, B., and A. Gonzalez. 2005. Stable coexistence in a fluctuating environment: an experimental demonstration. Ecology 86:2815–2824.

Ducobu, H., J. Huisman, R. R. Jonker, and L. R. Mur. 1998. Competition between a prochlorophyte and a cyanobacterium under various phosphorus regimes: comparison with the Droop model. Journal of Phycology 34:467–476.

Flöder, S., and U. Sommer. 1999. Diversity in planktonic communities: an experimental test of the intermediate disturbance hypothesis. Limnology and Oceanography 44:1114–1119.

Gilbert, J. J. 1985. Competition between rotifers and *Daphnia*. Ecology 66:1943–1950.

Goldman, J. C., W. J. Oswald, and D. Jenkins. 1974. The kinetics of inorganic carbon-limited algal growth. Journal of the Water Pollution Control Federation 46:554–571.

Grover, J. P. 1991*a*. Algae grown in non-steady continuous culture: population dynamics and phosphorus uptake. Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen 24:2661–2664.

———. 1991*b*. Dynamics of competition among microalgae in variable environments: experimental tests of alternative models. Oikos 62:231–243.

———. 1997. Resource competition. Chapman & Hall, London.

Hansen, S. R., and S. P. Hubbell. 1980. Single-nutrient microbial competition: qualitative agreement between experimental and theoretically forecast outcomes. Science 207:1491–1493.

Harder, W., and H. Veldkamp. 1971. Competition of marine psychrophilic bacteria at low temperatures. Antonie van Leeuwenhoek 37:51–63.

Hassell, M. P., H. N. Comins, and R. M. May. 1994. Species coexistence and self-organizing spatial dynamics. Nature 370:290–292.

Holm, N. P., and D. E. Armstrong. 1981. Role of nutrient limitation and competition in controlling the populations of *Asterionella formosa* and *Microcystis aeruginosa* in semicontinuous culture. Limnology and Oceanography 26:622–634.

Hu, S., and D. Y. Zhang. 1993. The effects of initial population density on the competition for limiting nutrients in two freshwater algae. Oecologia (Berlin) 96:569–574.

Huisman, J., and F. J. Weissing. 1999. Biodiversity of plankton by species oscillations and chaos. Nature 402:407–410.

Huisman, J., R. R. Jonker, C. Zonneveld, and F. J. Weissing. 1999. Competition for light between phytoplankton species: experimental tests of mechanistic theory. Ecology 80:211–222.

Huisman, J., J. Sharples, J. M. Stroom, P. M. Visser, W. E. A. Kardinaal, J. M. H. Verspagen, and B. Sommeijer. 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. Ecology 85:2960–2970.

Huston, M. A., and D. L. DeAngelis. 1994. Competition and coexistence: the effects of resource transport and supply rates. American Naturalist 144:954–977.

Jannasch, H. W. 1967. Enrichments of aquatic bacteria in continuous culture. Archives of Microbiology 59:165–173.

Jost, J. L., J. F. Drake, A. G. Frederickson, and H. M. Tsuchiya. 1973. Interactions of *Tetrahymena pyriformis*, *Escherichia coli*, *Azotobacter vinelandii*, and glucose in a minimal medium. Journal of Bacteriology 113:834–840.

Kilham, S. S. 1984. Silicon and phosphorus growth kinetics and competitive interactions between *Stephanodiscus minutus* and *Synedra* sp. Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen 22:435–439.

———. 1986. Dynamics of Lake Michigan natural phytoplankton communities in continuous cultures along a Si-P loading gradient. Canadian Journal of Fisheries and Aquatic Sciences 43:351–360.

Kirk, K. L. 2002. Competition in variable environments: experiments with planktonic rotifers. Freshwater Biology 47:1089–1096.

Kreutzer, C., and W. Lampert. 1999. Exploitative competition in differently sized *Daphnia* species: a mechanistic explanation. Ecology 80:2348–2357.

Kuenen, J. G., J. Boonstra, H. G. J. Schroder, and H. Veldkamp. 1977. Competition for inorganic substrates among chemoorganotrophic and chemolithotrophic bacteria. Microbial Ecology 3:119–130.

Laanbroek, H. J., A. J. Smit, G. Klein Nulend, and H. Veldkamp. 1979. Competition for L-glutamate between specialised and versatile *Clostridium* species. Archives of Microbiology 120:61–66.

Litchman, E. 2003. Competition and coexistence of phytoplankton under fluctuating light: experiments with two cyanobacteria. Aquatic Microbial Ecology 31:241–248.

MacIsaac, H. J., and J. J. Gilbert. 1989. Competition between rotifers and cladocerans of different body sizes. Oecologia (Berlin) 81:295–301.

Matin, A., and H. Veldkamp. 1978. Physiological basis of the selective advantage of a *Spirillum* sp. in a carbon-limited environment. Journal of General Microbiology 105:187–197.

Megee, R. D., III, J. F. Drake, A. G. Frederickson, and H. M. Tsuchiya. 1971. Studies in intermicrobial symbiosis: *Saccharomyces cerevisiae* and *Lactobacillus casei*. Canadian Journal of Microbiology 18:1733–1742.

Mickelson, M. J., H. Maske, and R. C. Dugdale. 1979. Nutrient-determined dominance in multispecies chemostat cultures of diatoms. Limnology and Oceanography 24:289–315.

Miller, T. E., J. H. Burns, P. Munguia, E. L. Walters, J. M. Kneitel, P. M. Richards, N. Mouquet, and H. L. Buckley. 2005. A critical review of twenty years' use of the resource-ratio theory. American Naturalist 165:439–448.

Mur, L. R., H. J. Gons, and L. Van Liere. 1977. Some experiments on the competition between green algae and bluegreen bacteria in light-limited environments. FEMS Microbiology Letters 1:335–338.

Olsen, Y., O. Vadstein, T. Andersen, and A. Jensen. 1989. Competition between *Staurastrum luetkemuellerii* (Chlorophyceae) and *Microcystis aeruginosa* (Cyanophyceae) under varying modes of phosphate supply. Journal of Phycology 25:499–508.

Passarge, J., S. Hol, M. Escher, and J. Huisman. 2006. Competition for nutrients and light: stable coexistence, alternative stable states, or competitive exclusion? Ecological Monographs 76:57–72.

Pengerud, B., E. F. Skjoldal, and T. F. Thingstad. 1987. The reciprocal interaction between degradation of glucose and ecosystem structure: studies in mixed chemostat cultures of marine bacteria, algae, and bacterivorous nanoflagellates. Marine Ecology Progress Series 35:111–117.

Rothhaupt, K. O. 1988. Mechanistic resource competition theory applied to laboratory experiments with zooplankton. Nature 333: 660–662.

———. 1996. Laboratory experiments with a mixotrophic chrysophyte and obligately phagotrophic and phototrophic competitors. Ecology 77:716–724.

Schulze, P. C., H. E. Zagarese, and C. E. Williamson. 1995. Competition between crustacean zooplankton in continuous cultures. Limnology and Oceanography 40:33–45.

Sommer, U. 1985. Comparison between steady state and non–steady state competition: experiments with natural phytoplankton. Limnology and Oceanography 30:335–346.

———. 1986*a*. Nitrate- and silicate-competition among Antarctic phytoplankton. Marine Biology 91:345–351.

———. 1986*b*. Phytoplankton competition along a gradient of dilution rates. Oecologia (Berlin) 68:503–506.

Spijkerman, E., and P. F. M. Coesel. 1996. Competition for phosphorus among planktonic desmid species in continuous-flow culture. Journal of Phycology 32:939–948.

Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58:338–348.

———. 1980. Resources: a graphical-mechanistic approach to competition and predation. American Naturalist 116:362–393.

———. 1981. Tests of resource competition theory using four species of Lake Michigan algae. Ecology 62:802–815.

———. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ.

Tilman, D., and R. W. Sterner. 1984. Invasions of equilibria: tests of resource competition using two species of algae. Oecologia (Berlin) 61:197–200.

Tilman, D., and D. Wedin. 1991. Dynamics of nitrogen competition between successional grasses. Ecology 72:1038–1049.

Tilman, D., M. Mattson, and S. Langer. 1981. Competition and nutrient kinetics along a temperature gradient: an experimental test of a mechanistic approach to niche theory. Limnology and Oceanography 26:1020–1033.

van Donk, E., and S. S. Kilham. 1990. Temperature effects on silicon- and phosphorus-limited growth and competitive interactions among three diatoms. Journal of Phycology 26:40–50.

Zevenboom, W., J. van der Does, K. Bruning, and L. R. Mur. 1981. A non-heterocystous mutant of *Aphanizomenon flos-aquae*, selected by competition in light-limited continuous culture. FEMS Microbiology Letters 10:11–16.

Associate Editor: James P. Grover
Editor: Donald L. DeAngelis