COMPETITION FOR NUTRIENTS AND LIGHT: STABLE COEXISTENCE, ALTERNATIVE STABLE STATES, OR COMPETITIVE EXCLUSION?

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Abstract. Competition theory has put forward three contrasting hypotheses: Competition for nutrients and light may lead to (i) stable coexistence of species, (ii) alternative stable states, or (iii) competitive exclusion. This paper presents a detailed investigation of competition among phytoplankton species to test these three different hypotheses. First, we developed a competition model combining competition for nutrients and light. Next, we ran monoculture experiments in phosphorus-limited and light-limited chemostats to estimate the model parameters for five freshwater phytoplankton species. Finally, we tested the model predictions in competition experiments, using phosphorus levels ranging from oligotrophic to eutrophic conditions. The population dynamics in the competition experiments were all in agreement with the model predictions. This demonstrates that competition for nutrients and light can be accurately predicted over a wide range of productivities. The experiments revealed that the intensity of competition remained constant or even decreased with increasing nutrient supply. Contrary to expectation, there were no trade-offs between competitive abilities for phosphorus and light. Species that were strong competitors for phosphorus were strong competitors for light as well. Hence, we found neither stable coexistence nor alternative stable states. All competition experiments led to competitive exclusion. Furthermore, the physiological traits of the species indicated that, if one would find trade-offs in competitive abilities, competition for phosphorus and light would lead to alternative stable states rather than to stable coexistence. These results suggest that stable coexistence mediated by competition for phosphorus and light is rare, and hence an unlikely explanation for the high biodiversity commonly found in phytoplankton communities.

Key words: aquatic ecosystems; biodiversity; competition model; continuous culture; cyanobacteria; green algae; neutral coexistence; phosphate; photosynthesis; productivity gradient; resource competition; stoichiometry.

INTRODUCTION


At one extreme, in oligotrophic ecosystems with an ample supply of light, primary producers typically compete for limiting nutrients. Theory predicts that, in a well-mixed and constant environment, the species with the lowest critical nutrient requirements ($R^*$) will be the superior nutrient competitor (Stewart and Levin 1973, Hsu et al. 1977, Armstrong and McGehee 1980, Tilman 1982). This prediction is supported by numerous competition experiments (e.g., Tilman 1977, Tilman et al. 1981, Kilham 1984, Sommer 1985, 1986, van Donk and Kilham 1990, Ducobu et al. 1998).

At the other extreme, in eutrophic ecosystems with an ample nutrient supply, primary producers typically compete for light. Theory predicts that, in a well-mixed and constant environment, the species with the lowest “critical light intensity” ($I_{out}^*$) will be the superior competitor for light (Huisman and Weissing 1994). The critical light intensity of a species corresponds to the light intensity at the bottom of a well-mixed water column at which this species can just survive. This prediction is supported by competition experiments with light-limited phytoplankton (Huisman et al. 1999, Litchman 2003).

How does competition affect the species composition in ecosystems of intermediate productivity, between these two extremes? Here, competition theory puts forward three contrasting hypotheses (Tilman 1982, Huisman and Weissing 1995). The first hypothesis assumes there is no trade-off between competitive abilities for nutrients and light: species with low critical nutrient requirements have low critical light intensities as well.
Theoretical representation of the outcome of competition for nutrients and light between two species. The solid lines represent the zero net growth isoclines (ZNGIs) of the species. The dashed lines represent the slopes of the consumption vectors of the species. In each region of the graphs, the outcome of competition is indicated for supply points falling into that region. (A) No trade-off between competitive abilities for light and nutrients. Competition will lead to competitive exclusion. (B) Trade-off between competitive ability for light and competitive ability for nutrients, where the stronger nutrient competitor absorbs relatively more light while the stronger light competitor consumes relatively more nutrients. Competition will lead to stable coexistence. (C) Trade-off between competitive ability for light and competitive ability for nutrients, where the stronger nutrient competitor consumes relatively more nutrients while the stronger light competitor absorbs relatively more light. Competition will lead to alternative stable states. The figure is adapted from Tilman (1982) and Huisman and Weissing (1995).

Fig. 1A; the zero net growth isoclines do not intersect. Hence, the strongest competitor excludes all other species. In a sense, this corresponds to Grime’s (1979) concept of universal competitive ability. Grime further predicts that the intensity of competition increases with productivity, since species grow faster in productive environments. The second hypothesis assumes a trade-off between competitive abilities for nutrients and light (Fig. 1B; the zero net growth isoclines intersect), reflecting Tilman’s (1982, 1988) resource-ratio hypothesis. This hypothesis predicts that competition intensity remains unchanged along productivity gradients, while the species interactions gradually shift from competition for nutrients to competition for light with increasing nutrient supply. This yields stable coexistence of species at intermediate nutrient supply rates. The third hypothesis (Fig. 1C) again assumes a trade-off between competitive abilities for nutrients and light. However, the superior nutrient competitor consumes relatively more nutrients, and thereby favors its own dominance by generating nutrient limitation. Conversely, the superior light competitor absorbs relatively more light, and thereby generates light-limited conditions. Hence, the winner depends on the initial conditions. This hypothesis matches the concept of alternative stable states proposed by Scheffer et al. (1997, 2001), which predicts that gradual changes in nutrient loading may induce catastrophic shifts in species composition.

All three hypotheses have been supported by a variety of observational arguments (Grime 1979, Tilman 1982, 1988, Scheffer et al. 1997, 2001). Several of the predictions have been experimentally tested in terrestrial plant communities (Wilson and Tilman 1991, Campbell and Grime 1992, Reader et al. 1994, Gold-berg et al. 1999). However, the long generation times of plants make it difficult to test the predictions in plant competition studies. As a result, the three hypotheses have so far not been investigated to their full extent (Miller et al. 2005). Contrary to terrestrial plants, phytoplankton can be grown in microcosms for numerous generations. Phytoplankton studies may thus provide ideal model systems to test competition theory under highly controlled conditions.

In this paper, we investigate competition for nutrients and light along a productivity gradient using chemostat experiments with phytoplankton species. Our aims are (1) to provide a quantitative test of competition theory under nutrient and light limitation, (2) to reveal the experimental validity of the three contrasting hypotheses in Fig. 1, and (3) to elucidate how competition intensity varies along productivity gradients. We chose phosphorus as limiting nutrient, because phosphorus is a major limiting nutrient in aquatic ecosystems (Vollenweider 1968, Schindler 1974, Sommer 1989, Elser et al. 1990, Sterner 1994, Thingstad et al. 1998). First, we present a model to describe competition for phosphorus and light. We then use monoculture experiments to estimate the model parameters for five freshwater phytoplankton species. From these monoculture experiments, we predict the outcome of competition for phosphorus and light. Finally, we test the model predictions in a series of competition experiments at three different nutrient levels.

**Theory**

To investigate competition for phosphorus and light, we combine a nutrient-based with a light-based com-
petition model (Tilman 1982, Huisman and Weissing 1995). The competition model is described in full detail in Appendix A. Here we outline only its essential features. We consider a well-mixed water column, with a vertical light gradient, a limited amount of phosphorus, and several phytoplankton species. We use a variable-internal-stores approach to model the phosphorus contents of the phytoplankton species (Droop 1973, Grover 1991b, Ducobu et al. 1998, Sterner and Elser 2002). The variable-internal-stores model allows rapid uptake of phosphorus, which is stored in the cells and later used for growth. Furthermore, we assume that the underwater light gradient changes dynamically due to shading by the phytoplankton populations (Huisman and Weissing 1994, Huisman et al. 1999). That is, an increase of the phytoplankton populations results in more turbid water, with less light penetrating to the bottom of the water column. The transition from nutrient-limited to light-limited phytoplankton growth has earlier been described as a multiplicative function (Huisman and Weissing 1995). However, pilot experiments with our species revealed a rather abrupt shift in the intracellular phosphorus contents and in the specific light extinction coefficients in response to a slight change in the phosphorus load. This indicates a sharp transition from phosphorus-limited to light-limited growth, which is represented in our model by Von Liebig’s (1840) “Law of the Minimum.”

More specifically, let \( N_i \) denote the population density of phytoplankton species \( i \), let \( Q_i \) denote its intracellular phosphorus content, let \( R \) denote the phosphorus concentration in the water column, and let \( I_{\text{sat}} \) denote the light penetration to the bottom of the water column. Accordingly, the general structure of our model reads:

\[
\frac{dN_i}{dt} = \min\{\mu_{\text{in}}(Q_i); \mu_{\text{out}}(I_{\text{sat}})\}N_i - DN_i, \quad i = 1, \ldots, n \tag{1}
\]

\[
\frac{dQ_j}{dt} = v_j(R, Q_j) - \min\{\mu_{\text{in}}(Q_j); \mu_{\text{out}}(I_{\text{sat}})\}Q_j, \quad i = 1, \ldots, n \tag{2}
\]

\[
\frac{dR}{dt} = D(R_{\text{m}} - R) - \sum_{j=1}^{n} v_j(R, Q_j)N_j \tag{3}
\]

\[
I_{\text{sat}} = I_{\text{a}}\exp\left(-K_{\text{bg}}z_{\text{m}} - \sum_{j=1}^{n} k_jN_jz_{\text{m}}\right). \tag{4}
\]

The first equation describes the population dynamics of \( n \) competing phytoplankton species, where \( \mu_{\text{in}}(Q) \) is the specific growth rate of species \( i \) under phosphorus limitation as described by the Droop equation (Droop 1973), \( \mu_{\text{out}}(I_{\text{sat}}) \) is the specific growth rate of species \( i \) under light limitation as a function of the vertical light gradient, and \( D \) is the dilution rate.

The second equation describes the dynamics of the intracellular phosphorus contents of the phytoplankton species. The term \( v_j(R, Q) \) is the phosphorus uptake rate of species \( i \), which increases with the external phosphorus concentration according to Michaelis-Menten kinetics, while it decreases with the intracellular phosphorus content according to Morel (1987) and Ducobu et al. (1998).

The third equation describes the dynamics of the external phosphorus concentration in the water column, which depends on the phosphorus input concentration, \( R_{\text{m}} \), losses of phosphorus from the system, and phosphorus uptake by the phytoplankton species.

Finally, the fourth equation describes the vertical light gradient according to Lambert-Beer’s law, where \( I_{\text{a}} \) is the incident light intensity at the water surface, \( K_{\text{bg}} \) is the background turbidity caused by water, dissolved organic matter, and other light-absorbing substances, \( k_j \) is the specific light attenuation coefficient of phytoplankton species \( j \), and \( z_{\text{m}} \) is the total depth of the water column.

This mathematical model generates the predictions illustrated in Fig. 1 (Tilman 1982, Huisman and Weissing 1995). Each species has its own critical phosphorus requirements (\( R^* \)) and its own critical light intensity (\( I_{\text{sat}}^* \)). Under constant conditions, the variable-internal-stores model predicts that, if all species are limited by phosphorus, the species with the lowest \( R^* \) for phosphorus will be the superior competitor for phosphorus (Grover 1991b, Smith and Waltman 1994). Likewise, if all species are limited by light, the species with the lowest \( I_{\text{sat}}^* \) will be the superior competitor for light (Huisman and Weissing 1994, Huisman et al. 1999). Furthermore, the model predicts the existence of an intermediate region, where some species may be limited by phosphorus while others may be limited by light. In this intermediate region, depending on the parameter combinations of the species, the model predicts either competitive exclusion (Fig. 1A), or stable coexistence (Fig. 1B), or a winner that depends on the initial conditions (Fig. 1C). We test which of these three scenarios is most likely using microcosm experiments.

**METHODS**

**Species**

After a series of pilot experiments with 25 species of freshwater phytoplankton, we selected five species that were most compatible with the experimental requirements (i.e., species that were able to grow in our culture system and mineral medium with minimal wall growth and without aggregation of cells). The selected species were the green algae *Chlorella vulgaris* Beyerick (strain UTEX 1648), *Selenastrum capricornutum* Printz (strain UTEX 151); and *Monoraphidium griffithii* (Berk.) Kom.-Legn. (strain CCAP 202/15); the yellow-green alga *Monodus subterraneus* Petersen (strain UTEX 151); and the cyanobacterium *Synechocystis* (strain PCC-6803). The cultures were not grown axenically, but regular microscopic inspection revealed
that biomass of heterotrophic bacteria remained well under 1% of the total biomass.

Light and culture conditions

The species were grown in laboratory-built chemostats, specially tailored to study population dynamics of light-limited phytoplankton. The design of the chemostats and the general set-up of our experiments are described in detail in Huisman et al. (1999). The temperature in the chemostats was maintained at 20°C. The dilution rate of the chemostats was set at $D = 0.015$ h$^{-1}$ in all experiments. Flat chemostat vessels with an optical path length of $z_m = 5$ cm were used to obtain a unidirectional light gradient. Light intensities (PAR from 400 to 700 nm) were measured with a LI-190SA quantum sensor attached to a LI-250 light meter (LI-COR, Lincoln, Nebraska, USA). To account for spatial variation, the incident light intensity ($I_{in}$) and the light intensity penetrating through the cultures ($I_{out}$) were measured at 14 regularly spaced positions at the front surface and back surface of the chemostat vessel, respectively. Based on pilot experiments, the incident light intensity was set at $I_{in} = 40 \mu$mol photons·m$^{-2}$·s$^{-1}$ in all experiments.

Phosphorus

The chemostats were provided with a mineral medium, using three different levels of phosphorus supply. We used $R_m = 350 \mu$mol/L $K_2HPO_4·3H_2O$ to induce light limitation, $R_m = 4.5 \mu$mol/L $K_2HPO_4·3H_2O$ to induce phosphorus limitation, and $R_m = 15 \mu$mol/L $K_2HPO_4·3H_2O$ to induce conditions on the edge of phosphorus limitation and light limitation. In addition, the chemostats were provided with an ample supply of all other nutrients (see Appendix B). To avoid contamination with phosphorus from other sources, all materials were prewashed with hydrochloric acid. Since the chemostat vessels did not tolerate treatment with hydrochloric acid, they were pre-incubated for several weeks with mineral medium with the same phosphorus concentrations as in the subsequent experiment. Pilot experiments confirmed the imposed resource limitations: Under phosphorus-limited conditions, steady-state population densities increased only in response to an increase in the phosphorus supply. Under light-limited conditions, steady-state population densities increased only in response to an increase in the light supply.

Inorganic phosphorus concentrations were determined in triplicate after filtration of the samples through 0.45-$\mu$m nitrocellulose filters (Millipore Corporation, Bedford, Massachusetts, USA), which had been prewashed with hydrochloric acid. Phosphorus concentrations were determined according to Murphy and Riley (1962). Care was taken that the salinity and Fe(III)(NH$_4$)$_3$ citrate concentration of the phosphorus standard matched the concentrations in the samples, because our control measurements revealed that the method of Murphy and Riley was very sensitive to salinity and the redox state of iron. With these modifications, nanomolar phosphorus concentrations could be accurately determined.

Samples for intracellular phosphorus analysis were collected on 0.45-$\mu$m nitrocellulose filters (Millipore Corporation, Bedford, Massachusetts, USA), which had been prewashed with hydrochloric acid. The filters were then washed twice with 15 mL of phosphorus-free medium at 4°C before digesting the cells by K$_2$S$_2$O$_8$ according to Wetzel and Likens (2000). Subsequently, phosphorus concentrations were determined as described in the last paragraph.

Population densities

Population densities and biovolumes of the monoculture experiments were measured in triplicate with an automated cell counter (Casy Cell Counter, Schaefer System GmbH, Reutlingen, Germany). Since the cell counter could not distinguish between the different species, the population densities in the competition experiments were counted microscopically using Fuchs-Rosenthal counting chambers. However, because the cyanobacterium Synechocystis and the green alga Chlorella are of similar size and shape, they could not be accurately distinguished under the microscope either. Samples of the competition experiments with Synechocystis and Chlorella were therefore fixed in triplicate in a mixture of paraformaldehyde and glutaraldehyde (Tsuji and Yanagita 1981). Cell numbers were subsequently counted on a flow cytometer (Jonker et al. 1995) that distinguished cyanobacteria and green algae based on their different pigment composition. The three counting methods were calibrated to ensure that differences in methodology did not affect the results.

Parameter estimation

The model parameters were either experimentally controlled or estimated from monoculture experiments. The incident light intensity ($I_{in}$), the phosphorus concentration of the inflowing mineral medium ($R_m$), the dilution rate ($D$), and the water-column depth ($z_m$) were defined by the experimental conditions described in the preceding subsections.

The specific light extinction coefficients of the phytoplankton species and the background turbidity were calculated from the monoculture experiments, using Lambert-Beer’s Law. More precisely, for monocultures Eq. 4 can be written as $\ln(I_{in}/I_{out})/z_m = k_i N_i + K_{bg}$. We, therefore, monitored the full time course of population densities ($N_i$) and light penetration ($I_{out}$) from low initial population densities to steady state, and then applied linear regression to the term $\ln(I_{in}/I_{out})/z_m$ plotted against $N_i$. The specific light extinction coefficients of the phytoplankton ($k_i$) were estimated as the slopes of the regression, and the background turbidity ($K_{bg}$) was estimated as the intercept. Our experiments revealed that...
phytoplankton cells adjust their pigment composition to the prevailing phosphorus and light conditions. We therefore distinguished two different values for the specific light extinction coefficients of the phytoplankton species: the value of $k_{lj}$ under light limitation and the value of $k_{lji}$ under phosphorus limitation.

The maximal phosphorus uptake rates ($v_{\text{max}}$) were determined in separate batch culture experiments. The species were precultured in phosphorus-limited steady-state chemostats and then transferred to phosphorus-free batch cultures at approximately 3% of the steady-state population density. Light supply, aeration, and temperature in the batch cultures matched the conditions in the chemostats. After addition of a saturating pulse of phosphorus, the decline of the inorganic phosphorus concentrations in the batch cultures was closely monitored during several hours. The phosphorus concentrations were plotted vs. time, and $v_{\text{max}}$ was determined as the initial linear slope of the curve.

The maximal intracellular phosphorus contents ($Q_{\text{max}}$) were determined in triplicate in two exponentially growing batch cultures per species, after providing the cultures with saturating concentrations of inorganic phosphorus for several days. The minimal intracellular phosphorus contents ($Q_{\text{min}}$) were determined in triplicate in two phosphorus-starved batch cultures per species. The cells were precultivated in phosphorus-limited chemostats, centrifuged to remove external phosphorus in the medium, and then grown in batch cultures with phosphorus-free medium. Subsequently, intracellular phosphorus concentrations and cell numbers were monitored during several weeks. The minimal intracellular phosphorus contents were determined as the intracellular phosphorus contents when the cells had reached the stationary phase.

The remaining species parameters are the maximal specific growth rates ($\mu_{\text{max}}$), the half-saturation constants for phosphorus uptake ($H_{ci}$), and the half-saturation constants of light-limited growth ($H_{i}$). The maximal specific growth rates were calculated by solving the Droop equation (Eq. A1 in Appendix A) at equilibrium. The two half-saturation constants were estimated by fitting the model predictions of Eqs. 1–4 to the time courses of the observed population densities and resource availabilities in the monoculture experiments. Model fits were obtained by minimization of the residual sum of squares. For this purpose, population densities and resource availabilities were first log-transformed to homogenize the variances. Thereafter, the log-transformed population densities and resource availabilities were normalized, using their total sum of squares as a weighting factor, to give equal weight to each of these variables in the fitting procedure. Since the dynamical system defined by Eqs. 1–4 is nonlinear, minimization of the residual sum of squares requires an iterative process. The iteration process was based on the Gauss-Marquardt-Levenberg algorithm, using the software package PEST (Watermark Numerical Computing, Brisbane, Australia).

The parameter estimates thus obtained from the monoculture experiments were used to predict the dynamics and the outcome of the competition experiments.

RESULTS

Phosphorus limitation in monoculture

Short-term batch experiments, used to measure the phosphorus uptake kinetics of the species, showed that phosphorus uptake is a relatively rapid process occurring on a time scale of minutes to a few hours (Appendix C). In agreement with these results, the long-term chemostat experiments with phosphorus-limited monocultures revealed that the external phosphorus concentrations were rapidly depleted (Fig. 2). Population densities increased concomitantly, but on a slower time scale. Population densities reached a steady state after eight to 12 days, depending on the species. The difference in time scale between the rapid phosphorus uptake and the slow increase in population densities reflects temporary storage of intracellular phosphorus, as adequately described by the variable-intern-stores model (Appendix C). The population dynamics and phosphorus depletion predicted by the model generally fitted well to the monoculture experiments (Fig. 2). The model parameters obtained from the monoculture experiments are given in Table 1. Equilibrium population densities under phosphorus limitation differed up to twenty-fold among the species (Table 2). This difference was mostly caused by the large differences in cell size among the species. In terms of total biovolume, the population densities reached by the species were more similar (Table 2). The critical phosphorus concentrations ($R^*$) of the species were determined as the steady-state concentrations of external phosphorus in monoculture. Critical phosphorus concentrations were significantly different between the species (Table 2; ANOVA, $F_{3,75} = 41.49$, $P < 0.001$), ranging from $R^* = 30$ nmol phosphorus/L for Synechocystis to $R^* = 182$ nmol phosphorus/L for Monodus.

Light limitation in monoculture

Fig. 3 shows the time courses of the monoculture experiments with a high supply of phosphorus, thereby generating light-limited conditions. In each experiment, population density increased and, hence, light penetration ($I_{\text{up}}$) through the culture vessels decreased until a steady state was reached after 12 to 22 days. In contrast to the phosphorus-limited experiments, the light-limited experiments did not show a time lag between resource dynamics and population dynamics. The sudden increase in light penetration through the Synechocystis monoculture at days 11 to 13 (Fig. 3A) was caused by temporary aggregation of the cells.
FIG. 2. Monoculture experiments under phosphorus-limited conditions: (A) *Synechocystis* (gray squares), (B) *Chlorella* (“plus” symbols), (C) *Monoraphidium* (triangles up), (D) *Selenastrum* (black squares), and (E) *Monodus* (triangles down). Open diamonds indicate the external phosphorus concentration. Solid lines indicate the population densities predicted by the model (Eqs. 1–4), and dotted lines indicate the predicted external phosphorus concentrations. For parameter values, see Table 1.

**TABLE 1.** Model parameters estimated from the monoculture experiments.

<table>
<thead>
<tr>
<th>Parameter</th>
<th><em>Synechocystis</em></th>
<th><em>Chlorella</em></th>
<th><em>Monoraphidium</em></th>
<th><em>Selenastrum</em></th>
<th><em>Monodus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>$\mu_{\text{max}}$ (h$^{-1}$)</td>
<td>0.090</td>
<td>0.079</td>
<td>0.038</td>
<td>0.055</td>
<td>0.048</td>
</tr>
<tr>
<td>$H_L$ ($\mu$mol photons·m$^{-2}$·s$^{-1}$)</td>
<td>58</td>
<td>50</td>
<td>24</td>
<td>45</td>
<td>37</td>
</tr>
<tr>
<td>$k_i$ ($\times 10^{-11}$ m$^2$/cell)</td>
<td>3.45</td>
<td>9.32</td>
<td>13.70</td>
<td>16.66</td>
<td>2.31</td>
</tr>
<tr>
<td>$k_R$ ($\times 10^{-11}$ m$^2$/cell)</td>
<td>0.10 ± 0.006</td>
<td>0.24 ± 0.016</td>
<td>1.10 ± 0.036</td>
<td>0.46 ± 0.009</td>
<td>0.21 ± 0.005</td>
</tr>
<tr>
<td>$Q_{\text{min}}$ (fmol/cell)</td>
<td>6.45 ± 1.57</td>
<td>7.70 ± 1.15</td>
<td>22.35 ± 2.70</td>
<td>14.51 ± 0.89</td>
<td>32.54 ± 3.68</td>
</tr>
<tr>
<td>$Q_{\text{max}}$ (fmol/cell)</td>
<td>0.30 ± 0.02</td>
<td>1.23 ± 0.13</td>
<td>3.53 ± 0.21</td>
<td>1.94 ± 0.17</td>
<td>1.11 ± 0.63</td>
</tr>
<tr>
<td>$v_{\text{max}}$ (fmol·cell$^{-1}$·h$^{-1}$)</td>
<td>0.62 ± 0.06</td>
<td>3.51 ± 0.23</td>
<td>9.17 ± 0.27</td>
<td>3.22 ± 0.18</td>
<td>0.34 ± 0.01</td>
</tr>
</tbody>
</table>

**Notes:** Values are reported as means ± sd. Parameters are maximum specific growth rate, $\mu_{\text{max}}$; half-saturation constant of light-limited growth, $H_L$; half-saturation constant for phosphorus uptake, $H_R$; specific light attenuation coefficient for light-limited phytoplankton, $k_i$; specific light attenuation coefficient for phosphorus-limited phytoplankton, $k_R$; maximum intracellular phosphorus content, $Q_{\text{min}}$; minimum intracellular phosphorus content, $Q_{\text{max}}$; and maximum phosphorus uptake rate, $v_{\text{max}}$. System parameters were measured directly: dilution rate, $D = 0.015$ h$^{-1}$; total depth of the water column, $z_m = 0.05$ m; incident light intensity, $I_m = 40$ μmol photons·m$^{-2}$·s$^{-1}$; background turbidity, $K_m = 5.5–7.2$ m$^{-1}$ (varied between experiments); phosphorus input concentration, $R_{\text{in}} = 4.5$ μmol P/L under P limitation, $R_{\text{in}} = 15$ μmol P/L on the edge of phosphorus and light limitation, $R_{\text{in}} = 350$ μmol P/L under light limitation. For initial conditions used in the model simulations of the experiments, see Appendix D.
**Table 2. Steady-state traits of the phytoplankton species, measured in monoculture experiments under light limitation and under phosphorus limitation.**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Synechocystis</th>
<th>Chlorella</th>
<th>Monoraphidium</th>
<th>Selenastrum</th>
<th>Monodus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population density (×10^9 cells/L)</td>
<td>51.6 ± 2.3</td>
<td>20.6 ± 2.0</td>
<td>2.7 ± 0.1</td>
<td>6.6 ± 1.8</td>
<td>13.8 ± 0.4</td>
</tr>
<tr>
<td>Light limitation</td>
<td>12.6 ± 0.3</td>
<td>2.9 ± 0.3</td>
<td>0.7 ± 0.1</td>
<td>1.6 ± 0.1</td>
<td>2.6 ± 0.3</td>
</tr>
<tr>
<td>Phosphorus limitation</td>
<td>0.01 ± 0.00</td>
<td>0.08 ± 0.01</td>
<td>10.0 ± 0.01</td>
<td>0.17 ± 0.01</td>
<td>0.18 ± 0.01</td>
</tr>
<tr>
<td>Total biovolume (mL/L)</td>
<td>0.59 ± 0.03</td>
<td>0.59 ± 0.05</td>
<td>0.45 ± 0.02</td>
<td>0.50 ± 0.13</td>
<td>0.48 ± 0.02</td>
</tr>
<tr>
<td>Light penetration (μmol photons·m⁻²·s⁻¹)</td>
<td>2.17 ± 0.10</td>
<td>2.36 ± 0.21</td>
<td>5.50 ± 0.31</td>
<td>6.35 ± 0.10</td>
<td>6.86 ± 0.20</td>
</tr>
<tr>
<td>External P concentration (μmol P/mL)</td>
<td>220.0 ± 0.5</td>
<td>23.1 ± 0.3</td>
<td>22.4 ± 0.9</td>
<td>18.9 ± 0.8</td>
<td>20.2 ± 0.7</td>
</tr>
<tr>
<td>Light limitation</td>
<td>2.82 ± 19.8</td>
<td>269.5 ± 17.9</td>
<td>255.6 ± 12.4</td>
<td>262.0 ± 7.9</td>
<td>197.0 ± 10.7</td>
</tr>
<tr>
<td>Phosphorus limitation (R*)</td>
<td>0.030 ± 0.022</td>
<td>0.059 ± 0.045</td>
<td>0.117 ± 0.042</td>
<td>0.160 ± 0.054</td>
<td>0.182 ± 0.023</td>
</tr>
<tr>
<td>Intracellular P content (μmol P/L)</td>
<td>136.2 ± 18.7</td>
<td>142.1 ± 13.1</td>
<td>124.6 ± 13.8</td>
<td>123.9 ± 5.9</td>
<td>116.1 ± 10.1</td>
</tr>
<tr>
<td>Light limitation</td>
<td>55.14 ± 5.44</td>
<td>59.29 ± 6.29</td>
<td>42.37 ± 6.15</td>
<td>25.00 ± 2.79</td>
<td>23.82 ± 3.04</td>
</tr>
<tr>
<td>Phosphorus limitation</td>
<td>11.4 ± 0.9</td>
<td>28.6 ± 2.9</td>
<td>167.9 ± 6.1</td>
<td>75.0 ± 2.5</td>
<td>34.4 ± 0.9</td>
</tr>
<tr>
<td>Cell volume (fL/cell)</td>
<td>8.0 ± 0.1</td>
<td>27.1 ± 2.6</td>
<td>150.5 ± 17.6</td>
<td>106.0 ± 3.2</td>
<td>65.9 ± 8.6</td>
</tr>
</tbody>
</table>

**Notes:** Monocultures were maintained at steady state for several months. Steady-state traits were based on 16 measurements per monoculture. To reduce temporal autocorrelation, measurements were spaced at least three days apart. Values are reported as means ± SD. The R*, Iₘ*, and intracellular P contents were tested for differences between species, using ANOVA with Student-Newman-Keuls multiple comparisons test. Different letters indicate significant differences (P < 0.05).

Equilibrium population densities under these eutrophic conditions were several times higher than under phosphorus-limited conditions (Table 2). As under phosphorus limitation, the almost 20-fold differences in equilibrium population density among the species were mostly caused by differences in cell size among the species. We determined the critical light intensities (Iₘ*) of the species as the steady-state light penetration in monoculture. Critical light intensities were significantly different between the species (Table 2; ANOVA, F_5,24 = 2234.27, P < 0.001), ranging from 2.2 μmol photons·m⁻²·s⁻¹ for Synechocystis to 6.9 μmol photons·m⁻²·s⁻¹ for Monodus.

**Model predictions**

The species traits measured in monoculture (Tables 1 and 2) allow prediction of the dynamics of competition for nutrients and light. The monoculture experiments revealed a strong positive correlation between the critical external phosphorus concentrations and the critical light intensities of the species (Fig. 4A; Pearson correlation, r = 0.98, N = 5, P < 0.005). In fact, the ranking of the species according to their critical phosphorus concentrations was identical to the ranking according to their critical light intensities: Synechocystis < Chlorella < Monoraphidium < Selenastrum < Monodus. Hence, the model predicts that the best competitor for phosphorus will also be the best competitor for light. In graphical terms, the zero net growth isoclines of the species do not intersect (as in Fig. 1C; see Appendix E). Along the entire productivity gradient, Synechocystis should outcompete all other four species, Chlorella should outcompete all others except for Synechocystis, Monoraphidium should outcompete Selenastrum and Monodus, and so on. Theory thus predicts that competition for phosphorus and light among these species should lead to competitive exclusion.

The monoculture data also reveal other interesting correlations between species traits. There is a strong negative correlation between the critical light intensities of the species and their specific light extinction coefficients per unit biovolume (Fig. 4B; Pearson correlation, r = -0.99, N = 5, P < 0.002). That is, superior competitors for light absorb more light per unit biomass than weak competitors. Furthermore, there is also a strong negative correlation between the critical phosphorus concentrations of the species and their intracellular phosphorus contents per unit biovolume (Fig. 4C; Pearson correlation, r = −0.96, N = 5, P < 0.01). That is, superior phosphorus competitors have higher intracellular phosphorus contents than weak competitors.

**Competition for phosphorus**

In our first competition experiment at low phosphorus levels, we inoculated Synechocystis and Chlorella at low population densities (Fig. 5A). Both species initially increased. Moreover, owing to phosphorus uptake, the intracellular phosphorus concentrations of both species increased as well (not shown). Consequently, the external phosphorus concentration was rapidly depleted to the nanomolar range. After ~7 d, Chlorella started to decrease. Hence, Synechocystis competitively excluded Chlorella. In a similar fashion,
Fig. 3. Monoculture experiments under light-limited conditions: (A) *Synechocystis* (gray squares), (B) *Chlorella* (“+” symbols), (C) *Monoraphidium* (triangles up), (D) *Selenastrum* (black squares), and (E) *Monodus* (triangles down). Open circles indicate the light intensity $I_{\text{out}}$ penetrating through the cultures. Solid lines indicate the population densities predicted by the model (Eqs. 1–4), and dotted lines indicate the predicted light penetration. For parameter values, see Table 1.

*Chlorella* displaced *Monoraphidium* (Fig. 5B), *Monoraphidium* displaced *Selenastrum* (Fig. 5C), and *Selenastrum* displaced *Monodus* (Fig. 5D).

On the edge of competition for phosphorus and competition for light

In the competition experiments with intermediate levels of phosphorus, on the edge of phosphorus limitation and light limitation, species had to compete for both phosphorus and light. Similar to the previous competition experiments, *Synechocystis* displaced *Chlorella* (Fig. 6A), *Chlorella* displaced *Monoraphidium* (Fig. 6B), *Monoraphidium* displaced *Selenastrum* (Fig. 6C), and *Selenastrum* displaced *Monodus* (Fig. 6D). Measurements of the external and intracellular phosphorus concentrations and of the specific light extinction coefficients of the species suggested that, as predicted by the model, the species were mainly light limited during the first weeks of the experiments, while they were mainly phosphorus limited during the latter part of the experiments.

Competition for light

Fig. 7 shows the competition experiments at high phosphorus levels, generating light-limited conditions. The critical light intensities of *Chlorella* and *Synechocystis* were so close, that competitive exclusion of *Chlorella* by *Synechocystis* was predicted to take more than a year. Accordingly, competitive exclusion of *Chlorella* could not be observed within the time span of this experiment (Fig. 7A). *Chlorella*, in turn, was predicted to be a much stronger competitor for light than *Monoraphidium*. Indeed, *Chlorella* competitively displaced *Monoraphidium* within 60 days (Fig. 7B). Similarly, *Monoraphidium* excluded *Selenastrum* (Fig. 7C). Competitive exclusion of *Monodus* by *Selenastrum*...
COMPETITION FOR NUTRIENTS AND LIGHT

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Correlations between species traits. (A) Positive correlation between the critical light intensities \( I_{\text{out}} \) and critical phosphorus concentrations \( R^* \) of the species. (B) Species with a low critical light intensity \( I_{\text{out}} \) have a high specific light extinction coefficient per unit biovolume. (C) Species with a low critical external phosphorus concentration \( R^* \) have a high intracellular phosphorus content per unit biovolume. Key to symbols: Synechocystis, gray squares; Chlorella, “plus” symbols; Monoraphidium, up-pointing triangles; Selenastrum, black squares; Monodus, down-pointing triangles. Error bars show standard error of the mean \( N = 16 \). When not visible, the error bars do not exceed the size of the symbol.

Competition for a single resource

The results show that competition for nutrients and light can be accurately predicted over a wide range of productivities. At low phosphorus levels, theory predicts that the species with the lowest critical phosphorus concentration \( R^* \) will be the superior competitor for phosphorus (Armstrong and McGehee 1980, Tilman 1982). Consequently, Synechocystis should be a better competitor for phosphorus than Chlorella, which in turn should be a better competitor than Monoraphidium, and so on. The competition experiments confirmed this prediction. In line with earlier studies (Tilman 1977, Tilman et al. 1981, Sommer 1985, 1986, van Donk and Kilham 1990, Ducobu et al. 1998), the species with lowest \( R^* \) was consistently the better competitor for phosphorus.

Conversely, at high phosphorus levels, theory predicts that the species with lowest critical light intensity \( I_{\text{out}} \) will be the superior competitor for light (Huisman and Weissing 1994, Huisman et al. 1999; but see Stomp et al. 2004). Monoculture experiments showed that the critical light intensity of Synechocystis was only slightly lower than that of Chlorella (Table 2). Hence, theory predicts that competitive exclusion will be extremely slow, even though ultimately Chlorella should be excluded. Indeed, Synechocystis and Chlorella coexisted for more than two months (Fig. 7A, E). This is an experimental example of “neutral coexis-

Discussion

Would competitive exclusion at different phosphorus levels proceed at different rates? To address this question, we measured the intensity of competition in our experiments as the “rate of competitive exclusion,” following Grover (1991a). More precisely, the rate of competitive exclusion was calculated as the slope of the linear regression of \( \ln(\text{population density of the winner/population density of the loser}) \) vs. time. The results show that in the competition experiments with the species pair Chlorella versus Monoraphidium, the rate of competitive exclusion was identical along the entire gradient of phosphorus supply (Table 3). For the three other species pairs, competitive exclusion was significantly faster at low and intermediate phosphorus supply than at high phosphorus supply (Table 3).
Fig. 5. Competition experiments under phosphorus-limited conditions: (A) Synechocystis (gray squares) displaces Chlorella (‘‘plus’’ symbols); (B) Chlorella (‘‘plus’’ symbols) displaces Monoraphidium (up-pointing triangles); (C) Monoraphidium (up-pointing triangles) displaces Selenastrum (black squares); (D) Selenastrum (black squares) displaces Monodus (down-pointing triangles). Open diamonds indicate the external phosphorus concentration. Solid lines indicate the population densities predicted by the model (Eqs. 1–4), and dotted lines indicate the predicted external phosphorus concentrations. For parameter values, see Table 1.

...ence’’ (sensu Grover 1997), where competitors are sufficiently similar to coexist for prolonged periods of time. Examples of neutral coexistence have also been found in several other competition studies (Hansen and Hubbell 1980, Tilman 1981). Most other species combinations under light-limited conditions showed rapid competitive displacement. As predicted, in all experiments the species with lowest critical light intensity was the better competitor for light.

Trade-offs between competition for nutrients and light?

Rather surprisingly, the experiments did not reveal trade-offs between the competitive abilities for phosphorus and light. Instead, the experiments showed that the critical light intensities of the species were ranked in the same order as their critical phosphorus concentrations (Fig. 4A). That is, strong competitors for phosphorus were strong competitors for light as well. Thus, our findings deviate from the expectation of Tilman (1982, 1988) that competition for nutrients and light should favor stable coexistence. They also deviate from the opposite prediction by Scheffer et al. (1997, 2001), that competition for nutrients and light should generate alternative stable states. Instead, all our experiments point at competitive exclusion (Figs. 5–7).

Why is there no trade-off between competitive ability for phosphorus and competitive ability for light? It can, of course, be argued that we investigated only five species. The observed lack of a trade-off might be mere coincidence. Indeed, we cannot rule out the possibility that the trade-off does exist for numerous other phytoplankton species that we have not investigated. However, the probability that five species would, by chance, have the same ranking of their competitive abilities for both phosphorus and light is rather low. To be precise, for a single resource, the competitive abilities of five species can be ranked in $5! = 120$ different ways. Hence, the probability that, by chance, the competitive abilities of five species are ranked in the same order for two different resources is $1/120 = 0.008$. It is thus unlikely to find a strictly positive correlation between the competitive abilities for phosphorus and light by chance alone. More likely, the pattern is real.

One might further argue that we investigated only a limited set of environmental conditions. Theory predicts that $R^*$ depends on the dilution rate ($\tau$, Tilman 1982, Grover 1997), and that the critical light intensity ($I_{\text{out}*}$) depends on both the dilution rate and the incident light intensity (Huisman and Weissing 1994, Huisman 1999). The dependence of $R^*$ and $I_{\text{out}*}$ on these environmental conditions implies that trade-offs might have
been discovered with other dilution rates or other incident light intensities (i.e., the zero net growth isoclines shift position when $D$ and $I_{in}$ are changed). To investigate this potential caveat, we ran 10,000 simulations with the parameterized model using a wide range of different values of incident light intensity and dilution rate. In each simulation, two species were randomly chosen from our species pool, the incident light intensity was randomly chosen from the range $I_{in} = 10$ to $I_{in} = 200 \, \mu\text{mol photons m}^{-2}\text{s}^{-1}$, and the dilution rate was randomly chosen from the range $D = 0.005$ h$^{-1}$ to the highest $D$ that would just allow persistence of both species in monoculture. We found that 93.0% of the simulations led to competitive exclusion (the scenario in Fig. 1A), whereas only 2.8% led to stable coexistence (Fig. 1B) and 4.2% led to alternative stable states (Fig. 1C). This again illustrates the robustness of our findings. We therefore conclude that the lack of a trade-off between the competitive abilities for phosphorus and light is not an accidental observation but reflects a robust pattern, at least for freshwater phytoplankton.

What is the underlying mechanism? A first hypothesis might be that the positive correlation between competitive ability for phosphorus and for light is related to cell size. According to allometric scaling rules, smaller phytoplankton will have higher surface-to-volume ratios and higher specific growth rates, and will therefore generally be better competitors for limiting resources (Raven 1998, Irigoien et al. 2004). Indeed, *Synechocystis* was both the smallest species and the best competitor in our experiments (Table 2). Moreover, *Chlorella* was both the second-smallest species and the second-best competitor in the experiments. For the other species, however, the relation between size and competitive ability did not apply: *Monoraphidium* was the largest species, yet the third-best competitor. *Monodus* was smaller than *Monoraphidium* and *Selenastrum*, yet the poorest competitor in the series. Therefore, the positive correlation between the competitive abilities for phosphorus and light cannot be fully explained by cell size.

A possible alternative explanation for the positive correlation between competitive ability for phosphorus and light is linked to the role of phosphorus in cell physiology. Strikingly, strong competitors were able to maintain higher phosphorus contents under phosphorus limitation than weak competitors (Fig. 4C; see also Grover 1989). High phosphorus contents under phosphorus-limited conditions may indicate high RNA levels and ribosomal activity (Sterner and Elser 2002). Species investing more in RNA and ribosomal activity will be biochemically more active, and might therefore be superior competitors for both phosphorus and light.
If the nature of the limiting nutrient indeed plays a major role, trade-offs between competitive abilities for light and nutrients other than phosphorus might be more likely. For instance, although we did not find trade-offs for light and phosphorus, there might be trade-offs for light and nitrogen, or for light and iron (Smith 1986, Timmermans et al. 2001, Leonaridos and Geider 2004).

These various perspectives indicate that further study of the physiological basis of competitive abilities for nutrients and light is highly recommended.

**Stable coexistence or alternative stable states?**

Suppose that one would find trade-offs between competitive abilities for phosphorus and light in other phytoplankton species or under different growth condi-
tions. Would our results then suggest stable coexistence (Fig. 1B) or alternative stable states (Fig. 1C)? In graphical terms, the answer will depend on the configuration of the zero net growth isolines and the consumption vectors (Tilman 1982, Huisman and Weissing 1995). Interestingly, the monoculture data showed that superior competitors for light absorb more light per unit biomass than weak competitors (Fig. 4B). This pattern seems quite plausible from a physiological perspective, since efficient light absorption will enable survival at low light levels (i.e., a low critical light intensity). Furthermore, the monoculture data showed that superior competitors for phosphorus had higher phosphorus contents (Fig. 4C). In other words, superior light competitors absorb relatively more light, thereby generating light-limited conditions. Conversely, superior phosphorus competitors consume relatively more phosphorus, thereby generating phosphorus-limited conditions. Hence, if there would be a trade-off between competitive abilities for phosphorus and light, our results imply that the configuration of the zero net growth isolines and consumption vectors would resemble Fig. 1C. The physiological traits of the species are therefore more likely to promote alternative stable states than stable coexistence. This is consistent with the above-mentioned 10,000 simulations, which yielded more examples of alternative stable states than of stable coexistence.

**Competition intensity along productivity gradients**

The impact of habitat productivity on competition intensity has been one of the most hotly debated issues in ecology (Grace 1993, Reader et al. 1994, Foster et al. 2004). Some have argued that, since biomass increases with productivity, the intensity of competition will increase with productivity as well (Grime 1979, Keddy 1989, Campbell and Grime 1992). Others have argued that the intensity of competition does not change with productivity, but that there is a shift in competitive focus from competition for nutrients in environments with low productivity to competition for light in environments with high productivity (Newman 1973, Tilman 1988, Wilson and Tilman 1991).

An advantage of phytoplankton studies is that competitive interactions can be investigated over numerous generations. This allows an accurate estimation of competition intensity. To measure the intensity of competition we calculated the “rate of competitive exclusion,” which compares the relative rates of change of the winners and losers (i.e., it is a measure of relative competition intensity sensu Grace 1993). The competition experiments clearly show that competitive exclusion does not become faster with increasing productivity. In fact, for three of the four species pairs investigated, we found a tendency towards the opposite pattern: species were more rapidly excluded at low and intermediate phosphorus levels than at high phosphorus levels (Table 3, Figs. 5–7). These results demonstrate that resource competition may effectively suppress the growth of inferior competitors at low productivity. For phytoplankton, at least, the hypothesis that the intensity of competition will increase with productivity can be rejected.

**Productivity–biodiversity patterns**

The unexpected lack of a trade-off between competitive abilities for phosphorus and light, two key resources in freshwater ecosystems, has implications for the interpretation of biodiversity patterns along productivity gradients. Productivity–biodiversity patterns of primary producers often follow a unimodal curve, with maximum diversity at intermediate productivity (Grime 1973, Tilman 1982, Rosenzweig 1995, Dodson et al. 2000, Mittelbach et al. 2001, Irigoien et al. 2004). It is commonly argued that the high diversity at intermediate productivity reflects a competitive balance, where species coexist on the transition from competition for nutrients to competition for light. In the absence of a trade-off between competitive abilities for nutrients and light, however, this classic explanation cannot hold. Our results do support an alternative explanation based on keystone predation (Leibold 1996). Strong competitors had significantly higher intracellular phosphorus contents than weak competitors (Table 2; ANOVA; under phosphorus limitation, $F_{4,25} = 201.18, P < 0.001$; under light limitation, $F_{4,25} = 10.56$,

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**Table 3. Rates of competitive exclusion.**

<table>
<thead>
<tr>
<th>Species pair</th>
<th>Phosphorus</th>
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<tbody>
<tr>
<td></td>
<td>Low</td>
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<tr>
<td><em>Synechocystis</em> vs. <em>Chlorella</em></td>
<td>0.35$^a$ ± 0.02</td>
</tr>
<tr>
<td><em>Chlorella</em> vs. <em>Monoraphidium</em></td>
<td>0.17$^a$ ± 0.01</td>
</tr>
<tr>
<td><em>Monoraphidium</em> vs. <em>Selenastrum</em></td>
<td>0.13$^a$ ± 0.01</td>
</tr>
<tr>
<td><em>Selenastrum</em> vs. <em>Monodus</em></td>
<td>0.08$^a$ ± 0.00</td>
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</table>

**Notes:** Rates of competitive exclusion (in units of day$^{-1}$) were calculated according to Grover (1991a), as the slope of the linear regression of ln(population density winner/population density loser) vs. time. Values are reported as slopes ± SE. For each species pair, we tested whether different phosphorus levels yielded different rates of competitive exclusion, using a comparison of the slopes of the regression lines with Tukey’s test. Different letters indicate significant differences ($P < 0.05$).
Therefore, phytoplankton species that are good competitors for phosphorus and light may constitute a preferred food source for zooplankton (Andersen and Hessen 1991, Urabe and Sterner 1996, DeMott and Gulati 1999, Sterner and Elser 2002), hence exposing them to higher grazing pressure. This trade-off between competitive ability and susceptibility to grazing also produces unimodal productivity-biodiversity patterns (Leibold 1996).

Caveats and conclusions

Our approach shares both the strengths and limitations of microcosm experiments (Daehler and Strong 1996). One limitation, for instance, is that mixing in microcosms is very fast, which may have induced a sharp transition from phosphorus to light limitation. Mixing will be much slower in real aquatic ecosystems, such that cells may become nutrient-limited in the upper water column but light-limited below, which might produce a smoother transition from phosphorus to light limitation. Furthermore, our microcosms assumed homogeneous mixing in a constant environment. Deviations from these highly idealized conditions may shift the competitive dominance and/or promote species coexistence (SOMMER 1985, Grover 1991b, Litchman and Klausmeier 2001, Flöder et al. 2002, Huisman et al. 2004).

A major strength of microcosm experiments, however, is that they allow rigorous tests of proposed mechanisms under controlled conditions. Experimental tests are a crucial element in the advancement of ecological theory. Our experiments demonstrate that the dynamics of competition for nutrients and light can be predicted over a wide range of productivities. The experiments further show that the intensity of competition, as measured by the rate of competitive exclusion, does not increase with productivity. Contrary to expectation, however, we found neither stable coexistence nor alternative stable states. Instead, all our experiments point to the same conclusion: competition for phosphorus and light in a mixed water column favors competitive exclusion.

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Literature Cited


APPENDIX A
Detailed description of the competition model (Ecological Archives M076-004-A1).

APPENDIX B
Description of the mineral medium and inorganic carbon supply used in the experiments (Ecological Archives M076-004-A2).

APPENDIX C
Figures illustrating the phosphorus uptake kinetics and the dynamics of intracellular phosphorus storage (Ecological Archives M076-004-A3).

APPENDIX D
A table with the initial conditions used in the model simulations of the monoculture and competition experiments (Ecological Archives M076-004-A4).

APPENDIX E
A figure illustrating the zero net growth isoclines of the species (Ecological Archives M076-004-A5).