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Competition and coexistence of phytoplankton under fluctuating light: experiments with two cyanobacteria

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ABSTRACT: The effects of light fluctuations on phytoplankton competition were examined in the experiments with 2 freshwater cyanobacteria, *Anabaena flos-aquae* and *Phormidium luridum*. Light regimes had the same average irradiance of 50 µmol photons m^{-2} s^{-1} and included constant light, high-low light fluctuations of 8 and 24 h periods and light:dark fluctuations of a 24 h period. A mechanistic model of light competition was used to predict competitive outcomes under these light regimes. The parameter values were obtained experimentally for constant light conditions. In the experiments, *A. flos-aquae* was rapidly excluded under constant light but persisted under fluctuating light. The model predicted well the dynamics and the outcome of competition under constant light but performed poorly under fluctuating light. The results indicate that light fluctuations may change the dynamics and outcome of competition and slow competitive exclusion and also that competition under fluctuating light cannot necessarily be predicted from the constant light monoculture dynamics.

KEY WORDS: Cyanobacteria · Competition · Irradiance · Fluctuations

INTRODUCTION

Environmental variability plays an important role in ecological communities. Nonequilibrium environmental conditions were set forth to explain the paradox of the plankton, where many species of phytoplankton coexist in a relatively homogeneous environment (Hutchinson 1961, Richerson et al. 1970). One of the important aspects of nonequilibrium environmental conditions is fluctuation in resource levels. Theoretical investigations show that variable resource supply can promote coexistence and increase diversity (Levins 1979, Armstrong & McGehee 1980, Hsu 1980), thus supporting Hutchinson's explanation of 'the paradox of the plankton' (1961). Experimental studies with phytoplankton showed that fluctuations in major limiting nutrients can alter competitive interactions and increase diversity (Turpin & Harrison 1979, Sommer 1985, Suttle et al. 1987, Grover 1988, 1990).

Light is a major essential resource in aquatic systems and is highly variable in both time and space. However, surprisingly little attention has been paid to the effects of fluctuating light supply on phytoplankton competition. Brzezinski & Nelson (1988) considered competition between 2 diatoms for ammonia under fluctuating light of non-limiting levels. They found that a fluctuating light regime facilitated coexistence of both species, while constant light conditions led to competitive exclusion of one of the species. Similarly, van Gemerden (1974) demonstrated that 2 strains of sulfur bacteria were able to coexist under variable light conditions while competing for a substrate. However, no studies have looked at the effects of fluctuating light at limiting levels on competitive interactions among phytoplankton.

Here, I examine how fluctuating light at limiting levels affects competitive interactions in freshwater phytoplankton. Light-limited conditions are not uncommon in natural waters and may result from either a deep mixed layer, high background turbidity (e.g. dissolved organic carbon [DOC] or suspended particles) and/or high biomass of phytoplankton. In eutrophic

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lakes, dense cyanobacterial blooms often create light-limited conditions where algae compete for light by mutual shading (Klemer 1985, Reynolds 1987). Competition for light among phytoplankton under constant irradiance has been investigated in the experiments of Mur et al. (1977) and Huisman et al. (1999). They showed that a species capable of reducing incident light to the lowest level (I_{out}, the incident light level at the bottom of the water column; sensu Huisman & Weissing 1994) wins competition. At the same time, in natural waters, even in severely light-limited environments, more than 1 species can be found simultaneously, e.g. cyanobacterial blooms can consist of 2 or 3 species (e.g. *Anabaena* sp., *Aphanizomenon* sp. and *Microcystis* sp.) even if a single species dominates (Brock 1985). Could it be possible that fluctuations in light promote coexistence of several species under light-limited conditions as was demonstrated theoretically for limiting resources in general (e.g. Levins 1979, Armstrong & McGehee 1980) and confirmed experimentally for nutrient-limited phytoplankton (Turpin & Harrison 1979, Sommer 1984)? I investigate this hypothesis in experiments with 2 cyanobacteria. The 2 species frequently occurring in eutrophic lakes were grown together in constant and fluctuating light under light-limited conditions and their dynamics were monitored. Following Huisman & Weissing (1994), competitive abilities of each species were determined by growing them in monoculture and estimating I_{out} at equilibrium. A model of light competition was used to predict competitive outcomes under each light regime.

MATERIALS AND METHODS

Experimental setup. To investigate the effect of temporal variation in light supply on competition for light between phytoplankton, pairwise competition experiments were performed. Two species of freshwater cyanobacteria, *Anabaena flos-aquae* (Lyng.) Brébisson (American Type Culture Collection Clone 22664) (hereafter *Anabaena*) and *Phormidium luridum* var. *olivace* Boresch (University of Texas Culture Collection Clone 426) (hereafter *Phormidium*), were grown under 4 different light regimes. *Anabaena* often forms extensive blooms and the genus *Phormidium* is similar to the genus *Oscillatoria* in its ecological niche and can be either planktonic or benthic (Whitford & Schumacher 1984). The average incoming irradiance was the same in all treatments, i.e. 50 µmol photons m^{-2} s^{-1}; however, temporal patterns of light supply differed, i.e. there were the constant light treatment, square-wave fluctuations between 15 and 85 µmol photons m^{-2} s^{-1} with 8 or 24 h periods, and light:dark fluctuations between 0 and 100 µmol photons m^{-2} s^{-1} with a 24 h period. In all 3 fluctuating regimes, periods of low and high irradiance were of equal duration. Algae were grown in 1 l Erlenmeyer flasks (380 ml culture volume) at 20°C and gently shaken several times a day. Each treatment had 3 replicates. Treatments were assigned randomly to environmental chambers. Flask positions were determined so that the irradiance levels at the surface of the flasks were within 1 to 2 µmol photons m^{-2} s^{-1} of the required levels as measured with a quantum scalar sensor (Biospherical Instruments QSL-100). Light was provided by 'cool white' fluorescent tubes (Philips); flasks were illuminated from all sides except the bottom. Fluctuations in irradiance were imposed by periodically turning on and off additional light sources.

Full strength WC freshwater medium (Guillard 1975) with 2× standard concentration of $NaHCO_3$ was used to achieve high filament densities and light-limited conditions for both species as well as competition for light by mutual shading. A higher concentration of inorganic carbon was used to increase the buffering capacity of the medium and the availability of inorganic carbon (both species are known to successfully utilize HCO_3^- as a source of inorganic carbon; Allen & Spence 1981, Novak & Brune 1985, E. Litchman & J. Shapiro unpubl.) and have very high affinity for CO_2 (Shapiro 1997). The cultures were buffered with bicarbonate rather than synthetic buffers to avoid possible effects of buffer salts on growth by altering cell membrane permeability (Novak & Brune 1985). In nature, cyanobacterial blooms are often associated with mildly alkaline bicarbonate-rich waters (Klemer 1985, Reynolds 1987). $NaHCO_3$ was added aseptically after autoclaving to prevent precipitation.

Cultures were started at relatively low densities of each species (ca. 10^3 filaments ml^{-1}) and were grown for 6 d in batch regime. After reaching higher densities, cultures were switched to a semicontinuous regime: once per day, 65 ml of a culture was replaced by fresh sterilized WC medium with a doubled HCO_3^- concentration (dilution rate of 0.19 d^{-1}). Such a relatively low dilution rate was chosen to ensure that slow growing *Anabaena* (Fig. 1) would not be washed out. Growth-irradiance curves for each species were determined in separate experiments under constant irradiance (Litchman 2000) (Fig. 1). The minimum irradiance at which growth is non-negative under this dilution rate is 3 and 12 µmol photons m^{-2} s^{-1} for *Phormidium* and *Anabaena*, respectively, as determined from their growth-irradiance curves (Fig. 1). These values agreed well with the results of a pilot experiment where a monoculture of *Phormidium* was able to grow at I_{in} (incoming irradiance) = 5 µmol photons m^{-2} s^{-1}, while a monoculture of *Anabaena* could not persist at this irradiance and a given dilution rate.

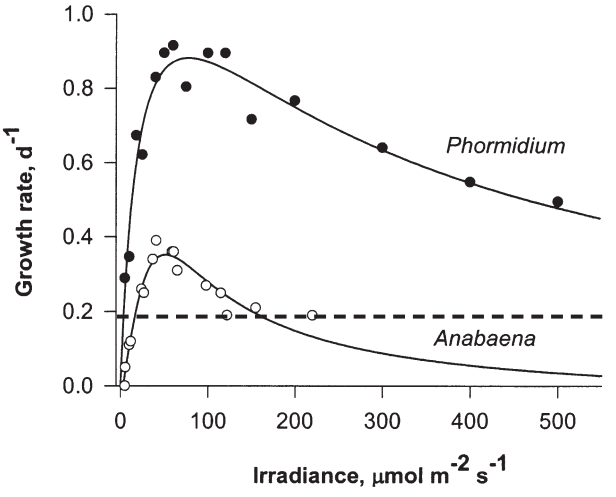

Fig. 1. *Phormidium* and *Anabaena*. Growth-irradiance curves of *Phormidium* and *Anabaena* determined in separate experiments under constant irradiance (Litchman 2000). Dilution (mortality) rate is shown with a dashed line. Parameter values of Eq. (2) are the following: $g_{max,Ana}$ = 1.19 d^{-1}, $g_{max,Phorm}$ = 1.4 d^{-1}, k_{Ana} = 42 µmol photons m^{-2} s^{-1}, k_{Phorm} = 22 µmol photons m^{-2} s^{-1}, $k_{inh,Ana}$ = 61 µmol photons m^{-2} s^{-1}, $k_{inh,Phorm}$ = 267 µmol photons m^{-2} s^{-1}

After species densities reached stationary phase, phosphorus (PO_4-P) and nitrogen (NO_3-N and NH_4-N) concentrations were measured according to Strickland & Parsons (1972) to check for nutrient-replete conditions. pH was measured periodically (in the middle of the low and high light periods in the fluctuating light regimes) to assess carbon availability. The experiment was run for 12 wk, samples were taken once or twice per week, preserved with Lugol's iodine and counted in a 1 ml Sedgwick-Rafter chamber. To determine species density, at least 500 filaments were counted for each sample, and if a species was rare in a sample, the whole chamber was scanned. Filament and cell sizes were measured with an ocular-micrometer and compared among treatments throughout the course of experiment. The average number of cells per filament for each treatment was determined by counting cells in 20 random filaments for each species in each treatment during the course of experiment.

To characterize the minimum light requirements of the species, each was grown in monoculture under constant light regime, and the incident light levels were estimated at equilibrium. According to resource competition theory, a species that is able to attenuate light to the lowest point (e.g. measured at the bottom of the water column, I_{out}), should win competition (Tilman 1982, Huisman & Weissing 1994). In contrast to nutrient competition where the minimum resource level (R^*) is independent of supply rate, the I_{out} depends on the incoming irradiance (Huisman & Weissing 1994). Therefore, it is necessary to determine I_{out} values under the same irradiance as was used in the pairwise experiment. I used the I_{out} as an estimate of species competitive abilities. This measure, although proposed by Huisman & Weissing (1994) for unidirectional light field, appears to be robust even when the assumption of unidirectionality is relaxed (Weissing & Huisman 1994). Light levels were measured directly outside the flask with a cosine quantum sensor connected to a Li-Cor data logger. Species-specific attenuation coefficients, a_i, were determined by estimating light attenuation in monocultures after they reached stationary phase:

$$a = \ln(I_{in}/I_z)/z$$

where I_{in} is the incoming light, and I_z is light at depth z (thickness of the culture volume), measured immediately outside the flask. The attenuation coefficient was then normalized by the filament density. The background attenuation was determined the same way, measuring the light attenuation in the growth medium without algae.

To determine whether monocultures reached equilibrium due to limitation by light, rather than another resource, a series of nutrient additions (nitrate, phosphate, bicarbonate and concentrated WC solution) were performed and the densities of species were monitored. Biomass responses were estimated by measuring optical densities of cultures at 750 nm (OD_{750}). At the end of experiment, cell densities in each monoculture were compared to the densities of monocultures grown under the same experimental conditions, but at higher irradiance: 75 µmol photons m^{-2} s^{-1}. Higher species densities at higher irradiances would indicate light-limited conditions.

Model. To describe light competition of the 2 species, I used a model based on the model proposed by Huisman & Weissing (1994):

$$\frac{db_i}{dt} = \frac{1}{z}\int_0^z g_i[I(s)]b_i ds - Db_i$$
$$i = 2 \qquad (1)$$
$$I(s) = I_{in}\exp\left[-\left(\sum_{i=1}^{n} a_i b_i s + a_{bg} s\right)\right]$$

where b_i is the filament density of the ith species (filaments ml^{-1}), t is time, z is the depth of the culture (cm), g_i is the irradiance-dependent growth function, D is mortality (d^{-1}), $I(s)$ is the irradiance at depth s, I_{in} is the incoming irradiance, a_i is the attenuation coefficient for species i (cm^2 $filament^{-1}$) and a_{bg} is the background attenuation (cm^{-1}). Attenuation coefficients were determined as desribed above. For the species used in the experiments, the growth is described by the following function with photoinhibition:

$$g_i = g_{\max,i} \frac{I}{I + k_i + \frac{I^2}{k_{\text{inh},i}}} \quad (2)$$

where $g_{\max,i}$ is the maximum growth rate (d^{-1}), I is the incident irradiance (µmol photons m^{-2} s^{-1}), k_i is the constant and $k_{\text{inh},i}$ is the photoinhibition constant (Megard et al. 1984). Growth parameters for both species were determined in separate experiments under constant irradiance (Litchman 2000) (Fig. 1).

RESULTS AND DISCUSSION

The temporal regime of light supply had a significant effect on the population dynamics of species and on competitive trends in the community. *Phormidium* was dominant under all 4 light regimes. *Anabaena* was excluded in the constant light treatment but was able to persist under fluctuating light regimes throughout the experiment (Fig. 2). Both species were able to grow

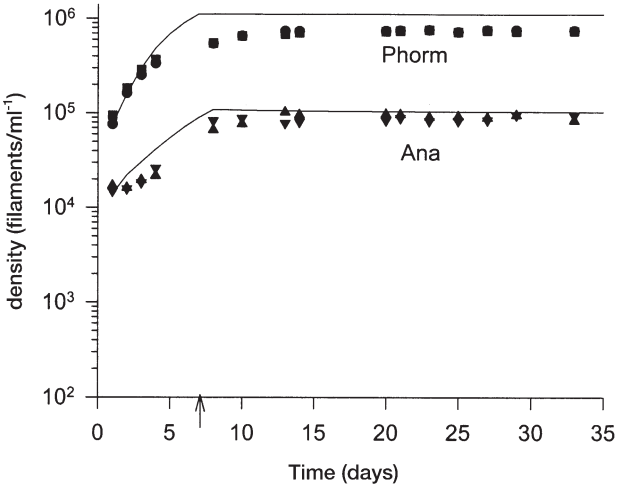

Fig. 3. *Anabaena* and *Phormidium.* Observed growth dynamics (symbols) of *Anabaena* and *Phormidium* in monoculture under constant light. The arrow shows when cultures were switched from batch to semicontinuous regime. The dynamics predicted by the model are also shown (lines)

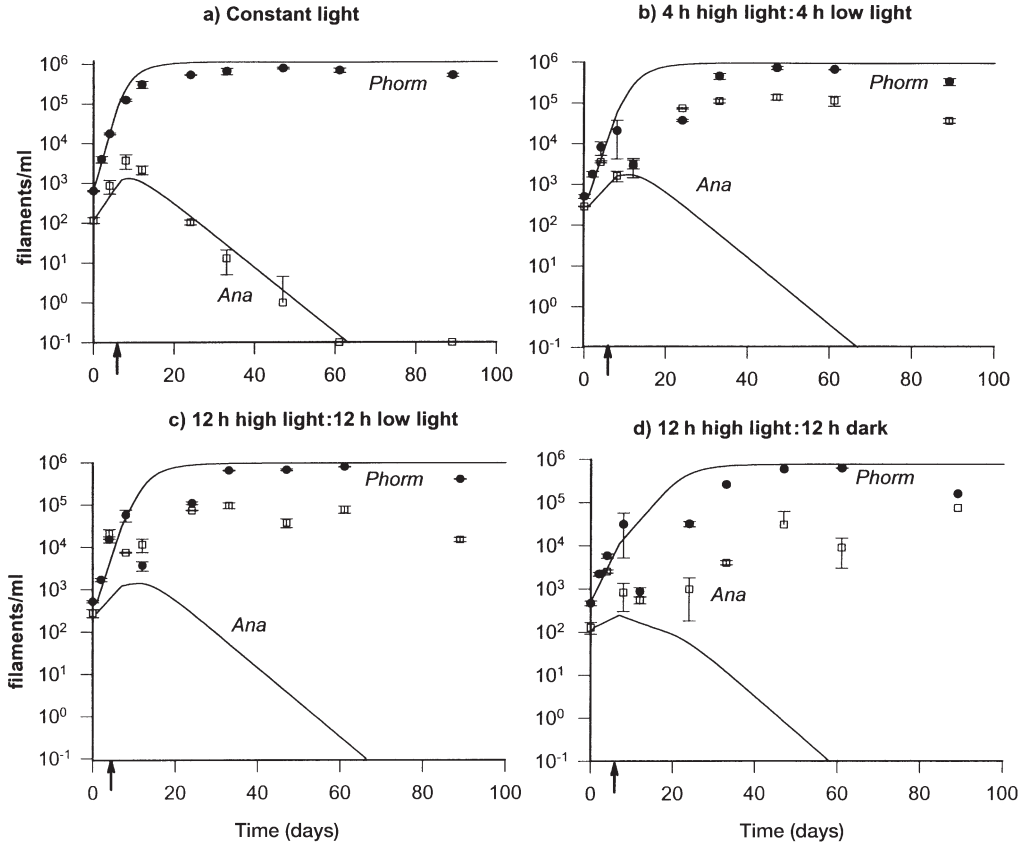

Fig. 2. *Phormidium* (●) and *Anabaena* (□). Species dynamics in the course of the pairwise experiment under 4 different light regimes. Means ± SEM are shown. (a) Constant light, (b) fluctuating light, 8 h period, (c) fluctuating light, 24 h period, (d) light:dark fluctuations, 24 h period. The vertical arrow on the abscissa marks the time of the first dilution. Lines are model predictions. Species parameters are as in Fig. 1 and D_{Ana} = 0.2 d^{-1}, D_{Phorm} = 0.19 d^{-1}, $k_{Ana} = 5.2 \times 10^{-6}$ cm^2 $filament^{-1}$, $k_{Phorm} = 1.7 \times 10^{-6}$ cm^2 $filament^{-1}$, k_{bg} = 0.066 cm^{-1}

in monoculture under these experimental conditions (Fig. 3), which suggests that *Anabaena*'s exclusion resulted from competitive interactions between the 2 species. I_{out} during *Anabaena*'s decline (24 d from the start of the experiment) was between 1 µmol photons m^{-2} s^{-1} (as estimated from the absorbance spectra of the cultures where $\overline{OD} = 0.56$) and 7 µmol photons m^{-2} s^{-1} (attenuation due to absorption only). Thus, the incoming light was reduced by more than 85 to 98 % by the species biomass. At the end of the experiment, the light attenuation was even higher ($\overline{OD} = 0.67$, $0.5 < I_{out} < 6$ µmol photons m^{-2} s^{-1}). The light attenuation in the light:dark treatments after 24 d from the start of experiment was lower than in the constant or fluctuating light treatments due to lower biomass of both species (as estimated from the OD measurements). There was a significant drop in species density in the fluctating light treatments after dilutions began and no such drop in the constant light treatment. Later in the course of experiment, the estimated light levels were not significantly different among treatments.

The average light at the bottom of the suspension (I_{out}) in the monoculture of *Phormidium* was significantly lower than that in the monoculture of *Anabaena* (0.8 to 1 µmol photons m^{-2} s^{-1} for *Phormidium* vs 5 µmol photons m^{-2} s^{-1} for *Anabaena*), indicating that under these experimental conditions *Phormidium* is a better competitor for light and should displace *Anabaena*, as was observed in the experiment.

Nitrogen and phosphorus concentrations were above limiting levels (10 µM phosphorus and 70 µM nitrogen; Horne & Goldman 1994); also, the occurrence of heterocysts in *Anabaena* in treatments was similar to that in dilute nutrient-replete cultures (an increase in heterocyst frequency could indicate nitrogen deficiency). Additions of nutrients did not affect the equilibrium densities of either species (as inferred from the OD_{750} measurements), which suggests that nutrients did not limit growth. The average pH values in the pairwise experiment were 9.1 ± 0.3 under constant light and ranged from 8.2 during the low light period to 9.7 during the high light period under fluctuating light. For light:dark fluctuations, the range was even wider: from ca. 7.6 in the dark to 9.8 during the light period. The pH values in monocultures after they reached equilibrium were comparable to the pH values in the pairwise experiment and did not exceed 9.4 for either species (under constant light), although both species are able to grow at pH ≥ 10 in water with similar concentrations of inorganic carbon (0.2 mM; Shapiro 1997). The addition of bicarbonate to the monocultures after they reached stationary phase did not change their densities (measured as OD_{750}), which indicates adequate carbon availability during the experiment, since both species can utilize bicarbonate (e.g. Allen & Spence 1981).

At higher incident light (75 µmol photons m^{-2} s^{-1}), the densities of each species were higher than at 50 µmol photons m^{-2} s^{-1} (9.9×10^5 filaments ml^{-1} for *Phormidium* and 1.2×10^5 filaments ml^{-1} for *Anabaena*), indicating the presence of light limitation under the experimental conditions.

To examine trends in competitive dynamics, linear regression was fitted to the time series of the natural logarithms of the ratio of population density of *Anabaena* to that of *Phormidium* (Grover 1988). The data from the first 12 d of the experiment were not included in the analysis to minimize transient effects associated with the change to semicontinuous regime. The rate of competitive exclusion for each light regime was estimated as a slope of the fitted regression line (Grover 1988). The rate was greatest under constant light; high:low light fluctuations of the 2 fluctuation periods had much lower, but still significantly non-0 rates. There was no significant difference in the rates of the 2 high-low light fluctuation regimes. In contrast, under the light:dark fluctuations, the slope of the regression line was not significantly different from 0 (Table 1), which suggests the possibility for stable coexistence under this light regime. To test whether stable coexistence was achieved in this case the invasion scenario experiments (Tilman & Sterner 1984) should be performed.

The average filament size of *Phormidium* was not significantly different among treatments throughout the experiment (average dimensions were 2×46 µm). The average filament length of *Anabaena*, however, was sensitive to the regime of light supply and, after about 2 wk from the start, was significantly shorter under constant light compared to the 3 fluctuating light regimes for all dates until *Anabaena*'s disappear-

Table 1. Linear regression of ln(*Anabaena* density/*Phormidium* density) versus time for different light regimes. The rate of competitive exclusion of *Anabaena* by *Phormidium* is determined as a slope of the regression line

Light regime		Estimate	SE	*t*-value	p-value
Constant light	Intercept	−5.39	1.68	−3.2	0.03
	Slope	−0.14	0.03	−4.2	0.01
Fluctuating light, $t = 8$ h	Intercept	0.49	0.59	0.84	0.44
	Slope	−0.05	0.01	−3.02	0.04
Fluctuating light, $t = 24$ h	Intercept	0.69	0.78	0.88	0.43
	Slope	−0.05	0.015	−3.36	0.03
Light:dark fluctuations, $t = 24$ h	Intercept	−2.9	1.53	−1.89	0.13
	Slope	0.005	0.03	0.17	0.87

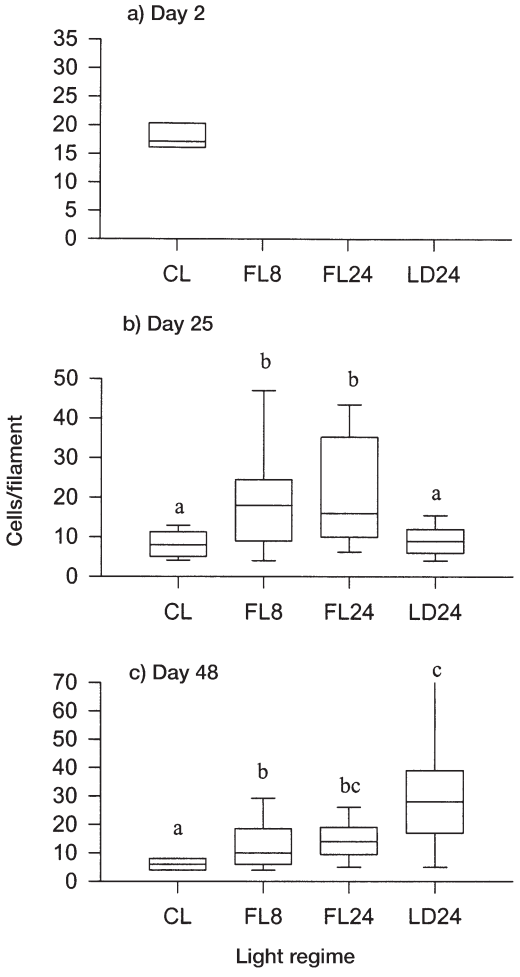

Fig. 4. *Anabaena.* Average number of cells per filament of *Anabaena* in the pairwise experiment under different light regimes. CL, constant light treatment; FL8 and FL24, high-low light fluctuations with 8 and 24 h periods, respectively; LD24, light:dark fluctuations of 24 h period. Kruskal-Wallis test was used for treatment comparisons. Treatments with no common letters are significantly different ($p < 0.05$)

ance from the constant light treatment (Fig. 4). Shorter filament length in cyanobacteria is often associated with lower growth rates and physiological stress (Meffert 1971).

The specific attenuation coefficients were 5.2×10^{-6} cm^2 filament^{-1} for *Anabaena* and 1.7×10^{-6} cm^2 filament^{-1} for *Phormidium*, which is comparable to the reported value for another filamentous cyanobacterium *Aphanizomenon flos-aquae* (Huisman et al. 1999). The higher specific attenuation coefficient of *Anabaena* could in part be explained by the higher concentration of chlorophyll *a* (chl *a*) in its filaments: under the given irradiance, chl *a* concentrations were 2.05 ± 0.07 pg filament^{-1} for *Phormidium* and 3.66 ± 0.05 pg filament^{-1} for *Anabaena* (as measured in a separate experiment; unpubl.).

Comparison of experimental dynamics with model predictions

In general, the predicted dynamics of species in monocultures agreed with the observed dynamics (Fig. 3). The model predicted slightly higher densities of *Phormidium* than were observed. There was also a noticeable lag phase in *Anabaena*'s growth in the experiment, which was not predicted by the model (Fig. 3).

The model predicted competitive exclusion of *Anabaena* by *Phormidium* under constant light regime. Overall, the predicted dynamics of both species in mixed cultures agreed well with the observed dynamics, although, similar to monoculture predictions, the model predicted higher densities of *Phormidium* than were observed in the experiment (Fig. 2). The model predicted competitive exclusion of *Anabaena* under fluctuating light, occurring at a rate similar to that under the constant light, while in the experiment under fluctuating light, no competitive exclusion was observed for the duration of the experiment (Fig. 2). Thus, the model was not able to adequately predict competitive interactions under fluctuating light regimes.

There are several possible reasons for the inadequate prediction of the competition dynamics under fluctuating light. First, dynamic responses of algae to fluctuations not included in the models might have altered the dynamics of competition under fluctuating light. As growth experiments show (Litchman 2000), under the fluctuating light regimes used in this study, growth rates of *Anabaena* in monoculture increased, compared to the constant light regime, possibly due to a delayed onset of photoinhibition and/or a non-0 growth in the dark, while the growth rates of *Phormidium* did not. Such enhancement of growth by fluctuations that may have enabled *Anabaena* to persist under fluctuating light could not be predicted from *Anabaena*'s steady-state growth-irradiance curve on which the model was based. Other studies have shown that growth rates change in response to light fluctuations (Nicklisch & Fietz 2001). It is conceivable that the inability of the steady-state model to describe species responses to fluctuations could also lead to poor prediction of competition under fluctuating light. A model that includes the dynamic responses of species to fluctuations and, thus, better describes growth in monoculture may be needed to model competition under fluctuating light. Alternatively, growth-irradiance curves would have to be obtained for each fluctuation regime. If the persistence of both species under fluctuating light is due to species-specific growth rate changes, then coexistence may not have occurred if both species would respond to fluctuations in a similar way.

Another possible reason for increased persistence of *Anabaena* under fluctuating light regimes is that fluc-

tuations might have altered the minimum light requirements of species compared to constant light, so that *Anabaena* was able to grow at lower light levels. A decrease in the minimum light requirements under 24 h light:dark cycles compared to constant light was documented previously for some species (Reynolds 1987).

The persistence of *Anabaena* under fluctuating light regimes could have also been due to buoyancy changes of the *Anabaena* filaments. Low light levels (5 to 35 µmol photons m^{-2} s^{-1}) were shown to increase buoyancy of *Anabaena* (Reynolds 1997), possibly due to lower carbohydrate content (Gibson 1978). Brookes et al. (1999) found that light fluctuations maintained higher buoyancy of *Anabaena circinalis* compared to the continuous high light conditions. If fluctuating light regimes caused increase in buoyancy, *Anabaena* could have greater access to light (since no constant mixing was imposed), thus increasing its competitive ability. Theoretical studies showed that a spatial segregation of species along the light gradient may promote coexistence of several species (e.g. Britton & Timm 1993, Klausmeier & Litchman 2001). To focus on non-spatial mechanisms of persistence, well-mixed cultures need to be used.

It is also possible that, despite light limitation, the exclusion of *Anabaena* by *Phormidium* occurred due to competition for other resource, possibly carbon. Although monocultures did not respond to additions of bicarbonate, the decreased availability of free CO_2 with increased pH may have contributed to *Anabaena*'s decline. Even though the average pH values in the constant and fluctuating light treatments were not significantly different, the temporal variation in pH and, consequently, in the availability of inorganic carbon could have been important. As the modeling investigation (Litchman & Klausmeier 2001) and the experiments by Brzezinski & Nelson (1988) suggest, light fluctuations, by mediating competition for a nutrient, may lead to a reversal of competitive outcome reached under constant light or increased perisistence of both competitors. Additional experiments are needed to test these hypotheses and to identify the exact mechanism for *Anabaena*'s increased persistence under fluctuating light.

The results of this study demonstrate that fluctuations in light supply may significantly affect competitive interactions of species and promote coexistence. Light fluctuations can increase diversity in multispecies communities as well (Litchman 1998, Flöder et al. 2002). Low light levels and relatively high pH values are common in productive lakes, often dominated by cyanobacteria. As results of this study suggest, fluctuations in light supply, including daily light:dark cycles, may lead to a long-term (several months) persistence of more than 1 species of cyanobacteria, depending on their responses to light fluctuations. This time is comparable to time-scales of successional sequence in temperate lakes. Thus, temporal heterogeneity in light supply may contribute to phytoplankton diversity in nature.

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