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Interactive effects of temperature and nutrient limitation on the response of alpine phytoplankton growth to ultraviolet radiation

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Abstract

We performed bag-enclosure experiments for 7 d in a lake in the Beartooth Mountains (in Montana and Wyoming) using natural phytoplankton assemblages. Ultraviolet radiation (UVR) (exposed or blocked), temperature (6°C and 14°C), and nutrients (nitrogen, phosphorus, and nitrogen plus phosphorus) were manipulated in a factorial design to determine how these factors interact to affect phytoplankton growth. Four major phytoplankton taxa (two diatoms, one chrysophyte, and one dinoflagellate) were found in the water samples across all treatments. Greater growth rates were observed at the higher temperature for all taxa, except the chrysophyte. UVR depressed the growth rates of all phytoplankton at 6°C regardless of nutrient conditions. In contrast, at 14°C, a negative effect of UVR was not observed for any species in the absence of nutrient additions; only with the addition of nutrients did UVR exposure depress the growth of one diatom species and the dinoflagellate. Our results suggest that in alpine lakes, the effects of UVR exposure on phytoplankton depend on temperature and nutrient availability, indicating that climate change and enhanced atmospheric nitrogen deposition are likely to alter UV–temperature–nutrient relationships of plankton in high-UV systems.

Incident levels of ultraviolet radiation (UVR) have increased at the Earth's surface over the past 20 yr as a result of decreased stratospheric ozone (Shindell et al. 1998). In aquatic ecosystems, UVR is selectively absorbed by chromophoric dissolved organic matter (CDOM), which provides protection to organisms from UVR damage (Morris et al. 1995). The concentration of CDOM is expected to decline in lakes if drought conditions become more frequent, further increasing the exposure of aquatic organisms to potentially damaging UVR (Schindler et al. 1996; Williamson and Zagarese 2003). The low CDOM levels and high UVR exposure in alpine lakes make them some of the most susceptible to climate change–induced alterations in UVR.

Several studies have revealed that UVR can negatively affect the growth (Nilawati et al. 1997; Davidson and van der Heijden 2000) and photosynthetic rates (Roos and Vincent 1998; Litchman et al. 2002) of phytoplankton and can alter phytoplankton community composition (Karentz et al. 1991; Cabrera et al. 1997). However, a number of studies have also indicated a lack of effect of UVR on the growth rates of algae (Halac et al. 1997). This inconsistency may be due to acclimation in high-UVR environments (Sommaruga 2001) or to differences in physicochemical factors, such as temperature or nutrients, across different experiments.

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Photoprotection and photorepair are two mechanisms employed by phytoplankton to deal with UVR exposure. To prevent UVR damage, some phytoplankton use photoprotective compounds such as mycosporine-like amino acids (MAAs) or carotenoids, with the concentration of these compounds positively correlated with the level of UVR exposure (Sommaruga and Garcia-Pichel 1999; Laurion et al. 2002). Phytoplankton may also use photorepair processes, either exclusively or in conjunction with photoprotection and other repair mechanisms such as nucleotide excision repair (Karentz et al. 1991). Photorepair relies on enzymatic activity; thus, it is a temperature-dependent process that is likely less effective at low temperatures. In contrast, photoprotection should not exhibit temperature dependence; rather, the synthesis of photoprotective pigments may rely more heavily upon nutrient availability (Litchman et al. 2002).

Alpine lakes serve as excellent systems for investigating the influence of temperature and nutrient availability on the response of phytoplankton to UVR because ice-off typically occurs in these high-UVR systems during the summer solstice, thereby creating high-UVR : low-temperature conditions. Colimitation of primary production by nitrogen (N) and phosphorus (P) is typical of alpine lakes (Morris and Lewis 1988); this limitation may cause phytoplankton to be more sensitive to increased UVR (Litchman et al. 2002; Xenopoulos and Frost 2003). For example, Litchman et al. (2002) found that N limitation can affect UVR sensitivity in phytoplankton due to less efficient DNA repair, coupled with a decrease in cell size and in the concentrations of photoprotective compounds.

While the effects of nutrient limitation and temperature on the response of phytoplankton to UVR have been investigated separately, the interactions of all three variables have

not been previously examined. These three variables are all part of various global change scenarios; thus, assessing how they interact to influence phytoplankton communities may provide more realistic predictions of future change. To investigate how nutrient availability and temperature affect the growth response of alpine phytoplankton to UVR, a factorial experiment was established during the early summer of 2003 using the natural phytoplankton assemblage from a lake in the Beartooth Mountain Range (Montana/Wyoming). Both N and P were manipulated in these treatments, and two temperatures (6°C and 14°C) were tested by incubating the experiment simultaneously in the surface waters of two lakes with different temperature regimes.

Methods

Site location—The Beartooth Mountain Range is located on the southwest Montana–Wyoming border, directly adjacent to the northeast entrance of Yellowstone National Park, and comprises much of the Absaroka–Beartooth Wilderness Area. There are over 600 permanent lakes in the 900 km^2 Beartooth area. Silica (Si) and phosphorus (P) concentrations in these lakes are low due to slow-weathering bedrock; the concentration of N is also relatively low, although it has increased in surface waters in recent years (Saros et al. 2003). The elevation range for these lakes is 2,450 to 3,100 m, with tree line ranging between 2,750 and 3,000 m. Beartooth Lake has a maximum depth of 30 m, with the thermocline typically forming in early July between 5 and 7 m. Additional physical and chemical characteristics of Beartooth Lake are provided in Saros et al. (in press A).

In situ experiments—Lake water from Beartooth Lake was used in this experiment; the phytoplankton species composition of this lake is representative of lakes in this area. Water was collected on 3 July 2003 with a van Dorn bottle from the depth of the chlorophyll maximum (7 m), as determined by in vivo fluorometric measurements with a 10-AU field fluorometer (Turner Designs), to ensure an adequate cell density for the experiment. The phytoplankton taxa found at this depth were present throughout the photic zone. The collected water was passed through a 153-μm mesh to remove zooplankton grazers and stored in carboys for no longer than 24 h. Initial nutrient concentrations at this depth were analyzed by standard methods (APHA 2000). Nitrate plus nitrite was measured by the cadmium reduction method, and soluble reactive phosphorus (SRP) by the ascorbic acid method. Dissolved Si was measured by the heteropoly blue method. Material retained on 0.4-μm polycarbonate filters was analyzed for particulate P by persulfate digestion followed by measurement of SRP and for particulate Si by sodium carbonate digestion followed by measurement of soluble reactive Si. Particulate C and N were collected on filters (Whatman GF/F) and measured via combustion and gas chromatography with an elemental analyzer (Carlo Erba 1106). Total phosphorus and total nitrogen were estimated by summing dissolved and particulate measurements of each nutrient (in μmol L^{-1}). This approach provides conservative low-end estimates of total nutrient pools because dissolved organic fractions are not represented.

Four nutrient treatments were created: no added nutrients (control), N enrichment (18 μmol L^{-1} N), P enrichment (5 μmol L^{-1} P), and N + P enrichment (18 μmol L^{-1} N + 5 μmol L^{-1} P). Nitrogen was added in the form of $NaNO_3$; P was added in the form of NaH_2PO_4. The amended water was added to 500-ml liquid-tight specimen bags (Bitran S Series) made of UVR-transmitting polyethylene (transmits 94% photosynthetically active radiation [PAR] 400–800 nm and 86% of solar UVR 295–399 nm, 50% transmittance at 234 nm).

Two incubation systems were selected based on epilimnetic temperature differences, as measured with a temperature probe (Hydrolab) initially and temperature loggers (Optic Stowaway, Onset Computer, accuracy ±0.2°C) over the course of the experiment. A pond was used as the warm incubation system (average temperature of 14.0°C, range of 8.7–19.3°C during the experiment), and a lake that was still partially frozen at the beginning of the experiment was used as the cold incubation system (average epilimnetic temperature of 6.1°C, range of 3.7–9.6°C during the experiment).

A series of 66 cm × 38 cm racks was constructed from 2.5-cm polyvinyl chloride pipe to incubate the bags. Two types of plastic films were used for the cover of the racks: Aclar, a long-wave-pass plastic that in water transmits both PAR (100% 400–800 nm) and most UVR (98% of UV-B 295–319 nm, 99% UV-A 320–399 nm, with a sharp wavelength cutoff and a 50% transmittance point at 212 nm), and Courtgard, a long-wave-pass plastic that transmits PAR (95% 400–800 nm in water) but blocks most UVR (transmits no UV-B 295–319 nm, and only 9% of UV-A 320–400 nm with a sharp wavelength cutoff and a 50% transmittance point at 400 nm). The two plastics were alternated in a checkerboard design on each rack. A small piece of rope with an attached carabineer was fastened to the middle of each rack and secured the rack to a buoy attached to an anchored rope. This design allowed the racks to float at the very surface of the water, prevented shading of the rack by the buoy, and eliminated problems with differential attenuation of light by lake water among lakes. Although no measurements of upwelling UV were made in the incubation lakes, upwelling UV at the shorter, more damaging wavelengths is generally less than 1% of downwelling UV in lakes of similar transparency to our study lakes (Kirk 1994). To compensate for the high light levels at the surface, a layer of window-screen mesh was placed over every bag to act as a neutral density filter and further reduce incident levels of light to 62% of ambient levels.

Four replicates of each treatment were created, and the bags were incubated for 7 d in each incubation system. Although no instrumentation was available for continuous monitoring of UV at this remote site, the weather throughout the 7-d period was generally very clear and sunny and free of any haze or clouds, except for brief periods in the afternoon on several of the days when mixed light clouds formed and later dissipated.

At the end of the experiment three 50-ml subsamples from each bag were preserved with Lugol's iodine solution. Final SRP measurements on 0.4-μm filtered aliquots from each bag were used as an indicator of final nutrient conditions in

Table 1. Initial nutrient conditions in the lake water used in the experiments. All nutrient concentrations are reported in μmol L^{-1}. The detection limit for dissolved phosphate was 0.02 μmol L^{-1}.

	Dissolved nutrients			Seston ratios			Total	
Lake	PO_4	NO_3	Si	C : N	C : P	N : P	N	P
Beartooth (7 m)	<0.02	1.66	36.0	12.6	345	27.3	3.66	0.08

the bags and as verification that nutrients were not depleted over the course of the experiment.

Cell counts and data analysis—The entire subsample was settled in an Utermöhl-style chamber for at least 8 h, and individuals of the dominant phytoplankton species were counted under an inverted microscope (Nikon TS-100) at ×400. For each sample, four transects or at least 200 cells (whichever was greater) were counted. The percentage change in each dominant phytoplankton taxon was determined by comparing initial and final cell densities in each treatment; these values were used to compare changes in growth for each taxon across treatments

A three-way analysis of variance (ANOVA) was performed on the percentage change data for each dominant species to assess the effects of UVR, nutrients, and temperature on growth. Data were log transformed when nonnormal distribution occurred, and a significance level of $p < 0.05$ was used. Because multiple three- and two-way interactions occurred, we also investigated differences among the eight treatments by conducting a one-way ANOVA with Tukey post hoc tests for each species. Based on the results of the post hoc tests, treatments that differed significantly from each other ($p < 0.05$) were categorized into different subsets for each species so that overall effects of each variable could be assessed.

Results

Initial dissolved and total nutrient concentrations were low in Beartooth Lake water (Table 1). Based on the Redfield ratio, seston ratios suggested strong P limitation as well as possible N limitation, as indicated by the high C : P and moderate C : N ratios. The phytoplankton assemblage did not respond to N or P additions alone in any of the treatments (i.e., never differed from the control [$p < 0.05$]), likely due to colimitation by N and P that often occurs in alpine lakes (Morris and Lewis 1988). Therefore, only the control and N + P (hereafter referred to as the nutrient addition) treatments will be presented here. SRP concentrations within the experimental bags remained relatively constant over the course of the experiment and did not change by more than 10% in any case.

A total of four major taxa were found in the water samples across all treatments: *Fragilaria crotonensis* Kitton, *Asterionella formosa* Hassall, *Dinobryon* sp., and *Gymnodinium* sp., hereafter referred to by genus only. Other taxa present in lower densities included *Aulacoseira distans* Ehrenberg, *Tabellaria flocculosa* Roth, small *Fragilaria* sensu lato species (i.e., *Staurosira* and *Staurosirella* sensu Round et al. 1990), *Cryptomonas* sp., and *Rhodomonas* sp., but these collectively comprised less than 10% of the total assemblage density. As a result, their final densities in the various treatments were sporadic and not reliably quantifiable.

Results of the three-way ANOVAs revealed significant three-way interactions among temperature, nutrients, and UVR for both *Dinobryon* ($p = 0.037$) and *Fragilaria* ($p < 0.001$) (Table 2). Two-way interactions between UVR and nutrients ($p < 0.001$) as well as temperature and nutrients ($p < 0.001$) were observed for *Asterionella*.

Subsets delineated for each species by one-way ANOVA (Table 3) were used in conjunction with results of three-way ANOVA to identify consistent effects of these three variables on phytoplankton growth. In the absence of UVR, direct temperature effects were observed for all four taxa; growth of *Gymnodinium*, *Fragilaria*, and *Asterionella* was greatest at 14°C, while growth of *Dinobryon* was highest at 6°C. Temperature strongly affected the response of all four taxa to UVR regardless of their temperature optimum for growth (Table 3), with negative UVR effects at 6°C in all cases (Fig. 1). In contrast, a negative effect of UVR was not observed at 14°C for any species in the absence of nutrient additions. Only with the addition of nutrients did UVR exposure depress the growth of both *Fragilaria* and *Gymnodinium* at 14°C (Table 3: 14°C-blocked/exposed UVR high-nutrient treatments).

For both diatom species (*Fragilaria* and *Asterionella*), the combination of higher temperature and nutrient enrichment

Table 2. Results of the three-way ANOVA to assess the effects of temperature, nutrients, and UVR on phytoplankton growth. Significant results ($p < 0.05$) are shown in bold.

Treatment	*Fragilaria*	*Asterionella*	*Dinobryon*	*Gymnodinium*
Temperature	**<0.001**	**<0.001**	**<0.001**	**0.003**
Nutrient	**<0.001**	**<0.001**	**0.049**	0.932
UVR	**<0.001**	**<0.001**	**<0.001**	**<0.001**
UVR×temperature	**<0.001**	0.958	**<0.001**	**0.001**
UVR×nutrient	**<0.001**	**<0.001**	0.173	0.944
Temperature×nutrient	**<0.001**	**<0.001**	**0.013**	0.961
UVR×temperature×nutrient	**<0.001**	0.881	**0.037**	0.968

Table 3. Results of the one-way ANOVA for each species. Treatments that differ significantly are separated into different subsets; subsets containing the same letters do not differ significantly ($p < 0.05$).

Species	% change	Temp (°C)	UVR	Nutrients	Subset
Fragilaria	84,953	14	blocked	high	A
	33,568	14	exposed	high	B
	4,633	14	blocked	low	C
	3,385	14	exposed	low	C
	3,067	6	blocked	high	D
	1,054	6	blocked	low	D
	323	6	exposed	low	E
	294	6	exposed	high	E
Asterionella	1,874	14	blocked	high	A
	1,172	14	exposed	high	AB
	577	6	blocked	high	BC
	276	14	blocked	low	CD
	235	14	exposed	low	CD
	126	6	blocked	low	D
	−2	6	exposed	low	E
	−25	6	exposed	high	E
Dinobryon	502	6	blocked	high	A
	308	6	blocked	low	B
	85	14	exposed	low	C
	44	14	exposed	high	CD
	44	14	blocked	low	CD
	−12	14	blocked	high	CD
	−70	6	exposed	high	CD
	−79	6	exposed	low	D
Gymnodinium	433	14	blocked	high	A
	267	14	blocked	low	AB
	255	14	exposed	low	AB
	237	6	blocked	low	ABC
	229	14	exposed	high	BC
	192	6	blocked	high	BCD
	46	6	exposed	high	CD
	20	6	exposed	low	D

had a strong positive effect on growth, regardless of UVR exposure (Table 3). Blocking UVR further stimulated the growth of *Fragilaria* under these conditions.

Growth of the chrysophyte *Dinobryon* was greatest under the combined effects of lower temperature and blocked UVR; the addition of nutrients further promoted growth under these conditions (Table 3). In contrast, nutrient additions had no effect when UVR was blocked at 14°C.

Discussion

A coupled effect of UVR and temperature on phytoplankton growth has been found in cyanobacteria (Roos and Vincent 1998) and in early life stages of intertidal algae (Hoffman et al. 2003). While Lotze and Worm (2002) found synergistic effects of nutrient enrichment, grazing, temperature, and UVR exposure on a green macroalga, the complex interaction observed here among UVR, temperature, and nutrients has not been previously documented in phytoplankton. Because of the high degree of interaction among these variables, our results reveal that inconsistencies across prior investigations of the effects of UVR on phytoplankton may be partly explained by differences in temperature and nutrient limitation conditions, and suggest that future studies must carefully control and describe these conditions.

Our study also reveals that the importance of UVR in determining phytoplankton growth patterns can be expected to vary along gradients of temperature and nutrient limitation. Furthermore, these patterns of response are likely to vary among phytoplankton species. For example, the temperature-dependent response of phytoplankton growth to UVR suggests that the relative importance of UVR in structuring phytoplankton communities may be greatest shortly after ice-off, particularly in high-elevation and high-latitude aquatic systems in which the ice-off occurs near summer solstice, i.e., during the highest annual UVR exposures. UVR may continue to influence community structure as thermal stratification initially sets up. This is because temperatures have increased but nutrient concentrations still remain relatively high, thus creating conditions in which some phytoplankton taxa are more sensitive to UVR than others.

The strong effect of temperature on the response of phytoplankton growth to UVR exposure reveals the temperature-dependent nature of UVR protection and/or repair. The UVR inhibition of growth was much greater at 6°C than at 14°C (Table 3). These results are consistent with the fact that repair of both thymine dimers and 6–4 photoproducts is temperature dependent, and incomplete repair of UVR-induced DNA damage can lead to a reduction in algal growth rates (Pakker et al. 2000). The synthesis of photoprotective pigments may also have been enhanced at the higher temperature.

Growth rates of *Fragilaria* and *Gymnodinium* were depressed by UVR exposure at 14°C only under nutrient-replete conditions. Xenopoulos and Frost (2003) also found stronger negative UVR effects on total phytoplankton growth under P enrichment. For *Fragilaria,* this difference may have been the result of higher overall growth rates with the addition of nutrients at this temperature, since populations increased in these treatments by more than 30,000% from initial values. In alpine lakes, the growth of *F. crotonensis* has been strongly stimulated by N and P additions (Yang et al. 1996; Saros et al. in press B). During periods of rapid growth and hence high rates of DNA synthesis, UVR-induced DNA damage may be more prone to occur (Karentz et al. 1991). Thus a UVR effect would be more apparent in these treatments. In contrast, the growth of *Gymnodinium* in the 14°C/UVR-exposed treatments was similar in high- and low-nutrient conditions (Table 3). The greater growth in the 14°C/UVR-blocked/high-nutrient treatment may have been the result of a synergistic effect among all three variables, but a clear trend is not yet apparent because of the high degree of overlap among subsets for this species.

An increasing number of studies reveal coregulation of phytoplankton growth by various factors, including N, P, trace elements, UVR, and ionic composition (Morel et al. 1994; Saros and Fritz 2000; Xenopoulos and Frost 2003). Our data provide evidence not only for colimitation but also for trilimitation of alpine phytoplankton populations by various factors. A strong interactive effect of higher temperature and nutrient additions was apparent for both diatom species. Under these warmer, nutrient-replete conditions, the growth

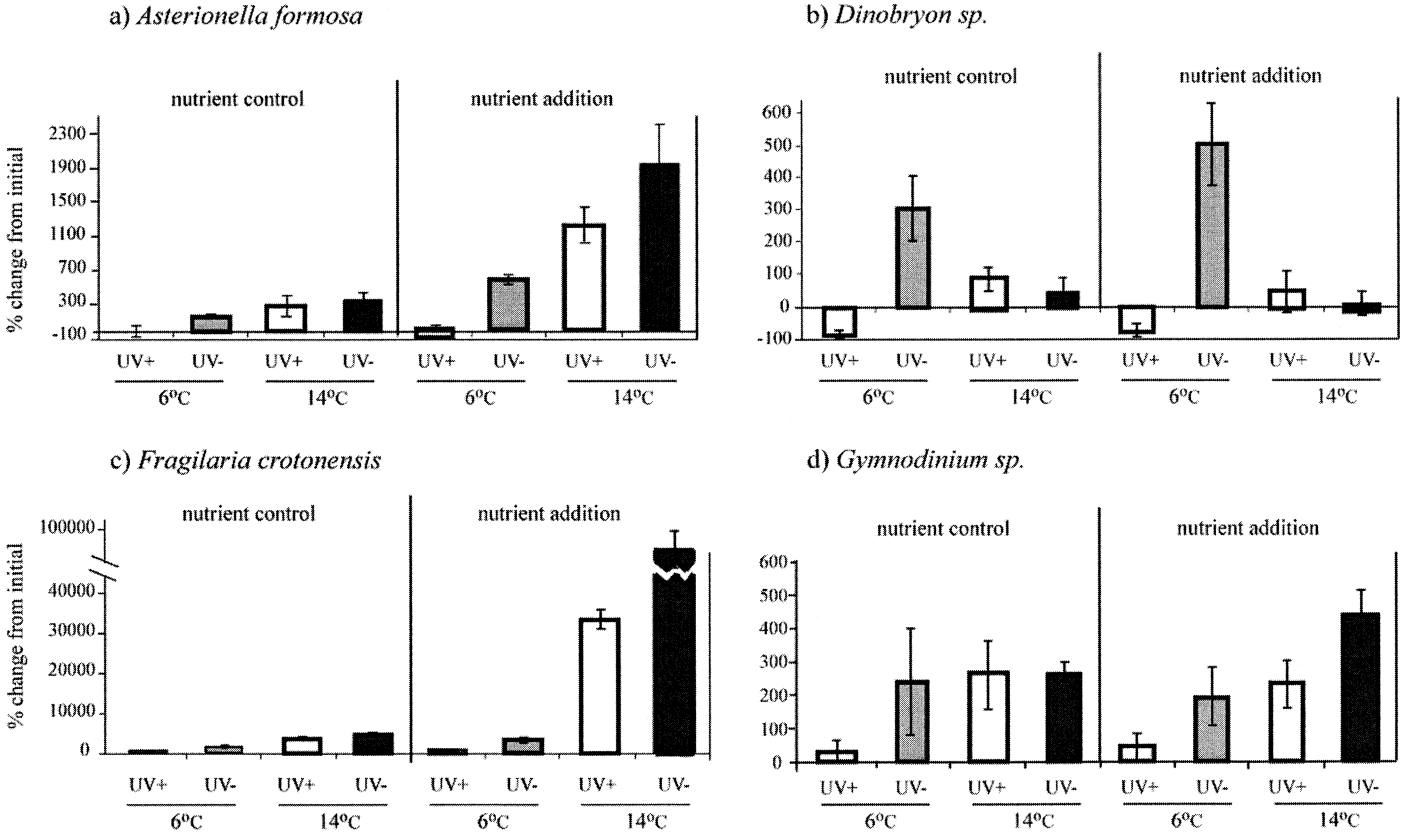

Fig. 1. Changes in cell densities (based on percentage change from initial densities) of (a) *Asterionella formosa,* (b) *Dinobryon* sp., (c) *Fragilaria crotonensis,* and (d) *Gymnodinium* sp. in response to variation in ultraviolet radiation (UV), temperature, and nutrients. Treatments under ''nutrient addition'' were enriched with nitrogen and phosphorus, whereas ''nutrient control'' treatments did not receive any additional nutrients. Black and gray shaded bars indicate that UV was blocked from these treatments, whereas unshaded bars represent treatments that were transparent to UV. Temperatures are indicated below the bars.

of *Fragilaria* was further promoted by blocking UVR. The combination of lower temperature and blocked UVR was the only condition that strongly stimulated the growth of *Dinobryon;* this was the only condition under which the addition of nutrients further promoted growth.

Vertical profiles of lakes in the Beartooth Mountains have provided data on phytoplankton distributions in this region (Saros et al. in press B). *Dinobryon,* for example, typically dominates the deep chlorophyll maximum (DCM) of these lakes, which always occurs well below the 1% attenuation depth for 320 nm and typically has a temperature of 4°C (Saros et al. in press A). The high growth rates of *Dinobryon* at low temperatures in the absence of UVR reported here are consistent with this distribution pattern and suggest that multiple factors are likely driving the formation of the DCM in these systems. The distributions of *Asterionella* and *Fragilaria* appear more strongly correlated to nutrient availability than to temperature or light (Saros et al. in press B), although these species are generally more abundant than *Dinobryon* in the warmer epilimnia of these lakes. Both of these diatoms increased substantially in relative abundance across the southern and central Rocky Mountains during the 20th century (Wolfe et al. 2001; Saros et al. 2003, in press B); this increase has been attributed to enhanced atmospheric N deposition. Our results for temperature and nutrient interactions for these two species suggest the possibility that higher epilimnetic temperatures and/or longer ice-free periods could be acting in conjunction with higher N concentrations to promote the growth of these diatom taxa.

Across alpine lakes of western North America, the three factors investigated here are currently changing or are expected to change in the near future. Enhanced atmospheric N deposition has already altered phytoplankton communities in lakes of the southern (Wolfe et al. 2001) and central (Saros et al. 2003) Rocky Mountains; future patterns in N loading to these systems will depend upon emission regulations. The magnitude and direction of both precipitation and temperature changes are predicted to vary across the Rocky Mountains (Kittel et al. 2002), creating a myriad of temperature and UVR conditions in these lakes. The interactions among UVR, temperature, and nutrients in their effect on phytoplankton growth reveal that the response of alpine phytoplankton communities to global change will be complex, varying across regions and among species.

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