Climatic control of ultraviolet radiation effects on lakes

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Abstract

Ultraviolet radiation (UVR) damages most biota, yet little evidence exists for its long-term effects on natural ecosystems. We used paleoecological techniques at three low-elevation lakes to show that algal abundance in lakes was depressed 10-fold by UVR during the first millennium of lake existence. Likewise, analysis of data from a lake near treeline showed that algal biomass declined 10–25-fold both early in the lake history and during the last ~4000 yr, when inputs of UVR-absorbing dissolved organic matter (DOM) declined despite constant nutrient levels since ~10,000 ^{14}C yr before the present. This rapid (−1.25% yr^{-1}), sustained (>600 yr) suppression of algal abundance arose from directional climate change that reduced DOM inputs and occurred despite initial reservoirs of photoprotective DOM that are typical of most boreal lakes. Hence, we conclude that many lakes may be vulnerable to order-of-magnitude declines in algal abundance arising from future climate-DOM-UVR interactions.

Despite increasing evidence for the detrimental effects of ultraviolet radiation (UVR) on individual lake biota (Karentz et al. 1994), there have been few demonstrations of its long-term effects on natural ecosystems (Xenopoulos et al. 2000). Most laboratory and field experiments have suggested that exposure to intense UVR reduces the rates of individual or population growth (Karentz et al. 1994). However, quantification of the net effects of UVR on total primary production remains difficult, because the sensitivity to UVR varies among algae (Vinebrooke and Leavitt 1999*a*), herbivores (Bothwell et al. 1995), their predators (Williamson et al. 1997), and biota in different lake habitats (Vinebrooke and Leavitt 1999*a*), and because recent variance in UVR exposure is slight relative to past changes (Leavitt et al. 1997; Pienitz and Vincent 2000). Here we use the wide range of past UVR exposures seen during the Holocene era to show

that algal abundance in lakes is regulated by complex interactions between UVR and climate change.

Recent studies of lake ecosystems have demonstrated that changes in inputs of terrestrial dissolved organic matter (DOM) are a more important control of UVR penetration into lakes than are variations in UVR flux to surface waters (Schindler et al. 1996*b*; Yan et al. 1996). Consistent with this idea, paleoecological analyses have demonstrated that changes in forest and soil development following climate change control DOM export to lakes and, thus, the exposure of aquatic biota to UVR (Leavitt et al. 1997; Pienitz and Vincent 2000). On the basis of these observations, we hypothesized that exposure of lake biota to UVR should be greatest immediately after deglaciation and that algal biomass should be greatly suppressed prior to the development of terrestrial sources of UVR-absorbing DOM.

We tested these hypotheses by analyzing changes in UVR penetration, total algal abundance, and gross algal community composition during the past ~12,000 yr at three lakes on an interior plateau (~1,000 m a.s.l.) of British Columbia, Canada, and at one treeline lake (1,940 m a.s.l.) in the adjacent Rocky Mountains. These paleoecological analyses were combined with a survey of 75 modern mountain lakes

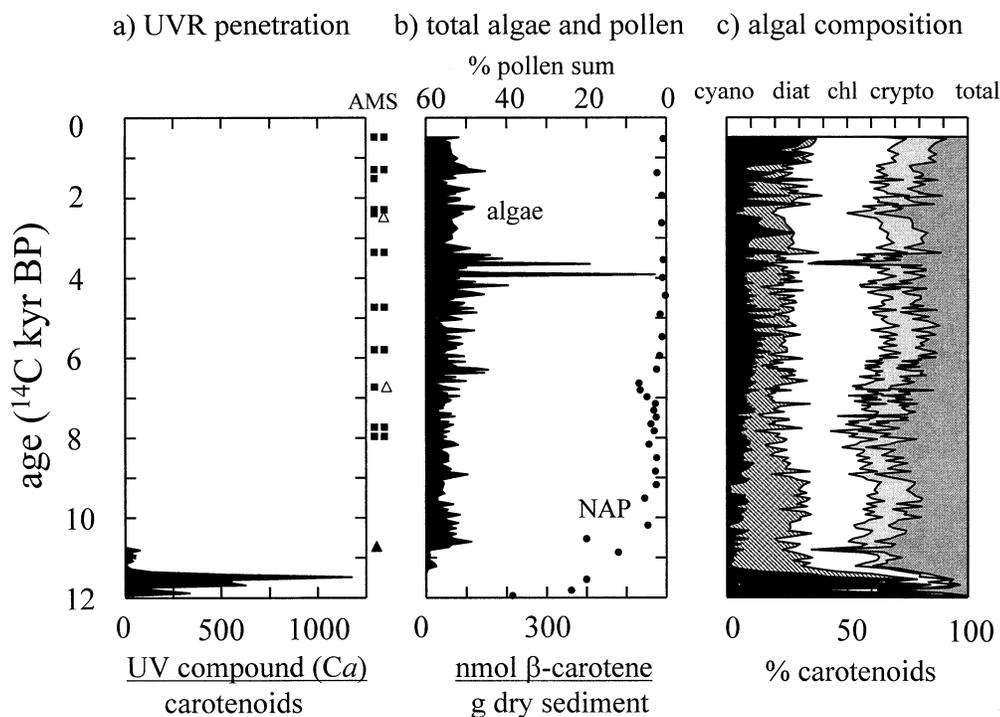a) UVR penetration   b) total algae and pollen   c) algal composition

Fig. 1.   Changes in (a) UVR penetration, (b) total algal abundance, and (c) gross algal community composition in Big Lake, British Columbia, Canada, during the Holocene era. UVR penetration was measured as a ratio of photoprotective pigment C_a to the sum of chemically stable carotenoids. Algal community composition (%) was estimated as pigments from cyanobacteria (cyano; myxoxanthophyll), diatoms (diat; diatoxanthin), chlorophytes and cyanobacteria (chl; lutein-zeaxanthin), cryptophytes (crypt; alloxanthin), and total algae (total; β-carotene). UVR penetration was elevated and algal abundance was at a historical minimum before ~10,700 ^{14}C yr BP. Details of accelerator mass-spectrometric [14]C (AMS; black squares), volcanic ash (open triangles), and clay interface (black triangles) dates are as in Bennett et al. (2001) and Heinrichs et al. (1999). Replicate analyses are indicated with multiple symbols. Nonarboreal pollen (NAP) abundance (as % fossil pollen sum; panel b) was modified from Bennett et al. (2001).

(Leavitt et al. 1997) to identify the potential mechanisms that cause long-term ecosystem change.

Methods

Big (51°40.1′N, 121°27.0′W), Valentine (51°35.2′N, 121°26.9′W), and Burnell (49°12.6′N, 119°36.7′W) lakes are located within 300 km of each other in south-central British Columbia, Canada. Our analysis focused on Big Lake, a site characteristic of the region but with prior paleoecological study of climate change and lake response during the Holocene era (Bennett et al. 2001). Big Lake is located within a mixed coniferous forest zone and presently has DOM levels (>20 mg dissolved organic carbon [DOC] L^{-1}) sufficient to limit UVR penetration to a few centimeters. In contrast, Crowfoot Lake (51°61′N, 116°31′W) is situated 300 km east of Big Lake in the upper Bow Valley of Banff National Park and lies near the upper elevational limit of subalpine coniferous vegetation (Hickman and Reasoner 1998). Low-elevation sites experienced their most recent glacial retreat ~10,700 yr before the present (yr BP) (Mathewes and King 1989; Hebda 1995; Heinrichs et al. 1999), whereas the mountain lake was above treeline early in its history, was

subalpine for ~6,000 yr but has been near treeline since ~4,000 yr BP (Reasoner et al. 1994; Reasoner and Huber 1999).

Low-elevation lakes were cored using a standard combination of Livingstone piston and Glew gravity corers (Bennett et al. 2001), whereas Crowfoot Lake sediments were collected using a light-weight percussion corer (Reasoner et al. 1994). Full postglacial sequences were recovered in all instances (~12,000 ^{14}C yr). Sediment ages were determined using accelerator mass spectrometric (AMS) analyses of ^{14}C activities in Crowfoot and Big lakes (10–18 dates core^{-1}; Reasoner et al. 1994; Bennett et al. 2001), volcanic ash layers (tephra), including the Bridge River (2,360 ^{14}C yr BP) and Mazama eruptions (6,730 ^{14}C yr BP) in all lakes (e.g., Reasoner et al. 1994), and AMS-dated lithostratigraphic transitions at the base of each core (Heinrichs et al. 1999; Reasoner and Huber 1999).

Fossil pigments were isolated and quantified using standard high-performance liquid chromatography (Leavitt et al. 1997, 1999). Algal abundance was measured as changes in fossil concentrations (nmol pigment g^{-1} dry sediment) of chemically stable carotenoids, including β-carotene (all algae), alloxanthin (cryptophytes), diatoxanthin (diatoms), my-

xoxanthophyll (colonial cyanobacteria), and lutein-zeaxanthin (chlorophytes and cyanobacteria). Similar stratigraphic profiles were obtained when fossils were expressed as accumulation rates or as organic matter–specific concentrations. Sediment organic content was determined as the percentage mass loss on ignition (LOI) at 500°C for 1 h (Leavitt et al. 1999).

UVR penetration (as UV-b radiation, 280–320 nm) was measured in all lakes as a ratio of UVR-absorbing pigments: algal carotenoids, an index that is linearly related to the depth of UVR penetration (as depth of 1% surface irradiance of UV-b) in whole-lake experiments (Leavitt et al. 1997). Mass spectrometry using negative ion-atmospheric pressure chemical ionization analysis showed that our UVR-absorbing pigment, C_a, had a gram molecular weight of 635. Surveys of alpine (Leavitt et al. 1997) and boreal lakes (Donahue et al. 2003) have demonstrated that C_a is produced by benthic algae in response to damaging levels of UVR. In contrast, ratios of C_a to the sum of chemically stable carotenoids (alloxanthin, diatoxanthin, and lutein-zeaxanthin) are 0 when the average algal exposure to UVR is not sufficient to initiate the production of photoprotective compounds.

For subalpine Crowfoot Lake, the depth of UVR penetration was inferred independently from historical changes in the organic matter content of sediment core samples. A survey of 75 alpine lakes (Leavitt et al. 1997; *see below*) revealed a strong linear correlation between the sediment organic matter content (LOI) and the DOM content of overlying waters in montane lakes ($r = 0.77$, $p < 0.0001$). Past DOM concentrations (as mg DOC L^{-1}) were reconstructed from organic matter (LOI) profiles in lake sediments and were converted to a depth of UVR penetration (as 1% surface irradiance of UV-b) using optical models published elsewhere (Morris et al. 1995; Schindler et al. 1996*b*). The mean lake depth was based on modern area-weighed basin morphology.

Historical changes in the nutrient content of Crowfoot Lake were inferred from prior analyses of fossil diatom community composition (Hickman and Reasoner 1998) and from a weighted-averaging regression model that inferred total phosphorus concentrations in British Columbia freshwater lakes from fossil diatoms (as total phosphorus [TP], μg L^{-1}; Bradbury et al. 2002). All key diatom taxa were well represented in our calibration set (no analog mismatches; *see figure 4 in* Hickman and Reasoner 1998), and the model performed well, with a coefficient of determination of 0.66. Although TP and total nitrogen (TN) concentrations were correlated both in modern alpine lake surveys and in our fossil reconstructions, we also used accumulation rates of pollen (grains cm^{-2} yr^{-1}) to quantify the variability in populations of N$_2$-fixing terrestrial plants (*Alnus* sp. and *Shepherdia canadensis*), the main source of N to lakes in recently deglaciated environments (Engstrom et al. 2000). Fossil pollen assemblages have been analyzed previously for both Crowfoot (Reasoner and Huber 1999) and Big (Bennett et al. 2001) lakes.

Statistical relationships among fossil time series from Crowfoot Lake were explored using basic time-series analyses with SYSTAT version 10 software (SPSS Inc., Chicago, Illinois). Preliminary analysis indicated that all predictor and
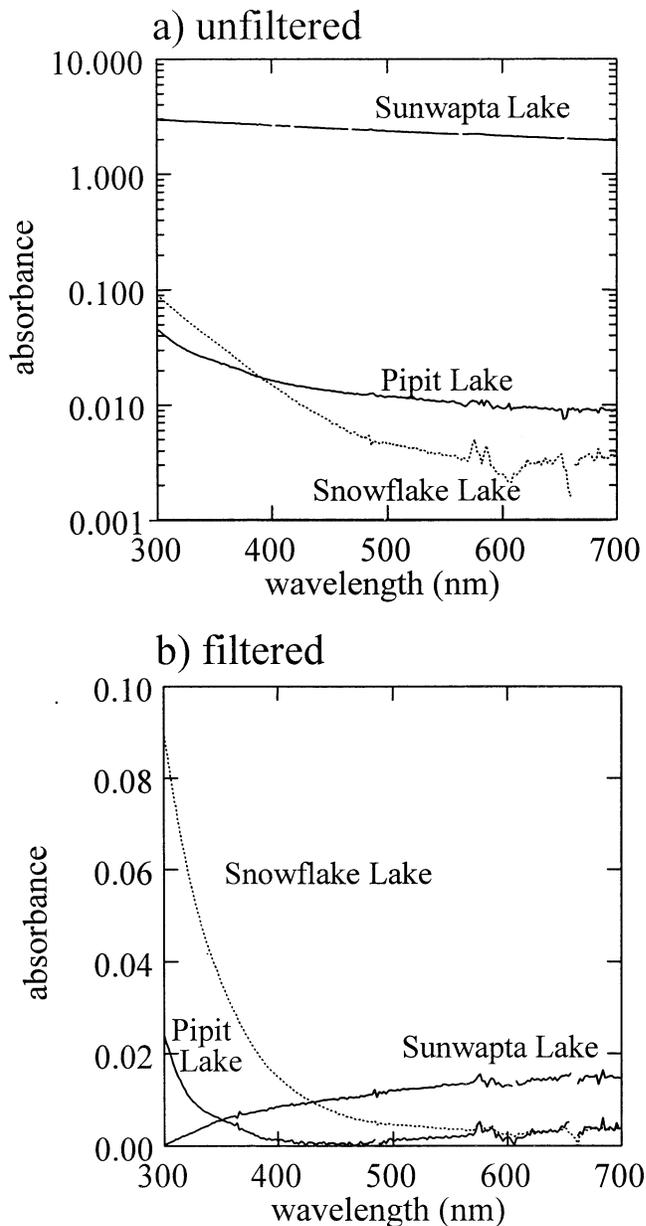

Fig. 2.   Optical properties of water from mountain lakes with (Sunwapta Lake) and without (Pipit and Snowflake lakes) inputs of inorganic particles from modern glaciers. (a) Absorbance of whole lake water as a function of light wavelength (nm) and (b) absorbance of water after filtration (0.45 μm pore) are shown. Ratios of absorbance of UVR:PAR show that, for a given photon flux of PAR, exposure to UVR is greater in turbid, glacial lakes than in clear, nonglacial systems (a) and that the DOM influence on UVR absorbance is absent from lakes with glacial particles (b).

response variables were not normally distributed and exhibited substantial temporal autocorrelations. Subsequently, all variables were subject to sequential log$_{10}$ and first-difference transformations to normalize the variance and remove autocorrelations. Cross-correlations were then calculated to determine whether there were significant lagged relationships among pairs of variables. No lagged relationships were sig-

a) Big Lake b) Burnell Lake c) Valentine Lake

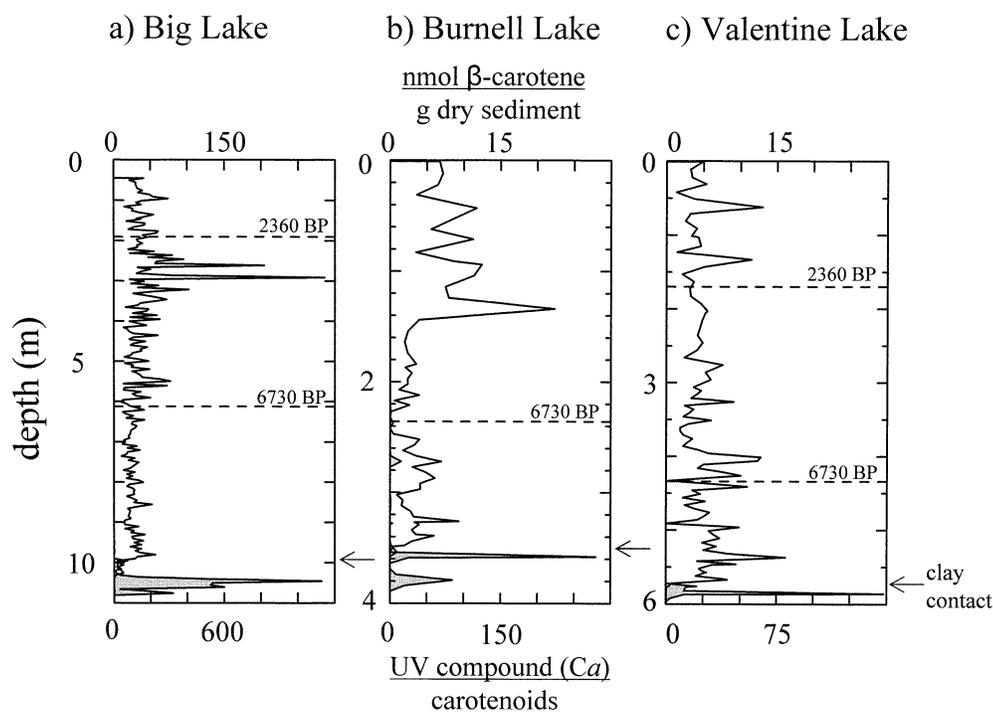$\dfrac{\text{nmol } \beta\text{-carotene}}{\text{g dry sediment}}$

Fig. 3.   Changes in UVR penetration (shaded) and total algal abundance (lines) in (a) Big, (b) Burnell, and (c) Valentine lakes, British Columbia, Canada. UVR penetration and total algal abundance as in Fig. 1, except for scale change. Comparison among lakes demonstrated that algal biomass is low when UVR penetration is great and that such periods occur after deglaciation. Approximate chronology is from Bridge River (2,360 ^{14}C yr BP) and Mazama volcanic ash (6,730 ^{14}C yr BP).

nificant, so we report only the lag = 0 relationships, calculated as Pearson correlation coefficients among the transformed variables. The relative importance of explanatory variables was determined by comparing the magnitude of correlation coefficients obtained from multiple regression analyses of fossil β-carotene profiles.

Finally, a survey of 75 lakes in the Rocky Mountains (Leavitt et al. 1997) was used to describe the relationships between algal abundance and the main gradients of environmental variability. Environmental variables included physical factors (ice-free season, summer water temperature, light and UVR attenuation, turbidity, and color), nutrients (DOM, dissolved and total N and P, major ions, and alkalinity), and morphometric features (depth, area, and catchment). The analytical details of chemical analyses are presented in Vine-brooke and Leavitt (1999b). Optical analyses were done on both filtered and unfiltered lake water, to estimate the effects of inorganic particles on biotic exposure to UVR (Vine-brooke and Leavitt 1998). Algal abundance was estimated as the β-carotene content of surface sediments (0–5 cm).

Results and discussion

Quantification of past UVR environments using fossil pigments documented that exposure to UVR in Big Lake was greatest early during the lake's history, prior to the development of regional forests ~10,700 ^{14}C yr BP (Fig. 1). For example, concentrations of photoprotective compounds were

elevated when nonarboreal pollen was abundant (>10% of fossil pollen sum) and when sediments lacked the physical remains of tree leaves. UVR-absorbing algal pigments were absent from sediments at all other times during the postglacial period, consistent with presently high levels of DOM in Big Lake. These patterns are also consistent with a recent analysis of lake chrono-series from Glacier Bay, Alaska, which demonstrated that the DOM content was exceptionally low during the first century after modern lake formation (Engstrom et al. 2000). Because DOM is the main factor regulating UVR flux in lakes (Morris et al. 1995; Schindler et al. 1996b), this early era also corresponds to the period of maximum UVR penetration.

The early exposure of algae to UVR may have been increased by the presence of fine inorganic particles from glaciers that, while reducing total irradiance, increased ratios of UVR relative to photosynthetically active radiation (PAR; 400–700 nm) within the photic zone of modern alpine lakes (Fig. 2). A comparison of the optical properties of unfiltered water from modern lakes with (e.g., Sunwapta Lake) and without (Pipit and Snowflake lakes) glacial inputs demonstrated that the absorbance of UVR was similar to that of PAR in turbid systems but was substantially greater than that of PAR in lakes without active glaciers (Fig. 2a). Similarly, when filtered waters were compared, glacial lakes apparently lacked the typical UVR attenuation normally imparted by DOM (Fig. 2b), possibly because DOM was adsorbed onto inorganic particles. Thus, for algae in turbid waters, the re-
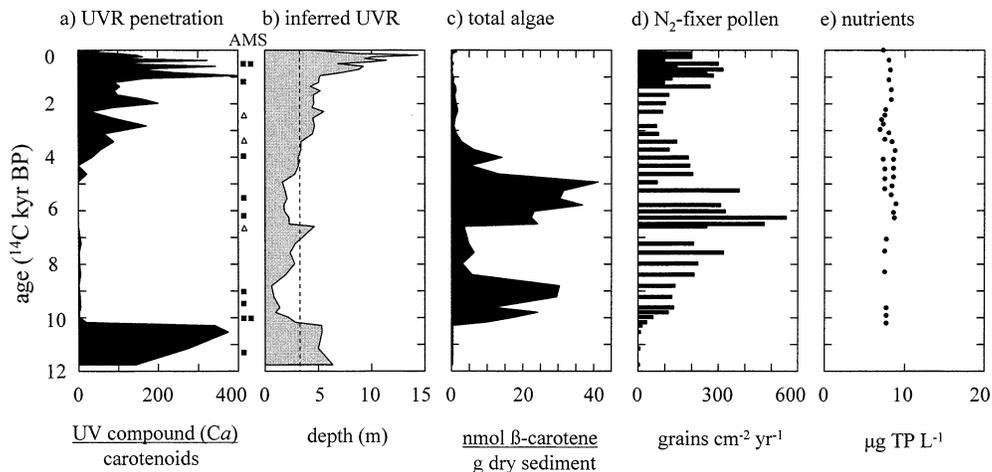
Fig. 4. Historical changes in (a) UVR exposure inferred from pigments, (b) the depth of UVR penetration inferred from sedimentary organic matter content, (c) total algal abundance, (d) the influx of pollen from N_2-fixing terrestrial plants, and (e) diatom-inferred total P concentrations at Crowfoot Lake, Alberta, Canada. The algal abundance was low and production of photoprotective pigments great whenever the depth of UVR penetration exceeded the mean depth of Crowfoot Lake (vertical dashed lines) during ~11,300–10,050 ^{14}C yr BP and ~4,000 ^{14}C yr BP to the present. Changes in algal abundance since 10,050 ^{14}C yr BP were uncorrelated with the historical variance in nutrient concentrations, measured as diatom-inferred TP. AMS ^{14}C (black squares) and volcanic ash (open triangles) chronologies are from Reasoner and Huber (1999). Chronological symbols are as in Fig. 1.

ceipt of sufficient PAR for photosynthesis is accompanied by unusually high exposure to UVR and may necessitate the production of photoprotective pigment C_a, despite low photon flux. Such compounds are costly for algae to manufacture and are only produced as a consequence of exposure to damaging levels of UVR (Gracia-Pichel and Castenholtz 1991).

Reconstructed algal biomass was at a historic minimum during the entire period of elevated UVR exposure (Fig. 1), consistent with a strong suppression of primary producers by UVR. In addition, early algal communities were predominately composed of colonial cyanobacteria, as evidenced by a high abundance of the diagnostic pigment myxoxanthophyll relative to those from eukaryotic algae. Such high abundance of cyanobacteria early during the Holocene era is also known from boreal lakes in eastern Canada (Brown and Colman 1963), as well as from modern polar and alpine lakes with high UVR exposure (Vincent and Quesada 1994). Experiments in other Canadian mountain lakes have shown that cyanobacteria may benefit from high UVR exposure, both because of a preferential inhibition of competing eukaryotic algae and, potentially, because of enhanced nutrient availability following the UV photolysis of organic matter (Vinebrooke and Leavitt 1998, 1999a).

UVR penetration declined and algal biomass increased ~10-fold immediately after the development of regional forests ~10,700 yr BP (Fig. 1). In particular, concentrations of pigments from UVR-sensitive diatoms (Vinebrooke and Leavitt 1998, 1999a) increased as UVR levels declined and remained elevated for ~2,000 yr. However, despite the subsequent variation in algal biomass and community composition in response to climate change (Bennett et al. 2001), UVR penetration never again achieved levels seen before

~10,700 ^{14}C yr BP, nor did UVR-resistant cyanobacteria achieve as high a relative abundance.

A comparison among other regional lakes showed that elevated UVR penetration and reduced algal biomass are common features of early lake evolution (Fig. 3). Valentine and Burnell lakes are located within 20 and 300 km, respectively, of Big Lake and have experienced a similar deglaciation and climatic history. In all cases, UVR penetration was great and total algal abundance low prior to the development of terrestrial carbon sources ~10,700 yr BP. However, unlike Big Lake, there was no predominance of cyanobacteria early in the history of the other two lakes (data not shown). We speculate that this pattern may signify that changes in gross community composition only occur at the extremely high UVR exposures rather than at the more modest values seen in Burnell, Valentine, and 75 other montane lakes (Leavitt et al. 1997).

Because the reconstructed algal abundance was low only during the oldest sedimentary sequences of these lakes, there exists the possibility that fossil patterns are artifacts of poor pigment preservation or sedimentary transformations (Hurley and Armstrong 1991). To test this hypothesis, we quantified Holocene changes in the UVR environment and algal abundance in Crowfoot Lake, a regional site situated near the present-day treeline in the Rocky Mountains. Crowfoot Lake lay above treeline during the Younger Dryas era (~11,100–10,100 ^{14}C yr BP), was subalpine for the next ~6,000 yr, then returned to its present position near the timberline after regional climatic cooling ~4,000 yr BP (Reasoner et al. 1994; Reasoner and Huber 1999). Because of the close correlation among climate, the development of terrestrial carbon sources, and reductions in UVR penetration in lakes (Pienitz and Vincent 2000), we hypothesized that
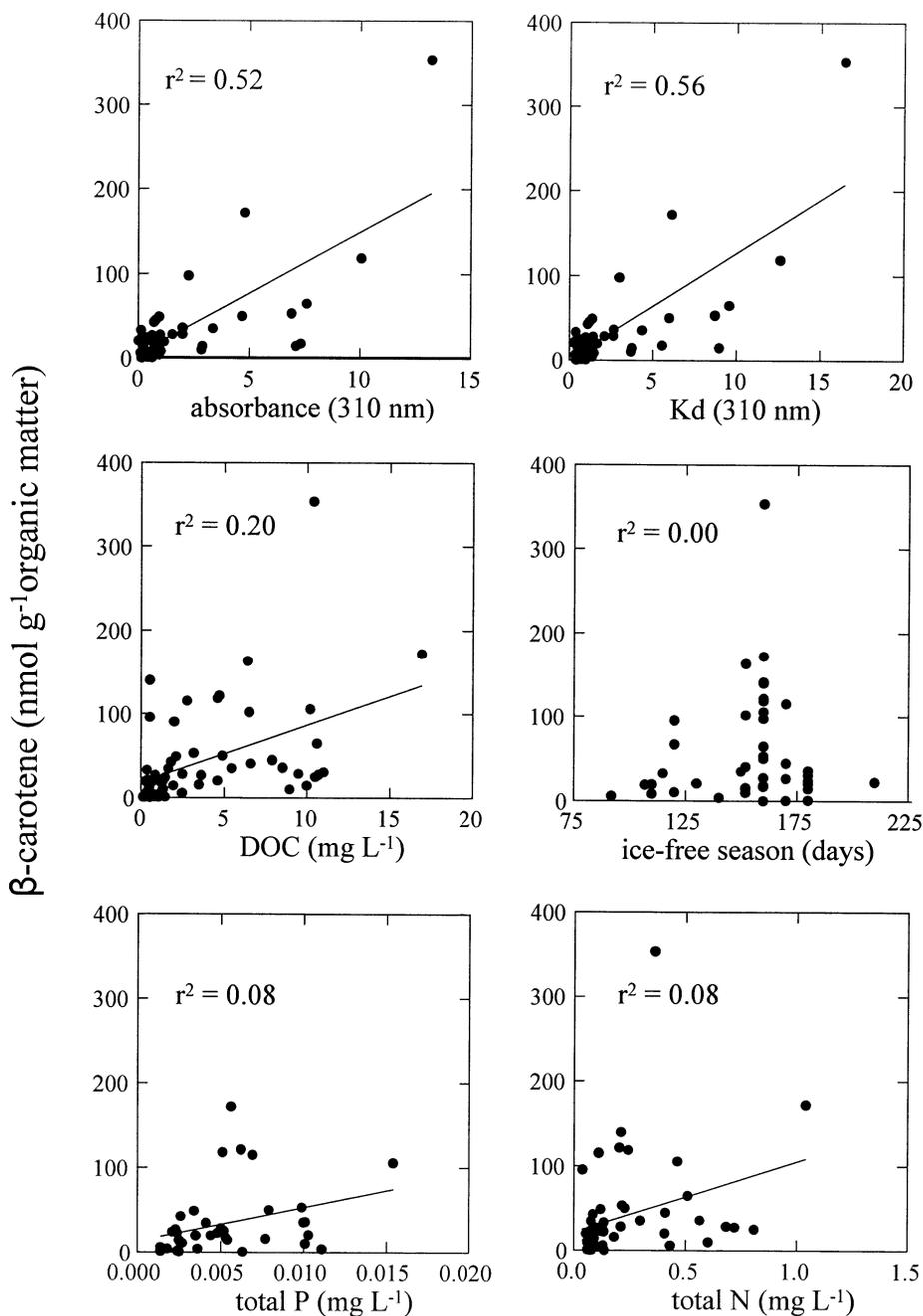
Fig. 5. Relationship between total algal abundance (as β-carotene concentration in surface sediments) in 75 mountain lakes and their optical properties (absorbance at 310 nm; diffuse attenuation coefficient, Kd_{310}), concentrations of DOM (mg DOC L^{-1}), duration of the ice-free season (days), and total nutrient concentrations (TN and TP; mg L^{-1}). The ability of lake water to attenuate UV-b radiation was a better predictor of total algal abundance than lake nutrient status, ice-free season duration, or summer water temperature (not shown).

the algal biomass should have been low during both the Younger Dryas era and recent cool periods but should have been greater in the intervening era, when terrestrial development and DOM export were greatest.

Analyses of fossil pigments from Crowfoot Lake confirmed that periods of reduced algal abundance coincided with those of high UVR penetration (Fig. 4). Furthermore, we used the strong correlation between sedimentary organic matter and the DOM content of alpine lakes ($r = 0.77$; $p < 0.001$) known from our modern surveys (Leavitt et al. 1997) to independently infer past changes in the DOM content of Crowfoot Lake. When this regression was coupled with standard DOM-UVR optical models (Morris et al. 1995; Schindler et al. 1996*b*), we could demonstrate that the algal abun-

dance was reduced 10–25-fold and photoprotective compounds were common only during periods when the estimated depth of UVR penetration exceeded the mean depth of Crowfoot Lake. After correction for autocorrelation, the time series of total algal abundance was negatively correlated with that of UVR exposure derived from both fossil pigments ($r = -0.72$, $p < 0.0001$) and sedimentary organic-matter metrics ($r = -0.68$, $p < 0.0001$), factors that themselves were correlated ($r = 0.51$, $p < 0.001$). In addition, the significant correlation between concentrations of sedimentary diatoms (Hickman and Reasoner 1998) and their unique biomarker pigment (diatoxanthin; $r = 0.64$, $p < 0.01$) in other cores from Crowfoot Lake confirmed that this fossil pigment mainly recorded changes in past algal abundance rather than pigment preservation. Because the chemical stability of diatoxanthin is similar to that of other carotenoids (Hurley and Armstrong 1991) and because other pigments are also deposited into sediments in proportion to the abundance of their respective producer populations in other lakes (e.g., Leavitt et al. 1997, 1999), we infer that our core analyses accurately reflect the major historical changes in total algal abundance.

Taken together, our analyses provide evidence that long-term changes in the algal biomass in lakes can be regulated largely by UVR and inputs of photoprotective DOM. This hypothesis is consistent with experiments in other Rocky Mountain lakes that demonstrated that DOM acts both as a screen of solar irradiance (Vinebrooke and Leavitt 1999*a*) and as a growth-enhancing nutrient for algae (Vinebrooke and Leavitt 1998). Although it is difficult to separate these functions, the close correspondence between the presence of metabolically expensive (Garcia-Pichel and Castenholtz 1991) UVR-absorbing pigments and the absence of refuges from UVR within Crowfoot Lake (Fig. 4) shows that UVR stresses were significant determinants of algal community development.

Three lines of evidence suggest that changes in algal abundance did not result from alterations in the mineral nutrient supply during the Holocene. First, a reconstruction of past nutrient levels using fossil diatoms showed that TP concentrations have not varied significantly during the past 10,000 yr (Fig. 4). These results are consistent with both geochemical (Filippelli and Slouch 1999) and modern glacial-analog studies (Engstrom et al. 2000) that have demonstrated that the phosphorus supply to lakes varies little as a consequence of terrestrial development in glaciated regions. Second, an analysis of fossil pollen demonstrated that populations of *Alnus,* the main source of nitrogen in recently deglaciated environments (Engstrom et al. 2000), have only been weakly correlated with algal abundance since ~10,050 ^{14}C yr BP ($r = 0.37$, $p < 0.01$; Fig. 4). Instead, an analysis using multiple regressions revealed that the variation in UVR penetration was eightfold (coefficient, -1.722) more important than changes in N_2-fixer populations (coefficient, 0.194) in explaining the variation in past algal abundance. Third, a survey of montane lakes confirmed that a modern algal abundance (as β-carotene) is more strongly correlated to the ability of lake water to attenuate UVR (Kd_{310}, A_{310}; $r^2 > 0.50$, $p < 0.001$) than to lake nutrient content (TP, TN; $r^2 = 0.08$, $p = 0.05$), the duration of ice-free seasons ($r^2 = $

0.00, $p = 1.00$), or the mean summer water temperature (not shown) (Fig. 5). Such a strong influence of DOM on algae and weak effects of nutrients and climatic variables are also known from other regional lake surveys (Vinebrooke and Leavitt 1999*b*). Taken together, these patterns suggest that changes in algal abundance during the Holocene era arose from the influence of DOM on lake optical properties rather than from direct climatic effects or variations in nutrient fluxes.

In conclusion, our analyses demonstrated that total algal biomass was reduced 10–25-fold during periods of extremely high UVR after lake formation. Because such episodes result from natural, climatically induced variations in the DOM flux in lakes, we believe that long periods of high UVR exposure are common to lakes of glacial origin. Consistent with this view, an analysis of modern analogs of lake ontogeny also demonstrated that concentrations of UVR-absorbing DOM are extremely low during the first ~100 yr of lake existence (Engstrom et al. 2000). Furthermore, because these changes are linked closely to long-term climatic variability, we suggest that future changes in global temperature and precipitation may fundamentally alter the UVR environment, gross community composition, and primary production of many boreal lake ecosystems by altering the inputs of UVR-absorbing DOM.

A modest extrapolation of our results suggests that modern lake communities may be poorly adapted to future UVR-climate interactions, despite apparently abundant reserves of photoprotective DOM in soils and surface waters. An analysis of Crowfoot Lake demonstrated that lakes can remain sensitive to changes in DOM and UVR fluxes even after 6,000 yr of continuous photoprotection. In particular, rates of decline of algal abundance in Crowfoot Lake ~4,500 ^{14}C yr BP (-1.25% yr^{-1}) were similar to those arising from DOM loss during modern climate change in North America (Schindler et al. 1996*a*), despite an inferred DOM content (2.5–5.5 mg DOC L^{-1}) that is typical of many modern boreal and montane lakes (Morris et al. 1995; Schindler et al. 1996*b*; Leavitt et al. 1997). However, unlike modern analyses, the present paleoecological investigation suggests that these reductions can persist for centuries, terminating in fundamental ecosystem reorganization and unprecedented declines in primary producers when the last refuges from UVR are lost.

References

BENNETT, J. R., B. F. CUMMING, P. R. LEAVITT, M. CHIU, J. P. SMOL, AND J. SZEICZ. 2001. Diatom, pollen, and chemical evidence of post-glacial climatic change at Big Lake, south-central British Columbia. Quat. Res. **55:** 332–343.

BOTHWELL, M. L., D. SHERBOT, AND C. M. POLLOCK. 1995. Ecosystem response to solar ultraviolet-B radiation: Influence of trophic-level interactions. Science **265:** 97–100.

BRADBURY, J. P., K. R. LAIRD, AND B. F. CUMMING. 2002. A 1500-year record of climatic and environmental change in Elk Lake, Minnesota III: Measures of past primary productivity. J. Paleolimnol. **27:** 321–340.

BROWN, S. R., AND B. COLMAN. 1963. Oscillaxanthin in lake sediments. Limnol. Oceanogr. **8:** 352–353.

DONAHUE, W. F., M. A. TURNER, D. L. FINDLAY, AND P. R. LEAVITT.

2003. The role of solar radiation in structuring the shallow benthic communities of boreal forest lakes. Limnol. Oceanogr. **48:** 31–47.

ENGSTROM, D. R., S. C. FRITZ, J. E. ALMENDINER, AND S. JUGGINS. 2000. Chemical and biological trends during lake evolution in recently deglaciated terrain. Nature **408:** 161–166.

FILIPPELLI, G. M., AND C. SOUCH. 1999. Effects of climate and landscape development on the terrestrial phosphorus cycle. Geology **27:** 171–174.

GRACIA-PICHEL, F., AND R. W. CASTENHOLTZ. 1991. Characterization and biological implications of scytonemin, a cyanobacterial sheath pigment. J. Phycol. **27:** 395–409.

HEBDA, R. J. 1995. British Columbia vegetation and climate history with focus on 6 ka BP. Geogr. Phys. Quat. **49:** 55–79.

HEINRICHS, M. L., I. R. WALKER, R. W. MATHEWES, AND R. J. HEBDA. 1999. Holocene chironomid-inferred salinity and paleovegetation reconstruction from Kilpoola Lake, British Columbia. Geogr. Phys. Quat. **53:** 211–221.

HICKMAN, M., AND M. A. REASONER. 1998. Late Quaternary diatom response to vegetation and climate change in a subalpine lake in Banff National Park, Alberta. J. Paleolimnol. **20:** 253–265.

HURLEY, J. P., AND D. E. ARMSTRONG. 1991. Pigment preservation in lake sediments: A comparison of sedimentary environments in Trout Lake, Wisconsin. Can. J. Fish. Aquat. Sci. **48:** 472–486.

LEAVITT, P. R., D. L. FINDLAY, R. I. HALL, AND J. P. SMOL. 1999. Algal responses to dissolved organic carbon loss and pH decline during whole-lake acidification: Evidence from paleolimnology. Limnol. Oceanogr. **44:** 757–773.

⸻, R. D. VINEBROOKE, D. B. DONALD, J. P. SMOL, AND D. W. SCHINDLER. 1997. Past ultraviolet environments in lakes derived from fossil pigments. Nature **388:** 457–459.

KARENTZ, D., AND OTHERS. 1994. Impact of UV-B radiation on pelagic freshwater ecosystems: Report of working group on bacteria and phytoplankton. Arch. Hydrobiol. Ergebn. Limnol. **43:** 31–69.

MATHEWES, R. W., AND M. KING. 1989. Holocene vegetation, climate and lake-level changes in the Interior Douglas-fir Biogeoclimatic Zone, British Columbia. Can. J. Earth Sci. **26:** 1811–1825.

MORRIS, D. P., AND OTHERS. 1995. The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. Limnol. Oceanogr. **40:** 1381–1391.

PIENITZ, R., AND W. F. VINCENT. 2000. Effect of climate change relative to ozone depletion on UV exposure in subarctic lakes. Nature **404:** 484–487.

REASONER, M. A., AND U. M. HUBER. 1999. Postglacial palaeoenvironments of the upper Bow Valley, Banff National Park, Alberta, Canada. Quat. Sci. Rev. **18:** 475–492.

⸻, G. OSBORN, AND N. W. RUTTER. 1994. Age of the Crowfoot advance in the Canadian Rocky Mountains: A glacial event coeval with the Younger Dryas oscillation. Geology **22:** 439–442.

SCHINDLER, D. W., AND OTHERS. 1996a. The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, northwestern Ontario. Limnol. Oceanogr. **41:** 1004–1017.

⸻, P. J. CURTIS, B. R. PARKER, AND M. P. STAINTON. 1996b. Consequences of climatic warming and lake acidification for UV-B penetration in North American boreal lakes. Nature **379:** 705–708.

VINCENT, W. F., AND A. QUESADA. 1994. Ultraviolet radiation effects on cyanobacteria: Implications for Antarctic microbial ecosystems. Antarc. Res. Ser. **62:** 111–124.

VINEBROOKE, R. D., AND P. R. LEAVITT. 1998. Direct and interactive effects of allochthonous dissolved organic matter, inorganic nutrients, and ultraviolet radiation on an alpine littoral food-web. Limnol. Oceanogr. **43:** 1065–1081.

⸻, AND ⸻. 1999a. Differential responses of littoral communities to ultraviolet radiation in an alpine lake. Ecology **80:** 223–237.

⸻, AND ⸻. 1999b. Phytobenthos and phytoplankton as potential indicators of climate change in mountain lakes and ponds: A HPLC-based pigment approach. J. North Am. Benthol. Soc. **18:** 15–33.

WILLIAMSON, C. E., S. L. METZGAR, P. A. LOVERA, AND R. E. MOELLER. 1997. Solar ultraviolet radiation and the spawning habitat of yellow perch, *Perca flavescens*. Ecol. Appl. **7:** 1017–1023.

XENOPOULOS, M. A., Y. T. PRAIRIE, AND D. F. BIRD. 2000. Influence of ultraviolet-B radiation, stratospheric ozone variability, and thermal stratification on the phytoplankton biomass dynamics in a mesotrophic lake. Can. J. Fish. Aquat. Sci. **57:** 600–609.

YAN, N. D., W. KELLER, N. M. SCULLY, D. R. S. LEAN, AND P. J. DILLON. 1996. Increased UV-B penetration in a lake owing to drought-induced acidification. Nature **381:** 141–143.