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Global warming and the export of dissolved organic carbon from boreal peatlands

John Pastor, Jeremy Solin, Scott D. Bridgham, Karen Updegraff, Cal Harth, Peter Weishampel and Bradley Dewey

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Peatlands occupy approximately 15% of boreal and sub-arctic regions, contain approximately one third of the world's soil carbon pool, and supply most of the dissolved organic carbon (DOC) entering boreal lakes and rivers and the Arctic Ocean. The high latitudes occupied by these peatlands are expected to see the greatest amount of climatic warming in the next several decades. In addition to increasing temperatures, climatic change could also affect the position of the water-table level and discharge from these peatlands. Changes in temperature, water tables, and discharge could affect delivery of DOC to downstream ecosystems where it exerts significant control over productivity, biogeochemical cycles, and attenuation of visible and UV radiation. We experimentally warmed and controlled water tables while measuring discharge in a factorial experiment in large mesocosms containing peat monoliths and intact plant communities from a bog and fen to determine the effects of climate change on DOC budgets. We show that the DOC budget is controlled largely by changes in discharge rather than by any effect of warming or position of the water-table level on DOC concentrations. Furthermore, we identify a critical discharge rate in bogs and fens for which the DOC budget switches from net export to net retention. We also demonstrate an exponential increase in trace gas CO_2–C and CH_4–C emissions coincident with increased retention of dissolved organic carbon from boreal peatlands.

J. Pastor and J. Solin, Dept of Biology, University of Minnesota, Duluth, MN 55812, USA. – J. Pastor, C. Harth and B. Dewey, Natural Resources Res. Inst., Univ. of Minnesota, Duluth, MN 55811, USA (jastor@sage.nrri.umn.edu). – S. D. Bridgham and P. Weishampel, Dept of Biological Sciences, Univ. of Notre Dame, Notre Dame, IN 46556, USA. Present address for PW: Dept of Natural Resources, Cornell Univ., Ithaca, NY 14850, USA. – K. Updegraff, Dept of Forest Resources, Univ. of Minnesota, St. Paul, MN 55108, USA.

Global climatic warming is expected be greatest in boreal and subarctic regions; midcontinental areas are also expected to become drier (Houghton et al. 1995). Peatlands occupy approximately 15% of boreal and subarctic regions (Bridgham et al. 2001), and contain approximately one third of the world's soil carbon pool (Gorham 1991), and they also supply most of the dissolved organic carbon (DOC) entering boreal lakes and rivers and the Arctic Ocean (Mulholland and Kuenzler 1979, Maybeck 1982, Urban et al. 1989, Dalva and Moore 1991, Molot and Dillon 1996), which represents a significant regional redistribution of terrestrial carbon.

The DOC exported from peatlands represents a significant regional redistribution of terrestrial carbon, exerts important controls on downstream aquatic net primary production (Carpenter and Pace 1997), bacterial production (Hobbie 1992, Wetzel 1992), and other biogeochemical cycles (Driscoll et al. 1980, Hemond 1980, Jackson and Hecky 1980, McKnight et al. 1985,

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Thurman 1985, Guildford et al. 1987), and DOC also attenuates visible solar and UV-B radiation in the water columns of downstream aquatic ecosystems (Schindler et al. 1990, 1996, Scully and Lean 1994, Morris et al. 1995, Williamson et al. 1999). Therefore, the redistribution of DOC from peatlands to downstream aquatic ecosystems could be a central factor in determining the overall response of aquatic ecosystems to climatic change.

The amount of DOC exported from peatlands may depend on interactions between the flow of water through the peatland and the production and consumption of DOC within the peatland, which in turn may depend on the diverse chemical nature of peat derived from different plant communities. Peatlands are dynamic ecosystems in which the accumulation of peat is determined by and in turn controls the flow patterns of water (Wright et al. 1992). Bogs are elevated portions of peatlands where peat accumulation has raised the surface above the water table; they receive their water from precipitation or from higher portions of the raised dome and deliver it to fens in lower topographic positions in the same peatland. Fens also receive groundwater inputs. *Sphagnum* mosses, and ericaceous shrubs, and black spruce dominate the vegetation of bogs while sedges and other graminoids dominate fens in North America (Wright et al. 1992). Additionally, the relative decomposability of bog and fen peats differ considerably (Bridgham et al. 1998). Consequently, DOC budgets of these two peatland ecosystems may respond to global warming in different ways.

Climatic change can affect the DOC budget of peatlands by several mechanisms. First, increased temperatures can increase the production (through increased decay rates) and/or microbial consumption of DOC, thereby changing DOC concentrations in drainage water. Second, changes in the position of the water-table level can change DOC concentrations as different portions of the peat profile become exposed to undergo aerobic and/or anaerobic decomposition regimes. Third, changes in the water budget and discharge could control DOC export independently of any changes in DOC concentrations.

In natural peatlands, it is difficult to separate the effect of water-table level on discharge and decomposition because water-table levels control both the proportion of the peat profile which is aerobic (controlling DOC concentration; but see Moore and Dalva 2001) and discharge (affecting the mass of DOC export independent of concentration; Boelter and Verry 1977, Brooks 1992). Separation of the multiple effects of water-table on DOC budgets requires experimentally decoupling the effect of water-table and exposure of the peat profile from that of discharge.

To examine the responses of peatlands to expected climate change, we have experimentally warmed and controlled the water table in mesocosms containing intact cylindrical monoliths of bog or fen vegetation and peat (Bridgham et al. 1999). Previous papers on this experiment have reported on the effect of warming and water-table levels on water and energy budgets (Bridgham et al. 1999), net primary productivity and species composition (Weltzin et al. 2000, 2001), and CO_2 and CH_4 fluxes (Updegraff et al. 2001). Here, we report the effect of these treatments on DOC export.

Methods

The source sites for the bog and fen monoliths cores are in the townships of Toivola and Alborn, respectively, in northern Minnesota (47° N, 92° W). The upper 60 cm of the bog is derived largely from *Sphagnum* mosses; the surface 0-25 cm has a pH of 4.1, 42.2% C, 8.4% ash, and 73.7% rubbed fiber content on a dry mass basis. The peat in the fen is derived almost entirely from sedges and graminoids; the upper 25 cm has a pH of 4.9, 38.6% C, 22.3% ash, and 29.2% rubbed fiber content on a dry mass basis.

The mesocosms, consisting of plastic insulated tanks 2.13 m^2 in area (1.65-m diameter) and containing a peat monolith approximately 60 cm thick with intact overlying vegetation, were sunk into the ground in a large open field. Infrared radiation was augmented with overhead heat lamps set at none (ambient), half, or full heat, beginning on July 27, 1994. These are identical to the lamps used in a similar experiment in alpine tundra (Harte et al. 1995). The net increase in infrared loading to the peat surfaces of the mesocosms (minus ambient solar inputs and canopy reflection) were approximately 45 and 90 $W\ m^{-2}$ for the medium and full heat treatments, respectively. The lamps did not alter the delivery of photosynthetically active radiation (1020 ± 73 sd $\mu mol\ m^{-2}\ s^{-1}$ under the lamps vs 1018 ± 75 sd $\mu mol\ m^{-2}\ s^{-1}$ ambient away from the lamps), UV-A radiation (9.92 ± 0.38 sd $W\ m^{-2}\ s^{-1}$ under vs 9.92 ± 0.35 sd $W\ m^{-2}\ s^{-1}$ ambient away), nor UV-B radiation (0.67 ± 0.03 sd $W\ m^{-2}\ s^{-1}$ under vs 0.67 ± 0.04 sd $W\ m^{-2}\ s^{-1}$ ambient away). Although these thermal energy loads were considerably above those predicted under a $2 \times CO_2$ atmosphere, soil temperature increases in the heated plots were approximately 1.6 to 4.1°C above ambient during the growing season (Bridgham et al. 1999), well within the range of temperature increases predicted by global climate models (Houghton et al. 1995). Seasonal changes in soil temperature in the heated plots parallel seasonal changes in ambient plots, although the heating effect of the lamps is dissipated in the winter (see Bridgham et al. 1999 for further details and discussion).

Water-table levels in each mesocosm were maintained by perforated PVC pipes that drain the base of each mesocosm into a PVC pipe manostat in a sump tank that collected discharge water. The manostat heights were set so that the water table treatments were approximately +1 cm, −10 cm and −20 cm relative to the lowest point in each plot (i.e. a datum hollow) the surface of the peat cores at the beginning of the growing season of 1994. Therefore, we have a fully crossed factorial design of two communities (bog and fen) × three infrared loadings × three water-table levels with three replicate tanks for each infrared loading-water table combination.

Water in the mesocosms was replenished by natural precipitation (measured with a wet/dry rain gauge) and – when necessary to maintain the desired water-table level – by weekly measured additions of water pumped from a ditch channel draining a nearby, 3.9 km^2 continuous bog. This bog water had similar pH, electrical conductivity, and nutrient status to the pore water of the bog source site (Updegraff et al. 2001). The bog water was added through a vertical PVC pipe installed in the center of each mesocosm to the bottom of the tanks. Both bog and fen mesocosms receive the same bog-derived water, which mimics the flow of water through bogs into fens in natural peatland complexes (Glaser 1992).

The volume of discharge was measured at least weekly or more often after rain events in the covered sump tanks into which the manostats drained. These measurements of discharge, precipitation, and weekly additions of water to each mesocosm, along with precipitation measurements using a standard rain gauge and the measured volume of water added weekly to the different water table treatments, allowed us to calculate water budgets during the unfrozen season at approximately a weekly time step. Details of the effects of warming and water-table levels on the water budget are reported in Bridgham et al. (1999).

Discharge water samples were collected monthly May through September for DOC analysis. Approximately 500 ml of water was pulled through the manostat drainage system (thus coming from the bottom of the mesocosms) from tubing placed to the bottom of the manostat pipes before collecting 60 ml samples. Rainfall water was collected as soon as possible after an event and applied bog water was collected at the time of application. All water samples were placed in coolers, returned to the lab and filtered through Fisherbrand G4 glass-fiber filters.

DOC was determined by first measuring DOC concentrations directly on a TOC analyzer (Doorman DC-80) for 50 randomly selected samples throughout the course of the growing season. These measurements of DOC concentrations were then regressed against UV absorbance at 320 nm wavelength measured with a Perkin Elmer Lambda 3B spectrophotometer on the same samples ($\mathrm{DOC} = (\mathrm{Abs@320} \times 60.255) - 18.61$, $r^2 = 0.83$, $P < 0.001$; EPA 1983). This regression was then applied to the remaining water samples after measuring their UV light absorbance at 320 nm to estimate their DOC concentrations. The residuals of the regression were randomly distributed across the entire growing season, and so the regression does not introduce any temporal bias in our estimates of DOC concentrations. The amount of uncertainty introduced in any one sample is less than the variation in mean DOC concentrations between treatments.

Along with quantitative measurements of the water budget during the period when the peat is unfrozen (late May–early October), these data on DOC concentrations allow us to examine the effect of warming and water-table level on DOC input–output budgets. Changes in DOC budgets with respect to infrared loading and water-table level manipulation during the first three years of the experiment from 1995 to 1997 were analyzed using repeated measures ANOVA.

Results and discussion

Increased infrared loading and higher water tables significantly decreased net DOC export in both communities (Fig. 1; $P < 0.001$ for both treatment effects in communities). Neither the heat × water table nor

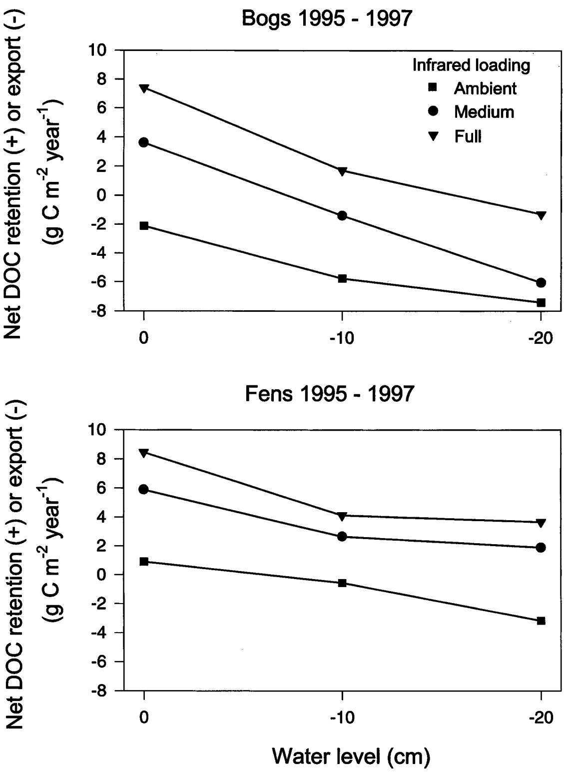

Fig. 1. The effects of water table level and infrared loading on the annual DOC budgets of bogs and fens. Each point represents the mean of each infrared loading-water table treatment combination over the period 1995–1997.

year × main effects interactions were statistically significant. While these results show that climate change can affect DOC budgets, they do not demonstrate whether the mechanisms are changes in DOC concentrations, discharge from the water budget, or both. To determine the mechanism responsible, we examined the effects of increased infrared loading and water table on DOC concentrations and the relationship between DOC and discharge water budgets.

DOC concentrations in discharge water from the bog mesocosms were significantly higher than those from the fens ($P < 0.001$). DOC concentrations increased slightly with increased infrared loading in the bog mesocosms ($P < 0.001$, from $68.9 \pm$ sd 14.2 mg l^{-1} under ambient infrared loading to $83.6 \pm$ sd 15.3 mg l^{-1} under the highest infrared loading), similar to that reported by Freeman et al. (2001) for acidic bogs in the United Kingdom. DOC concentrations in the fen discharge water were unaffected by infrared loading ($35.8 \pm$ sd 15.5 mg l^{-1} under ambient loading vs $36.8 \pm$ sd 15.7 mg l^{-1} under the highest infrared loading). They were not affected by water table levels in either the bog ($77.3 \pm$ sd 13.8 when the water table was at the surface vs $79.9 \pm$ sd 18.5 when the water table was -20 cm) or the fen mesocosms ($37.3 \pm$ sd 16.0 when the water table was at the surface vs $32.3 \pm$ sd 11.7 when the water table was -20 cm).

These DOC concentrations are within the ranges of those found in waters draining from natural peatlands (Hemond 1980, McKnight et al. 1985, Urban et al. 1989, Dalva and Moore 1991). The lower DOC concentrations in the fen discharge compared with bog discharge compare favorably with those found by Urban et al. (1989) in drainage waters from fens and bogs in a similar, nearby peatland complex to that studied here. Moreover, DOC concentrations in the mesocosm bogs and fens were similar to those we have observed in the natural bog and fen from which the peat monoliths were removed (unpubl).

Discharge accounted for a very small proportion of variations in DOC concentrations over the three years in both the bog ($r^2 = 0.03$) and fen mesocosms ($r^2 = 0.02$, albeit statistically significant in both cases ($P < 0.01$) because of the large sample size of 405 samples in each ecosystem type over three years). This weak correlation between DOC concentrations and discharge is in contrast to the stronger positive correlations often seen in drainage waters from watersheds with few wetlands (McDowell and Fisher 1976, Fiebig et al. 1990, Brown et al. 1999). In these upland-dominated watersheds, wetter conditions change flowpaths to include surface organic matter layers such as forest floors, thus enriching DOC concentrations over those from low flow conditions through deeper mineral soil horizons. In peatlands, flowpaths are always through organic layers. This alone would argue for a dilution of DOC concentrations under higher flows through these mesocosms, rather than the relatively constant DOC concentrations reported here. However, Qualls and Richardson (in press) suggested that DOC concentrations in water draining from the Everglades peatlands are regulated by rapid adsorption/desorption reactions between the DOC and the exchange and reactive surfaces of the undecomposed peat. Sorption equilibria for porewater DOC may also be operating in our peats as well. Our results thus suggest relatively stable, ecosystem-dependent DOC concentrations in peatlands, irrespective of input source, water-table level, or heat loading.

Because DOC concentrations were relatively stable with respect to infrared loading and water tables in both bog and fen mesocosms, the increased DOC retention upon warming in both bogs and fens (Fig. 1) resulted predominantly from the increased evapotranspiration and therefore decreased discharge under warmer conditions (Bridgham et al. 1999). This suggests that the effect of warming and changes in water tables on DOC budgets occurs primarily through changes they cause in discharge the water budget rather than any large effect they may have on DOC concentrations.

To examine how changes in the water budget affected net DOC retention (inputs > outputs) or export (outputs > inputs), we regressed DOC mass balance (inputs in precipitation plus added bog water-outputs in discharge) against volume of discharge (Fig. 2). DOC retention declined and export increased as volume of discharge increased in both ecosystems, but the rate of change differed between bogs and fens (Fig. 2). The correlation between net DOC retention/export and discharge was stronger for bogs ($r^2 = 0.91$, $P < 0.0001$) than fens ($r^2 = 0.46$, $P < 0.001$). DOC budgets switched from net export to net retention when water output declined below 150 l m^{-2} $year^{-1}$ in the bogs and 250 l m^{-2} $year^{-1}$ in the fens.

Since infrared loading affected DOC concentrations in the bogs, the DOC-discharge relationships in Fig. 2 could also depend on changes in DOC concentrations. To examine this, we regressed net DOC retention/export against discharge for each level of infrared loading in both ecosystems. Infrared loading significantly increased both the y-intercepts ($P < 0.001$) and the slopes ($P < 0.004$) of the DOC-discharge relationship in the bogs. The net effect of these changes is to increase DOC retention with warming when discharge was less than 150 l m^{-2} $year^{-1}$ but increase export when discharge was greater than 150 l m^{-2} $year^{-1}$. This is consistent with the increased DOC concentrations and with the increased infrared loadings as noted above. In contrast, infrared loading did not significantly explain any of the scatter in the data in Fig. 2 from the fens, consistent with the lack of effect of infrared loading on DOC concentrations in fen discharge water.

In a natural peatland, fens often naturally receive water from upslope bogs (Wright et al. 1992), and so

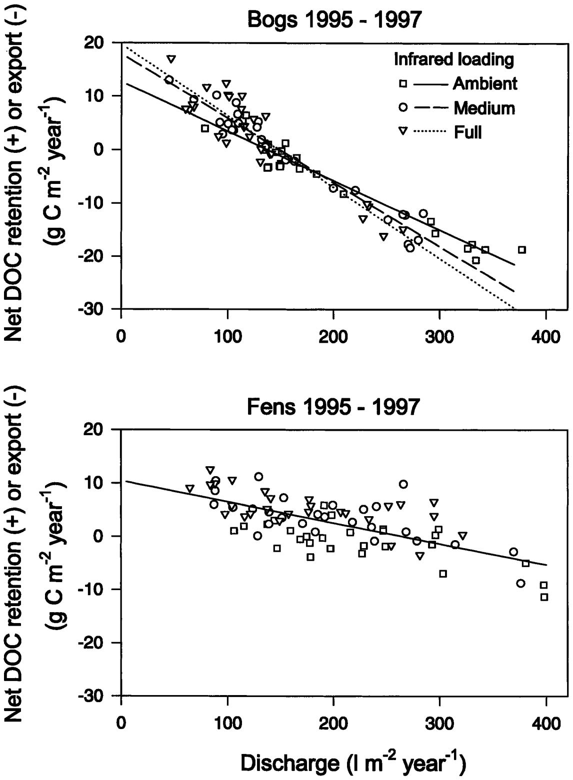

Fig. 2. Decreased water output switched the DOC budgets from net export to net retention in bogs (r^2 across all infrared loadings = 0.905, $P < 0.0001$) and fens (r^2 across all infrared loadings = 0.457, $P < 0.001$). The three regression lines in the bogs indicate the different relationships between DOC budgets and water output for different infrared loadings. Increased infrared loading increased net DOC retention in bogs when water output was less than 150 l m^{-2} yr^{-1}, but increased net DOC export when water output was greater than 150 l m^{-2} yr^{-1}. Infrared loading did not significantly affect the slopes and y-intercepts of similar regressions of the data from the fens, and therefore only a single overall regression line is shown. Each point is the annual output from each mesocosm for each of the three years during the period 1995–1997.

our addition of bog water as a supplementary water source to the fen mesocosms mimics this coupling between bogs and fens in a natural peatland. In these fen mesocosms, less DOC was discharged than was added in the supplementary water needed to maintain constant water tables when discharge was less than 250 l m^{-2} year^{-1}. Our results suggest that in natural peatlands bogs export DOC to fens, where it is partially retained with the balance being delivered from fens to downstream ecosystems. This results in a redistribution of DOC from bogs to fens in the peatland, with fens being the export venue from the peatland to downstream ecosystems. Our results suggest that as warming decreases discharge, bogs will deliver less DOC to fens and fens will in turn deliver even less DOC to downstream ecosystems.

This retained DOC could either be stored in the peat column or exported to the atmosphere by means of microbial respiration. CO_2–C and CH_4–C emissions were previously determined by enclosing the plots in dark tents biweekly and sampling the airspace, followed by gas chromatography analyses (Updegraff et al. 2001). Respiratory losses of CO_2–C and CH_4–C increased exponentially with increased DOC retention (Fig. 3) in both bogs ($r = 0.57$, $P < 0.001$) and fens ($r = 0.37$, $P < 0.001$). In fact, the rise in gaseous C emissions export happens only when the DOC budget switches from net export to net retention. It is likely that the same processes which retain DOC (warmer temperatures, lower discharge) also increase gaseous C emissions. However, the amount of DOC retained can potentially account for only 1.5 to 3% of net ecosystem respiratory losses (ER) of C in the bog and fen, respectively (ER ~ 620 m^{-2} year^{-1} in bog, 660 g m^{-2} year^{-1} in fen; Updegraff et al. 2001). Stable isotope analyses of DOC and gaseous carbon species are required to determine more precisely the relative contribution of DOC to gaseous C export. Nevertheless, the clear exponential rise of gaseous C emissions with DOC retention (Fig. 3) strongly suggests a redistribution of exported carbon from aquatic systems to the atmosphere as peatlands become warmer and drier.

These measured DOC export rates are small but not insignificant fractions of the carbon gains in net primary production. Net primary production was determined annually in 4 subplots per mesocosm using allometric relationships between linear measures of plant growth (current twig length, culm length, etc.) and mass (Weltzin et al. 2000). Maximum net DOC retention or loss in the bog mesocosms was as much as 8–9% of carbon gains in net primary productivity (243–273 g C m^{-2} year^{-1}; Weltzin et al. 2000) and in the fen mesocosms was approximately 5–8% of carbon

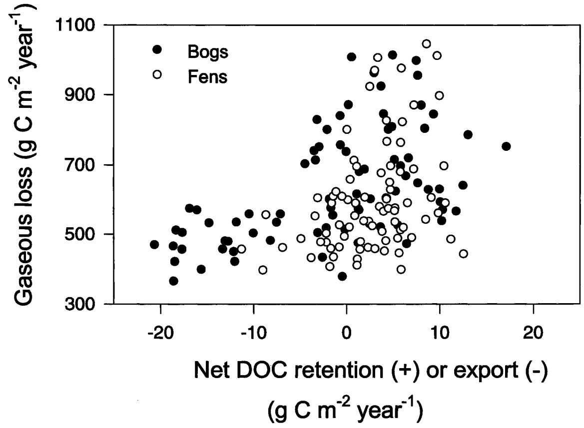

Fig. 3. Gaseous emissions of CO_2–C + CH_4–C increase exponentially with increased DOC retention in bogs and fens. Each point is the annual output from each mesocosm for each of the three years during the period 1995–1997.

gains in net primary productivity (125–182 g C m^{-2} $year^{-1}$; Weltzin et al. 2000).

These results indicate that the fate of DOC in boreal region catchments with significant peatland area depends on climatically controlled changes in the hydrologic and thermal energy budgets of these regions. If current climate trends in boreal regions continue as anticipated (Houghton et al. 1996) and discharge from peatlands decreases because of greater evapotranspiration, then DOC will be more strongly retained in bogs and especially in fens, where it will then be available for further decomposition and carbon emissions to the atmosphere as CO_2 or CH_4. Our results indicate that decreased hydrologic DOC export from peatlands will be more controlled by changes in their water balance than by changes in DOC concentrations in pore water due to in situ production–consumption dynamics. Our results for these peatlands contrast with the findings of Freeman et al. (2001) for bogs in the United Kingdom, where DOC export has increased in parallel with the observed warming trend of the past 20 years. However, in the United Kingdom peatlands, warming has caused an increase in DOC concentrations (as we have also seen in our bogs) but no change in discharge. Therefore, Freeman et al. (2001) observed an increased DOC export with warming because of increased concentrations while we have observed a decreased DOC export because of reduced discharge in spite of higher concentrations.

The redistribution of the carbon export of northern peatlands from aquatic ecosystems to the atmosphere may have profound influences on the regional carbon budget and the ecology of boreal and arctic surface waters. Our results are consistent with the observed large decreases in DOC loadings into lakes of the Precambrian Shield in northwestern Ontario during recent warmer- and drier-than-average years, which in turn significantly increased the depth and amount of UV-B penetration, likely exceeding lethal doses for many surface littoral organisms (Schindler et al. 1996). Such indirect effects on downstream ecosystems may be the most important consequence of reductions in DOC export from peatlands under a warmer climate.

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