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Author(s): David W. Schindler

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A Dim Future for Boreal Waters and Landscapes

Cumulative effects of climatic warming, stratospheric ozone depletion, acid precipitation, and other human activities

David W. Schindler

In the past 30 years, a combination of human activity and natural events has resulted in both dramatic and subtle changes to forests, wetlands, lakes, and streams in the boreal regions of North America. Consequently, future generations will not see natural boreal assemblage of plants, animals, and landscapes. In this article, I document some of the changes that have occurred and discuss how these changes may cause severe malfunctioning of boreal communities and ecosystems in the future.

Despite increasing public concern for the world's forests and waters, the boreal zone is seldom mentioned. At 1.3×10^9 ha, the boreal forest is second in size only to the moist tropical forests (Olson et al. 1983). Furthermore, boreal lakes are the most numerous on Earth. Although the exact number has never been compiled, there are over 700,000 lakes in temperate areas of eastern Canada alone (Minns et al. 1990). I estimate that Canada may contain from 1.5 to 2 million lakes. The vast areas of water in boreal Eurasia may double this number. Molot and Dillon (1996) estimate that, globally, lakes cover 1.25×10^6 km², or 10% of the total boreal area. The boreal region

David W. Schindler (e-mail: d.schindler@ualberta.ca) is Killam Professor of Ecology in the Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9 Canada. He has spent the last 30 years working and living in boreal ecosystems, much of it as leader of the Experimental Lakes Area in northwestern Ontario. © 1998 American Institute of Biological Sciences.

Despite increasing public concern for the world's forests and waters, the boreal zone is seldom noticed

also contains the world's largest expanse of wetlands and plays a major role in the global carbon cycle, as discussed below. However, North Americans and Europeans have focused much of their concern over the loss of biodiversity and greenhouse gas production on the tropics, ignoring the destruction of boreal ecosystems that is taking place under their very noses.

Large and small insults to the boreal region

Climatic warming, acid deposition, and increased exposure to ultraviolet (UV) radiation caused by stratospheric ozone depletion are considered by many to be the "Big Three" of global human stressors to natural ecosystems. All are likely to have serious environmental consequences for boreal regions.

Models of climate change indicate that the Canadian boreal zone will be among the regions that are most affected by climatic warming from increasing greenhouse gases (Environment Canada 1994). Throughout the twentieth century, but par-

ticularly in the 1970s and 1980s, average temperatures in boreal regions of Canada have increased considerably (Figure 1). Woodwell et al. (1995) predict that among terrestrial ecosystems, northern forests and wetlands will be most vulnerable to climate warming. Although it is not clear whether the extreme warming of the 1970s and 1980s was caused by increasing greenhouse gases or natural variability, the effects that were observed gave a disturbing "preview" of the effects of prolonged climatic warming on boreal regions, indicating that Woodwell et al.'s predictions may become a reality.

Acid precipitation, caused by human emissions of sulfur and nitrogen oxides to the atmosphere, has stressed ecosystems throughout eastern North America (Figure 2; Schindler 1988a, Schindler et al. 1989). Thousands of fish populations and perhaps millions of invertebrate populations from boreal waters of Canada have been lost as a result of acid precipitation (Minns et al. 1990).

Finally, stratospheric ozone depletion caused incident UV-B radiation at boreal latitudes in Canada to increase by 35% per year from 1989 to 1993 (Kerr and McElroy 1993). The biological effects of increased UV radiation are only beginning to be studied, but it is clear that many organisms are sensitive to UV radiation (e.g., Bothwell et al. 1994, Vinebrook and Leavitt 1996).

In addition to their individual effects, the three major stressors have cumulative and perhaps synergistic effects on boreal landscapes because

they interact in significant and complex ways (Figure 3; Schindler et al. 1996b, Yan et al. 1996). The stressors also dramatically change the nature of interactions among terrestrial, wetland, stream, and lake ecosystems, affecting the dynamics of the entire boreal landscape. Other, more localized human perturbations, such as reservoir construction and clearcut logging, also interact substantially with the “Big Three” stressors, causing them to have still greater impacts. Taken together, these studies suggest that the boreal landscape will undergo rapid, substantial changes in the future.

Climate warming effects on boreal catchments

During the warm, dry period of 1970–1990, the area burned by forest fires in Canada doubled in comparison to the previous several decades (Figure 4; Kurz et al. 1995a). Most of the increase occurred in remote areas, where fire suppression is not effective.

Among the boreal regions in which forest fire increased the most were the Experimental Lakes Area (ELA) and surrounding parts of northwestern Ontario. The ELA, which contains 46 small lakes and their catchments, was reserved beginning in 1968 for whole-ecosystem experiments and long-term ecological monitoring. Other human activities were restricted in the area (Johnson and Vallentyne 1971, Schindler 1988b). When I began work in the area in 1968, most of the forests were mature; they were dominated by jackpine (*Pinus banksiana*), black spruce (*Picea mariana*), trembling aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) of more than 80 years of age (Brunskill and Schindler 1971). Clearcut logging had just become mechanized, so its effects were

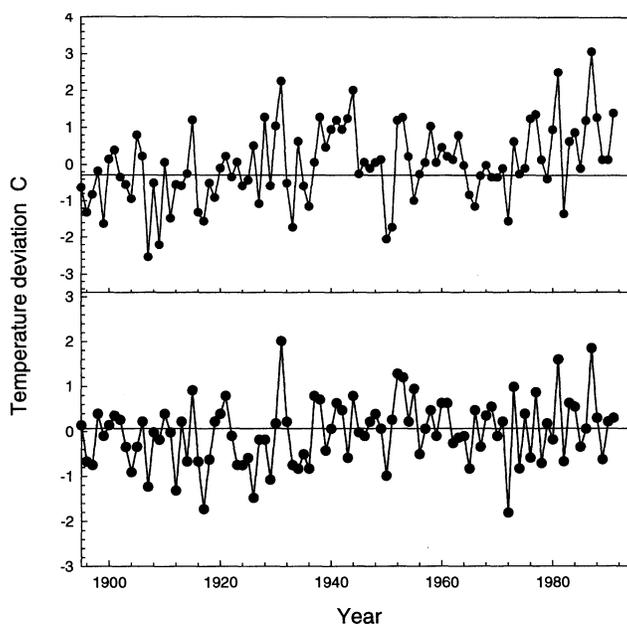


Figure 1. Annual average air temperature deviations from the 1950 to 1979 average in the boreal regions of northwestern Canada (top) and northeastern Canada (bottom) in the twentieth century. Reproduced from Gullett and Skinner (1992) with the permission of the Minister of Public Works and Government Services, Canada.

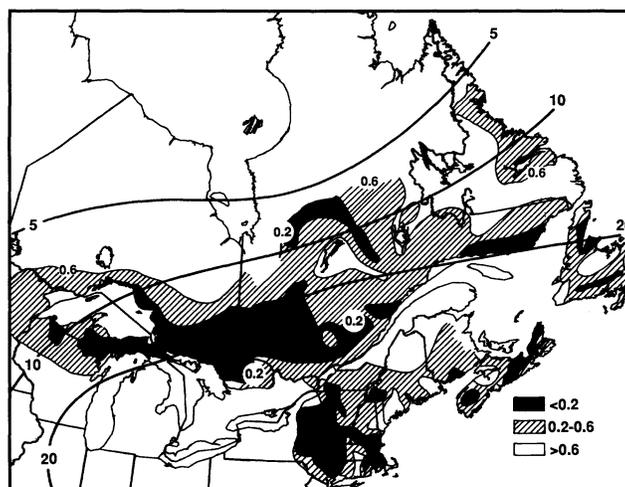


Figure 2. A map of eastern Canada showing the ratio of alkalinity to Ca^{2+} plus Mg^{2+} (equivalents). Values lower than 1.0 indicate that acid precipitation has depleted the capacity of lakes to buffer against acidification. Black indicates areas where the ratio is less than 0.2; crosshatching indicates areas where the ratio is 0.2–0.6; white indicates areas where the ratio is greater than 0.6 but less than 1.0. Heavy lines indicate sulfate deposition in $\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. Acid deposition depletes alkalinity but increases weathering of Ca^{2+} and Mg^{2+} . Reprinted with permission from Schindler (1998a). © 1988 American Association for the Advancement of Science.

relatively small in the region around ELA.

During the period 1970–1990, annual air temperature at ELA increased by 1.6 °C (Schindler et al. 1990,

1996a). As a result, evapotranspiration increased by nearly 50%, and precipitation declined by approximately 40% (Schindler et al. 1996a), leaving the landscape extremely dry. Several massive forest fires consequently burned, most of which were caused by lightning strikes. Burning in 1974 affected some of the monitored catchments in the ELA (Figure 5a; Schindler et al. 1976). After burning, the vegetation recovered rapidly and was dominated by the same fire-resistant tree species that had occupied the sites before the fire (Figure 5b). However, many of the young trees died during subsequent years of warming and severe drought (Figure 5c), providing a tremendous amount of dry fuel near the ground. Some monitored catchments burned a second time in 1980 (Bayley et al. 1992a, 1992b), resulting in a landscape that was almost denuded of organic matter (Figure 5d). After the second fire, vegetation recovered more slowly and was less dense. In fact, 17 years later, bare bedrock is still exposed in much of the area, which was once covered by organic mats 20–50 cm in depth and with mature forests. Even when it becomes mature, the forest will obviously be much less dense than it was originally. In addition, deciduous trees, such as trembling aspen and balsam poplar (*Populus balsamifera*), have replaced conifers as dominant tree species. Thus, the forests resemble those of the more arid aspen parklands of western Canada, as predicted by Hogg and Hurdle (1995).

Effects of climate warming on boreal waters and wetlands

Climatic warming and fires also affected wetlands, lakes, and streams

in northern Ontario during the 1970s and 1980s. Water levels in wetlands declined, allowing reoxidation of sulfur that had entered as sulfate from precipitation and had been reduced to sulfur during previous high water phases (Bayley et al. 1986, Devito and Hill 1997). Effects on the carbon budgets of wetlands during the 1970s and 1980s are less well known. Studies in other northern wetlands indicate a variety of responses, depending on the temperature, precipitation, and wetland type. In general, declining water levels allow the reoxidation of peat deposits that have been long-term carbon sinks and promote the oxidation of methane before it reaches the atmosphere. Woodwell et al. (1995) warn that if climatic warming and drought cause a sufficient decline in wetland water tables, peatland fires could accelerate the reoxidation of carbon stored as peat, thus increasing the rate of greenhouse gas accumulation in the atmosphere. Bridgham et al. (1995) review the known and predicted effects of climate warming on northern wetlands.

Also during the 1970s and 1980s, headwater streams that had flowed throughout the ice-free season in the late 1960s and early 1970s became ephemeral. By the late 1980s, these streams were dry for up to 150 days during the summer (Figure 6; Schindler et al. 1996a). As a result of the decreased streamflow, exports of almost all chemicals from catchments to lakes decreased (Schindler et al. 1996a, 1997).

Climatic warming over this 20-year period caused several direct changes to lakes in ELA (Schindler et al. 1990, 1996a): ice-free seasons averaged several days longer, and maximum surface water temperatures increased. Similar changes were observed at other northern sites (Anderson et al. 1996, McDonald et al. 1996). In addition, landscapes that had been denuded by fire allowed greater wind velocities to occur at the surface of small lakes (Schindler et al. 1990), thus creating larger surface waves with greater energy for mixing (Robertson and Imberger 1994).

Lakes also became clearer, largely as the result of reduced inputs of dissolved organic matter (usually mea-

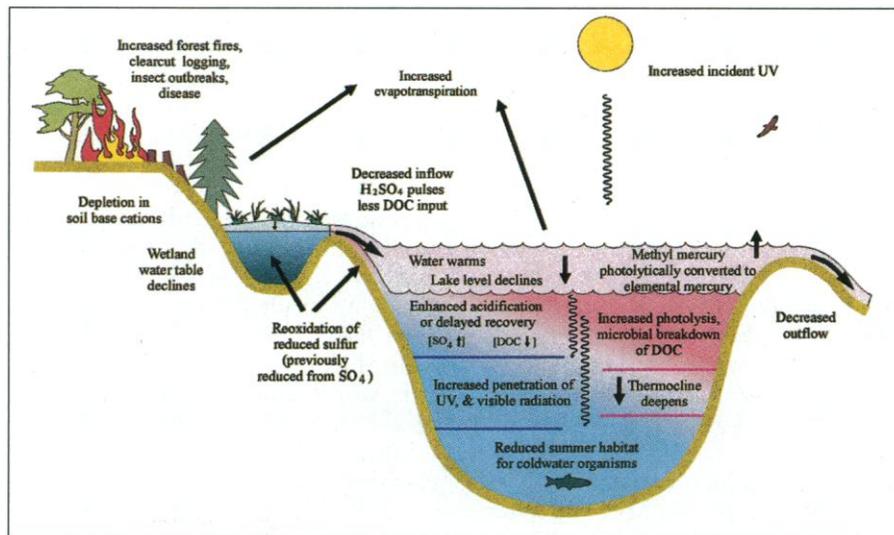
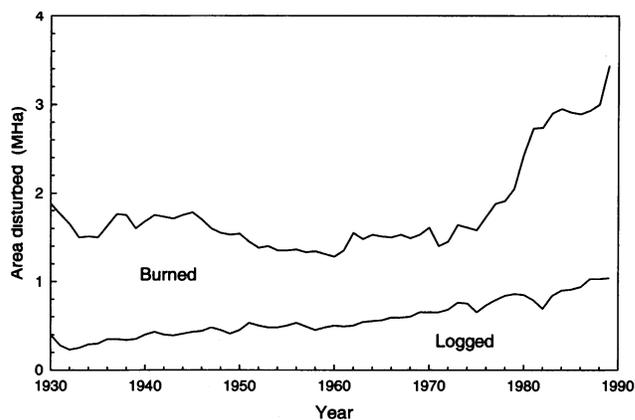


Figure 3. The combined effects of climatic warming, acid precipitation, stratospheric ozone depletion, and major human activities on boreal lakes and their catchments. Sulfate entering the wetlands and lakes with acid precipitation is stored as reduced sulfur when water tables are high. When climate warming and drought cause water tables to lower, the sulfur is reoxidized, causing acid pulses to enter lakes and streams. Both drought and acidification cause dissolved organic carbon (DOC) to decrease.

sured as dissolved organic carbon, or DOC) from catchments (Schindler et al. 1996a, 1997, Dillon and Molot 1997). This allochthonous (i.e., derived from terrestrial ecosystems) DOC is an important organic carbon source for food chains in pristine boreal lakes. It originates in wetlands or wet terrestrial soils in the catchments of lakes, where it is derived from decomposition of organic matter produced by terrestrial plants, and is typically highly colored (Figure 7). This dissolved color, rather than plankton or turbidity, is the chief factor attenuating both visible and ultraviolet radiation in boreal lakes (Schindler 1971, 1996b; Scully and Lean 1994, Williamson et al. 1996). As DOC declined, increased penetration of solar radiation warmed deeper layers of the lake, causing thermoclines to deepen. Together, thermocline deepening, in-

Figure 4. Increases in forest fires and clearcut logging in Canada during the twentieth century. The top line is the sum of both. Modified with permission from Kurz et al. (1995a).



concentrations of more biologically important chemicals, such as phosphorus and DOC, to decline (Schindler et al. 1996a, 1997).

Changes to the thermal regimes, transparency, and chemistry of the lakes in turn caused biological changes. The phytoplankton standing crop, expressed as chlorophyll *a*, declined in proportion to inputs and concentrations of phosphorus, as expected in phosphorus-limited systems. The depth distribution of phytoplankton production also changed, with photosynthesis occurring at much greater depths, although no trend in production per unit area was detected (Schindler et al. 1996a). There was a slight increase in phytoplankton diversity during the 1970s and 1980s (Schindler et al. 1990). The changed thermal regime also caused shrinkage of summer habitats for cold stenothermic organisms, such as lake trout (*Salvelinus namaycush*) and opossum shrimp (*Mysis relicta*), which are normally confined to the hypolimnion (the cold region below the lake's thermocline) in summer (Sellers et al. 1997). For example, in lake 239, which was monitored throughout the period, lake trout declined slowly, whereas northern pike (*Esox lucius*), a warm-water species that preys on small trout, increased (Ken H. Mills, Fisheries and Oceans Canada, Winnipeg, Manitoba, unpublished data). Although it is difficult to prove causality, fishing is prohibited in the lake, and alternative reasons for the change in predator species are not apparent.

Effects of acid deposition

Most of the boreal zone of Canada is underlain by the Precambrian Shield, which consists chiefly of granitic rocks that are several billion years old. Low rates of geochemical weathering cause lakes and soils in the region to have extremely low capacities to neutralize strong acids. During the twentieth century, thousands of boreal lakes in eastern Canada were acidified by deposition of strong acids, caused chiefly by sulfur oxide emissions from factories in the midwestern United States and from smelters in the Sudbury, Ontario, region. The biodiversity of many

lakes and streams in the Sudbury region was severely reduced (Hall and Ide 1987, Dixit et al. 1995), and smaller losses of biodiversity were widespread (Minns et al. 1990). Forests near sulfur oxide sources were also damaged or killed by sulfur oxide emissions, soil acidification, and toxic trace metal deposition, particularly in the regions around Sudbury and other smelters (Winterhalter 1995).

In the period from 1970 to 1990, deposition of acids decreased in much of the eastern boreal zone, largely because sulfur oxide emissions in eastern Canada decreased by approximately 60% (Environment Canada 1996). As a result, recoveries in pH were observed in many waters, particularly near Sudbury, where many lakes had been acidified to pH 5 and below. In addition, some sport fisheries that had been eliminated by acidification earlier in the century recovered (Schindler et al. 1991, Keller et al. 1992a). Substantial recoveries of damaged forests also occurred in the Sudbury area as local concentrations of sulfur oxides were reduced (Gunn 1995).

Although some lakes have recovered substantially, for others the recovery has been more limited, and many others continue to acidify (Dillon et al. 1987, Keller et al. 1992b). Overall, 33% of the acidified lakes in eastern Canada are recovering, 11% are still acidifying, and 56% show no signs of recovery (Environment Canada 1996). As Minns et al. (1990) predicted, atmospheric inputs of strong acids are still too high to allow many lakes to recover. In particular, US sulfur oxide emissions have remained stable at near 20 million metric tons (Environment Canada 1996). Full implementation of US emission reductions, to 14.4 million metric tons, is not expected until 2010. In addition, little has been done to curb emissions of nitrogen oxides, the precursors of nitric acid in precipitation. Thus, acid deposition continues to be a problem, and even with current levels of acid deposition, large numbers of lakes will be affected (Minns et al. 1990). Moreover, as described below, climate warming and drought have exacerbated the effects of acid deposition.

Interactions between climate warming and acidification

Climate warming has several effects on the responses of boreal lakes and streams to acid precipitation. In cooler, drier climates, much of the sulfate deposited by precipitation is reduced and stored as sulfur in vegetation, soils, and peatlands. Where anthropogenic emissions of sulfur oxides cause acid precipitation, this storage protects lakes and streams from acidification (Bayley et al. 1986, Rochefort et al. 1990). As noted earlier, however, under warmer, drier climatic conditions, increased exposure of peatlands and wet soils to atmospheric oxygen causes reoxidation of stored sulfur. As a result, pulses of sulfuric acid are released to streams and lakes during periods of high streamflow produced by rainstorms following periods of drought (Bayley et al. 1992b, Lazerte 1993, Devito 1995). The pulses appear to be more acidic in eastern Ontario, where high anthropogenic sulfate deposition has occurred for decades, than in northwestern Ontario, where sulfate deposition is lower and where less reduced sulfur is stored in soils and wetlands. In catchments with base-poor soils, the resulting concentrations of strong acids in streams can consistently exceed concentrations of base cations, decreasing the average pH (Schindler et al. 1996a). Forest fires also increase the mobilization of strong acid anions to a greater degree than base cations in such catchments (Bayley et al. 1992b).

Incoming sulfuric acid is also removed in the littoral areas of lakes. Microbial reduction of sulfate to sulfide occurs just below the mud-water interface, where anoxic conditions prevail. The reduced sulfur combines with ferrous iron or organic matter to form insoluble sulfides, neutralizing the sulfuric acid (Cook and Schindler 1983, Rudd et al. 1986). However, as lake levels decline during warming or drought, sulfur stored in upper areas of the littoral zone is reoxidized, causing lakes to reacidify (Yan et al. 1996). As a result of the reoxidation of sulfur in catchments and littoral zones, the recovery of some lakes and streams from acidification has been prevented or delayed, even in

ecosystems in which sulfur emissions to the atmosphere have been greatly reduced. Ecosystem-scale experiments in Norway, in which acid rain was neutralized, have also shown delays in recovery (Wright and Hauhs 1991).

In areas subjected to many years of acid deposition, recovery of lakes and streams may also be aggravated by the depletion of base cations in catchments (Likens et al. 1996). Together, the acid pulses caused by climatic warming and forest fires and the reductions in base cation yields from acidified, burned soils will make it necessary to reduce acidifying emissions by much more than originally predicted if lakes and streams are to recover.

Conversely, acidification also exacerbates the effects of climatic warming, via its effects on DOC. Acidification of lakes to below pH 5 greatly decreases DOC concentrations, as the result of increased precipitation (Effler et al. 1985, Schindler et al. 1992, Driscoll and van Dreason 1993), photolytic bleaching, and mineralization (Molot and Dillon 1996). Reductions in DOC concentrations of 90–95% have been observed in acidified lakes, greatly increasing the penetration of solar radiation and exacerbating thermocline deepening (Dillon et al. 1984).

Climate warming, DOC, and UV exposure

The increased residence time of DOC in lakes provides more time for microbial degradation, chemical flocculation, and photolytic bleaching and degradation to occur. Warmer temperatures, deeper UV penetration, and longer ice-free seasons accelerate these processes, contributing to increased in-lake degradation of DOC (Dillon and Molot 1997, Schindler et al. 1997). The higher transparency to UV radiation caused by declining concentrations of DOC and increased photobleaching of DOC greatly increases exposure of aquatic ecosystems to UV radiation (Schindler et al. 1996b, Williamson et al. 1996, Yan et al. 1996). This increased exposure amplifies by up to severalfold the increase in UV radiation that is already reaching boreal lakes as a result of the approximately 10% stratospheric

ozone depletion in boreal regions (Hengeveld 1991). As UV radiation penetrates deeper into lakes, it may become even more effective at removing or bleaching DOC, so that the process of increasing UV transparency may be self-accelerating. The increased penetration of solar radiation may also cause other chemical changes. For example, both UV and short visible wavelengths photodegrade methyl mercury to non-valent (Hg⁰) mercury, which is quickly lost to the atmosphere (Amyot et al. 1994, Sellers et al. 1996). The magnitude and fate of the released mercury are still not known.

The relationship between DOC and UV is a negative exponential, with UV penetration increasing rapidly as DOC concentrations decline below approximately 300 μM (3.6 mg/l). As a result, the effects of climate warming on UV penetration will be most pronounced in clearer lakes. In Ontario, the DOC of approximately 20% of the lakes is less than 300 μM (Neary et al. 1990). In subarctic and subalpine areas, an even higher proportion of lakes has low DOC.

A triple whammy

Climate warming, acid precipitation, and stratospheric ozone depletion act in concert to increase the exposure of aquatic organisms to UV radiation. As discussed above, both climatic warming and acidification contribute to increased UV radiation reaching aquatic ecosystems through their effects on DOC. The penetration of UV radiation into acidified lakes can therefore be several times higher than it would otherwise be (Schindler et al. 1996b, Yan et al. 1996). Even modest climatic warming and acidification contribute more than stratospheric ozone depletion to increasing UV exposure of aquatic systems (Schindler et al. 1996b), greatly exacerbating the effects of increased incident UV at the earth's surface.

Consequently, boreal lakes are under a "three-pronged attack" from the combined effects of climatic warming, acidification, and stratospheric ozone depletion, through their combined effects on UV (Gorham 1996). The biological consequences are still largely unknown,

but they are under active investigation by several research groups.

The effects of other human activities and other stressors

Other human activities and other stressors in boreal regions will add to the ecological problems caused by the "Big Three" stressors. Some will have effects that are exacerbated by interaction with the "Big Three."

For example, clearcut logging is increasing rapidly (Figure 4; Kurz et al. 1995a). In addition to causing decreased carbon storage in vegetation and soils, logging increases the exposure of small, shallow streams to UV radiation, causing dramatic changes to biota (David Kelly, University of Alberta, unpublished data).

Climate warming may cause increased damage due to forest pests. Outbreaks of several species of common forest insects are known to increase as the result of warmer, drier climatic conditions (Kurz et al. 1995a).

Building reservoirs in boreal regions floods wetlands and terrestrial soils, causing massive fluxes of DOC and methyl mercury to water. The accelerated decomposition of peat increases carbon dioxide and methane fluxes to the atmosphere (Duchemin et al. 1995, Kelly et al. 1997). Moreover, large areas of reservoirs in boreal regions would further amplify climatic warming by increasing greenhouse gas fluxes to the atmosphere. Already, the total area of boreal reservoirs in North America is similar to that of Lake Ontario (Rudd et al. 1993).

The boreal zone in the global carbon cycle

The boreal zone contains one of Earth's largest terrestrial carbon pools. Terrestrial vegetation is a relatively small part of the pool, a mere 64 Gt (Apps et al. 1993). Soils are estimated to contain an additional 247–286 Gt (Schlesinger 1984, Bonan and Van Cleve 1992), whereas boreal peatlands contain 419 Gt (Apps et al. 1993), nearly one-third of the global soil carbon pool (Gorham 1991). Until recently, lake sediments were overlooked as a carbon pool. Molot and Dillon (1996) estimate that 120 Gt of carbon are



Figure 5. Changes in the boreal forests of ELA during the period 1970–1990. (top left) The eastern half of the catchment of lake 239 in the midafternoon of 26 June 1974 as a forest fire approached. The fire burned the eastern half of the catchments of lakes 239 and 240. (top right) The eastern subbasin near the shore of lake 239 during the late summer of 1975 shows substantial regeneration of jackpine (*Pinus banksiana*), spruce (*Picea mariana*), and several deciduous species. (bottom left) Young jackpine in the catchment of lake 239 in 1980. After six years of drought and warmer than normal temperatures, dead and dying trees are prevalent. (bottom right) The eastern catchment of lake 240 following a second fire in 1980.

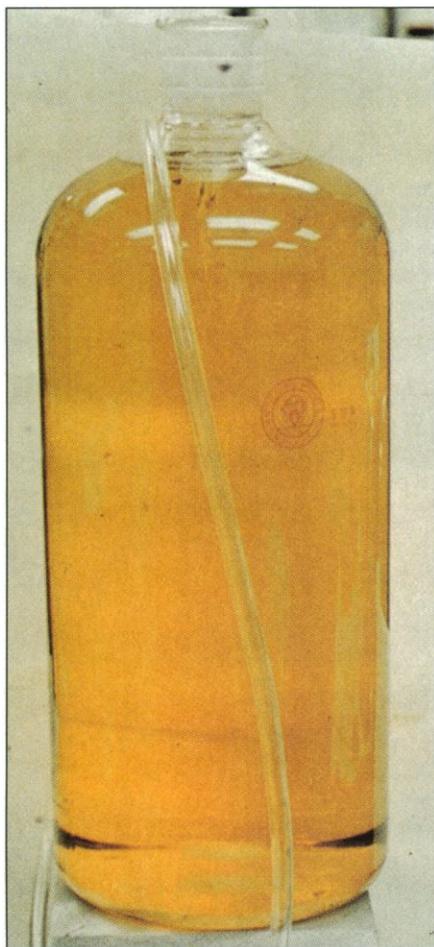


Figure 7. A 10-liter bottle of stream water from the eastern subbasin in the lake 239 catchment. This water shows the typical color of DOC, which attenuates UV and visible light, as well as providing organic carbon to the lake's food chain.

stored in the sediments of boreal lakes, so that the total carbon storage in boreal landscapes is approximately 830 Gt.

Altogether, recent estimates indicate that north temperate forests, of which the boreal forests are the major part, may equal the oceans as a net annual sink for atmospheric carbon (Tans et al. 1990), thus damping the increase in atmospheric carbon dioxide caused by fossil fuel burning (Keeling et al. 1996). In particular, lake sediments and peat deposits are long-term repositories (i.e., from 1000 to 10,000 years) for fixed carbon. Kurz et al. (1995b) estimate that the forested parts of the boreal region alone may remove carbon from the atmosphere at a rate of 0.2 Gt/yr; they present evidence that the boreal carbon “sink” weakened in the period 1970–1989 as the result of fires and other disturbances. If human insults significantly weaken or reverse the carbon flux to the

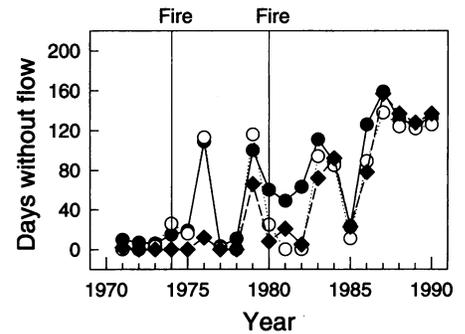


Figure 6. Flows in the three headwater streams entering lake 239 from 1970 to 1990. Solid circles indicate the north-east subbasin, open circles the north-west subbasin, and solid squares the east subbasin. Modified from Schindler et al. (1996a).

boreal sink, a significant increase in climatic warming may occur. Such a warming would, as discussed above, accelerate the “unraveling” of the sensitive boreal landscape.

When the combined effects of climate warming, acid precipitation, stratospheric ozone depletion, and other human activities are considered, the boreal landscape may be one of the global ecoregions that changes the most in the next few decades. Certainly, our descendants will know a much different boreal landscape than we have today.

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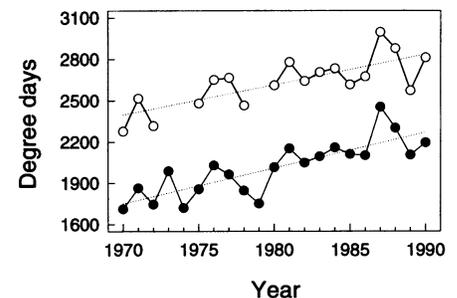


Figure 8. The thermal capacities of lakes 239 and 240 from 1970 to 1990. These capacities, as measured in degree days, increased as the result of longer ice-free seasons, warmer water temperatures, and deeper thermoclines. Open circles indicate lake 239; solid circles indicate lake 240. Reprinted from Schindler et al. (1996a).

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References cited

- Amyot M, Mierle G, Lean DRS, McQueen DJ. 1994. Sunlight-induced formation of dissolved gaseous mercury in lake waters. *Environmental Science & Technology* 28: 2366–2371.
- Anderson WL, Robertson DM, Magnuson JJ. 1996. Evidence of recent warming and El Niño-related variations in ice breakup of Wisconsin lakes. *Limnology and Oceanography* 41: 815–821.
- Apps MJ, Kurz WA, Luxmoore RJ, Nilsson LO, Sedjo RA, Schmidt R, Simpson LG, Vinson TS. 1993. Boreal forests and tundra. *Water, Air and Soil Pollution* 70: 39–53.
- Bayley SE, Behr RS, Kelly CA. 1986. Retention and release of S from a freshwater wetland. *Water, Air and Soil Pollution* 31: 101–114.
- Bayley SE, Schindler DW, Beaty KG, Parker BR, Stainton MP. 1992a. Effects of multiple fires on nutrient yields from streams draining boreal forest and fen watersheds: Nitrogen and phosphorus. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 584–596.
- Bayley SE, Schindler DW, Parker BR, Stainton MP, Beaty KG. 1992b. Effect of forest fire and drought on acidity of a base-poor boreal forest stream: Similarities between climatic warming and acidic precipitation. *Biogeochemistry* 17: 191–204.
- Bonan GB, Van Cleve K. 1992. Soil temperature, N mineralization and carbon source-sink relationships in boreal forests. *Canadian Journal of Forest Research* 22: 629–639.
- Bothwell ML, Sherbot DMJ, Pollock CM. 1994. Ecosystem response to solar ultraviolet-B radiation: Influence of trophic level interactions. *Science* 265: 97–100.
- Bridgman SD, Johnston CA, Pastor J, Updegraff K. 1995. Potential feedbacks of northern wetlands on climate change. *BioScience* 45: 262–274.
- Brunskill GJ, Schindler DW. 1971. Geography and bathymetry of selected lake basins, Experimental Lakes Area, northwestern Ontario. *Journal of the Fisheries Research Board of Canada* 28: 139–155.
- Cook RB, Schindler DW. 1983. The biogeochemistry of sulfur in an experimentally acidified lake. Pages 115–127 in Halberg RO, ed. *Ecological Bulletins (Stockholm)* Vol. 35.
- Devito KJ. 1995. Sulfate mass balances of Precambrian Shield wetlands: The influence of catchment hydrogeology. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 1750–1760.
- Devito KJ, Hill AR. 1997. Sulphate dynamics in relation to groundwater-surface water interactions in headwater wetlands of the southern Canadian Shield. *Hydrological Processes* 11: 103–110.
- Dillon PJ, Molot LA. 1997. Dissolved organic and inorganic carbon mass balances in central Ontario lakes. *Biogeochemistry* 36: 29–42.
- Dillon PJ, Reid R, de Grosbois E. 1987. The rate of acidification of aquatic ecosystems in Ontario, Canada. *Nature* 329: 45–48.
- Dillon PJ, Yan ND, Harvey HH. 1984. Acidic deposition: Effects on aquatic ecosystems. Pages 167–194 in *Critical Reviews in Environmental Control*. Vol. 13. Boca Raton (FL): CRC Press.
- Dixit S, Dixit AS, Smol JP, Keller W. 1995. Reading the records stored in lake sediments: A method of examining the history and extent of industrial damage to lakes. Pages 33–44 in Gunn JM, ed. *Restoration and Recovery of an Industrial Region*. New York: Springer-Verlag.
- Driscoll CT, van Dreason R. 1993. Seasonal and long-term temporal patterns in the chemistry of Adirondack lakes. *Water, Air and Soil Pollution* 67: 319–344.
- Duchemin E, Lucotte M, Canuel R, Chamberland A. 1995. Production of the greenhouse gases CH₄ and CO₂ by hydroelectric reservoirs in the boreal region. *Global Biogeochemical Cycles* 9: 529–540.
- Effler SW, Schafran GC, Driscoll CT. 1985. Partitioning light attenuation in an acidic lake. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1707–1711.
- Environment Canada. 1994. Modelling the global climate system. Ottawa (Canada): Minister of Supply and Services. *Climate Change Digest Report no. 94-01*.
- _____. 1996. Technical supplement to the environmental indicators of acid rain. Ottawa (Canada): Environment Canada, Minister of Supply and Services. *State of the Environment Technical Supplement no. 96-2*.
- Gorham E. 1991. Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* 1: 182–195.
- _____. 1996. Lakes under a three-pronged attack. *Nature* 381: 109–110.
- Gullett DW, Skinner WR. 1992. The state of Canada's climate: Temperature change in Canada 1895–1991. Ottawa (Canada): Environment Canada, Minister of Supply and Services. *State of Environment Report no. 92-2*.
- Gunn JM, ed. 1995. *Restoration and Recovery of an Industrial Region*. New York: Springer-Verlag.
- Hall RJ, Ide FP. 1987. Evidence of acidification effects on stream insect communities in central Ontario between 1937 and 1985. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 1652–1657.
- Hengeveld H. 1991. Understanding atmospheric change. Ottawa (Canada): Environment Canada, Minister of Supply and Services. *State of Environment Report no. 91-2*.
- Hogg EH, Hurdle PA. 1995. The aspen parkland in western Canada: A dry climate analogue for the future boreal forest? *Water, Air and Soil Pollution* 82: 391–400.
- Johnson WE, Vallentyne JR. 1971. Rationale, background, and development of experimental lake studies in northwestern Ontario. *Journal of the Fisheries Research Board of Canada* 28: 123–128.
- Keeling RF, Piper SC, Heimann M. 1996. Global and hemispheric CO₂ sinks deduced from changes in atmospheric O₂ concentration. *Nature* 381: 218–221.
- Keller W, Gunn JM, Yan ND. 1992a. Evidence of biological recovery in acid stressed lakes near Sudbury, Canada. *Environmental Pollution* 78: 79–85.
- Keller W, Pitblado JR, Carbone J. 1992b. Chemical responses of acidic lakes in the Sudbury, Ontario, area to reduced smelter emissions, 1981–89. *Canadian Journal of Fisheries and Aquatic Sciences* 49 (Supplement 1): S25–S32.
- Kelly CA, et al. 1997. Increases in fluxes of greenhouse gases and methyl mercury following flooding of an experimental reservoir. *Environmental Science & Technology* 31: 1334–1344.
- Kerr JB, McElroy CT. 1993. Evidence for large upward trends of ultraviolet-B radiation linked to ozone depletion. *Science* 262: 1032–1034.
- Kurz WA, Apps MJ, Stocks BJ, Volney WJ. 1995a. Global climate change: Disturbance regimes and biospheric feedbacks of temperature and boreal forests. Pages 119–133 in Woodwell GM, Mackenzie FT, eds. *Biospheric Feedbacks in the Global Climate System: Will the Warming Speed the Warming?* New York: Oxford University Press.
- Kurz WA, Apps MJ, Beukema SJ, Lekstrum T. 1995b. 20th century carbon budget of Canadian forests. *Tellus* 47B: 170–177.
- Lazerte BD. 1993. The impact of drought and acidification on the chemical exports from a minerotrophic conifer swamp. *Biogeochemistry* 18: 153–175.
- Likens GE, Driscoll CT, Buso DC. 1996. Long-term effects of acid rain: Response and recovery of a forest ecosystem. *Science* 272: 244–246.
- McDonald ME, Hershey AE, Miller MC. 1996. Global warming impacts on lake trout in arctic lakes. *Limnology and Oceanography* 41: 1102–1108.
- Minns CK, Moore JR, Schindler DW, Jones ML. 1990. Assessing the potential extent of damage to inland lakes in eastern Canada due to acidic deposition. IV. Predicting the response of potential species richness. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 821–830.
- Molot L, Dillon PJ. 1996. Storage of terrestrial carbon in boreal lake sediments and evasion to the atmosphere. *Global Biogeochemical Cycles* 10: 483–492.
- Neary BP, Dillon PJ, Munro JR, Clark BJ. 1990. The acidification of Ontario Lakes: An assessment of their sensitivity and current status with respect to biological damage. Dorset, Ontario: Ontario Ministry of Environment, Dorset Research Centre.
- Olson JS, Watts JA, Allison LJ. 1983. Carbon in live vegetation of major world ecosystems. Oak Ridge (TN): Oak Ridge National Laboratory. Technical Report no. ORNL-5862.
- Robertson D, Imberger J. 1994. Lake number, a quantitative indicator of mixing used to estimate changes in dissolved oxygen. *Internationale Revue der Gesamten Hydrobiologie* 79: 159–176.
- Rochefort L, Vitt DH, Bayley SE. 1990.

- Growth, production and decomposition dynamics of Sphagnum under natural and experimentally acidified conditions. *Ecology* 71: 1986–2000.
- Rudd JWM, Kelly CA, Furutani A. 1986. The role of sulfate reduction in long-term accumulation of organic and inorganic sulfur in lake sediments. *Limnology and Oceanography* 31: 1281–1291.
- Rudd JWM, Harris R, Kelly CA, Hecky RE. 1993. Are hydroelectric reservoirs significant sources of greenhouse gases. *Ambio* 22: 246–248.
- Schindler DW. 1971. Light, temperature and oxygen regimes of selected lakes in the Experimental Lakes Area, northwestern Ontario. *Journal of the Fisheries Research Board of Canada* 28: 157–169.
- _____. 1988a. Effects of acid rain on freshwater ecosystems. *Science* 239: 149–157.
- _____. 1988b. Experimental studies of chemical stressors on whole lake ecosystems. *Verhandlungen Internationale Vereinigung Limnologie* 23: 11–41.
- Schindler DW, Newbury RW, Beaty KG, Campbell P. 1976. Natural water and chemical budgets for a small Precambrian lake basin in central Canada. *Journal of the Fisheries Research Board of Canada* 33: 2526–2543.
- Schindler DW, Kasian SEM, Hesslein RH. 1989. Biological impoverishment in lakes of the midwestern and northeastern United States from acid rain. *Environmental Science & Technology* 23: 573–579.
- Schindler DW, Beaty KG, Fee EJ, Cruikshank DJ, DeBruyn DE, Findlay DL, Linsey GA, Shearer JA, Stainton MP, Turner MA. 1990. Effects of climatic warming on lakes of the central boreal forest. *Science* 250: 967–970.
- Schindler DW, et al. 1991. Comparisons between experimentally- and atmospherically-acidified lakes during stress and recovery. Pages 193–226 in Last FT, Watling R, eds. *Acidic Deposition: Its Nature and Impacts*. Vol. 97B. Edinburgh (UK): Proceedings of the Royal Society of Edinburgh.
- Schindler DW, Bayley SE, Curtis PJ, Parker BR, Stainton MP, Kelly CA. 1992. Natural and man-caused factors affecting the abundance and cycling of dissolved organic substances in Precambrian Shield lakes. *Hydrobiologia* 229: 1–21.
- Schindler DW, Bayley SE, Parker BR, Beaty KG, Cruikshank DR, Fee EJ, Schindler EU, Stainton MP. 1996a. The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, Northwestern Ontario. *Limnology and Oceanography* 41: 1004–1017.
- Schindler DW, Curtis PJ, Parker BR, Stainton MP. 1996b. Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. *Nature* 379: 705–708.
- Schindler DW, Curtis PJ, Bayley SE, Parker BR, Beaty KG, Stainton MP. 1997. DOC-mediated effects of climate change and acidification on boreal lakes. *Biogeochemistry* 36: 9–28.
- Schlesinger WH. 1984. Soil organic matter: A source of atmospheric CO₂. Pages 111–127 in Woodwell GM, ed. *The Role of Terrestrial Vegetation in the Global Carbon Cycle*. New York: John Wiley & Sons.
- Scully NM, Lean DRS. 1994. The attenuation of ultraviolet radiation in temperate lakes. *Ergebnisse der Limnologie. Archiv für Hydrobiologie, Beiheft* 43: 135–144.
- Sellers P, Kelly CA, Rudd JWM, MacHutchon AR. 1996. Photodegradation of methylmercury in lakes. *Nature* 380: 694–697.
- Sellers TJ, Parker BR, Schindler DW, Tonn WM. In press. The pelagic distribution of lake trout (*Salvelinus namaycush*) in small Canadian Shield lakes with respect to temperature, dissolved oxygen and light. *Canadian Journal of Fisheries and Aquatic Sciences*.
- Tans PI, Fung Y, Takahashi T. 1990. Observational constraints on the global atmospheric CO₂ budget. *Science* 247: 1431–1438.
- Vinebrook RD, Leavitt PR. 1996. Effects of ultraviolet radiation on periphyton in an alpine lake. *Limnology and Oceanography* 41: 1035–1040.
- Williamson CE, Stemberger RS, Morris DP, Frost TM, Paulsen SG. 1996. Ultraviolet radiation in North American lakes: Attenuation estimates from DOC measurements. *Limnology and Oceanography* 41: 1024–1034.
- Winterhalter K. 1995. Early history of human activities in the Sudbury area and ecological damage to the landscape. Pages 17–31 in Gunn JM, ed. *Restoration and Recovery of an Industrial Region*. New York: Springer-Verlag.
- Woodwell GM, Mackenzie FT, Houghton RA, Apps NJ, Gorham E, Davidson EA. 1995. Will the warming speed the warming? Pages 393–411 in Woodwell GM, Mackenzie FT, eds. *Biotic Feedbacks in the Global Climatic System*. New York: Oxford University Press.
- Wright RF, Hauhs M. 1991. Reversibility of acidification: Soils and surface waters. *Proceedings of the Royal Society of Edinburgh* 97B: 169–191.
- Yan ND, Keller W, Scully NM, Lean DRS, Dillon PJ. 1996. Increased UV-B penetration in a lake owing to drought-induced acidification. *Nature* 381: 141–143.