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EFFECTS OF ATMOSPHERIC CHANGE AND AGRICULTURE ON THE BIOGEOCHEMISTRY AND MICROBIAL ECOLOGY OF PRAIRIE WETLANDS

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Abstract. *Relatively little is known about the factors which regulate in-water biogeochemical processes and food chains in prairie wetlands. Climatic warming, increased UV-radiation and agricultural activities will have interacting effects on these wetlands. We examined the effects of these processes on prairie wetland functioning and productivity with particular emphasis on production and cycling of organic carbon, especially dissolved organic carbon (DOC). Autotrophic and heterotrophic production are temperature dependent and temperature increases or decreases could affect production under more extreme climate change scenarios. DOC concentrations could decrease with increasing bacterial production and photolysis, leading to increases in UV-radiation penetration. This is pertinent to prairie wetlands because of their general shallowness. Considering the potential consequences of climatic warming, increased UV-radiation and agricultural activity on biogeochemistry and food chains, it is imperative that we obtain an understanding of the major rate processes in prairie wetlands and how these may be affected by external processes.*

Over the last century, increases in levels of atmospheric pollutants have caused dramatic changes in the earth's atmosphere: atmospheric CO_2 has increased while levels of stratospheric ozone have decreased. The ultimate effects of these atmospheric changes have been climatic warming and increased levels of UV-B radiation on earth, both of which can significantly affect prairie wetland ecosystems. In addition, agricultural practices across the prairies pose a significant threat to these wetlands which are regularly interspersed among cultivated fields where both fertilizers and pesticides are commonly used. Herbicides and fertilizers make their way into water bodies through processes of runoff, groundwater flow, spray drift or aeolian deposition (Grover et al. 1988; Waite et al. 1992; Goldsborough and Crumpton

1998). Moreover, on the prairies where a high level of soil fertility is maintained by fertilizing, nutrient enrichment of surface waters may be considerable, especially at certain times of the year. Although the potential effects of these chemicals (and nutrients) on prairie wetlands are largely unknown (Johnson 1986), it has been hypothesized that pesticides might adversely affect primary production thus negatively affecting subsequent secondary production (Donald and Syrgiannis 1995).

Due to their geographical location, prairie wetlands will be subjected to the interacting effects of climatic warming, increased UV-radiation and agricultural activities. It is apparent that these stresses cannot be studied in isolation (Schindler and Curtis 1997). Here we examine the effects of these processes on prairie wetland functioning and productivity with particular emphasis on the production and cycling of organic carbon, especially dissolved organic carbon (DOC). The reason for this emphasis is that dissolved organic carbon participates in many biogeochemical reactions in lakes and presumably also in wetlands. For example, it flocculates chemical substances (including pesticides), "fuels" microbial food chains, and takes part in a number of photochemical reactions that produce reactive chemicals such as carbon monoxide and peroxide (Schindler et al. 1997). Its ability to attenuate photosynthetically active (PAR) and ultraviolet (UV) radiation not only restricts the depth of autotrophic production in aquatic ecosystems but also protects aquatic organisms from harmful light. In addition, DOC in prairie wetlands is probably terrestrial in origin and contains a high percentage of aromatic compounds (Clair and Sayer 1997; Waiser and Robarts unpublished data). Because of its highly aromatic character, this DOC is expected to be more intensely photoreactive and susceptible to photolytic changes by UV-B light than would be expected in marine systems (Clair and Sayer 1997).

Climatic Warming

Green-house gas accumulation in the atmosphere is predicted to warm the earth's climate and as a result, the interior of North America is expected to become more arid (Poiani and Johnson 1991). Mean summer temperatures will likely increase by 1-2°C , while winter temperatures may increase by as much as 3-4°C by the year 2030 (Covich et al. 1997). Wetlands are key ecological components of the vast prairie region of North America; unfortunately there has been little consideration of how climatic warming might affect them (Poiani and Johnson 1991), especially in-water processes.

Generally, these wetlands are shallow, water-holding depressions that vary in size, water permanence and water chemistry (LaBaugh et al. 1998). Usually they have no inflows or outflows, are relatively isolated from one another and have little interaction with groundwater (Covich et al. 1997; van der Kamp and Hayashi 1998). As well, they are highly dependent on precipitation for their water supply as most are refilled in spring from precipitation and snow melt runoff on frozen or saturated soils (Covich et al. 1997). Their location within a highly variable semi-arid climatic area where evaporation exceeds precipitation—annual evaporation is typically 30 cm more than annual precipitation (LaBaugh et al. 1996)—means that wetland water levels and vegetation fluctuate widely in response to seasonal wet/dry periods (van der Valk and Davis 1978; Poiani et al. 1996). Evapotranspiration causes the major water loss from semi-permanent prairie wetlands (Poiani et al. 1996) and as a result they are extremely vulnerable to climatic warming.

Poiani and Johnson (1993) used a spatially-defined, rule-based simulation model to assess the effects of climatic change on the hydrology and vegetation of a semi-permanent prairie wetland. Temperature and precipitation ranges used were +2 to +4°C and -20% to +20%, respectively. They found that maximum water depths were significantly less under enhanced greenhouse gas scenarios than under current climatic conditions. Moreover, precipitation increases predicted by the model were not great enough to offset water losses due to increased evapotranspiration. Therefore, in most years, the wetland dried out. As well, because of these predicted drier hydrological conditions, the emergent cover/open water ratio shifted from a nearly balanced condition to a completely closed basin with no open water areas. The predicted increased frequency of dry basins over the prairies could result in dramatic declines in habitat quality for breeding birds (Poiani and Johnson 1991; 1993) and concomitant decreases in waterfowl populations (Larson 1994).

Dryout of prairie wetlands will also affect overall production of both macrophytes and phytoplankton (Poiani and Johnson 1993). For example, total production for an Alberta pond (Fig.1) was negatively affected by decreasing pond volume even though volumetric rates of production could be high during times of low or declining water levels. Changes in nutrient concentrations and the standing stock of phytoplankton also influenced these relationships (Robarts et al. 1995).

Just how important are algae (pelagic and attached) to overall wetland production? Generalization of the quantitative contribution of algae to gross
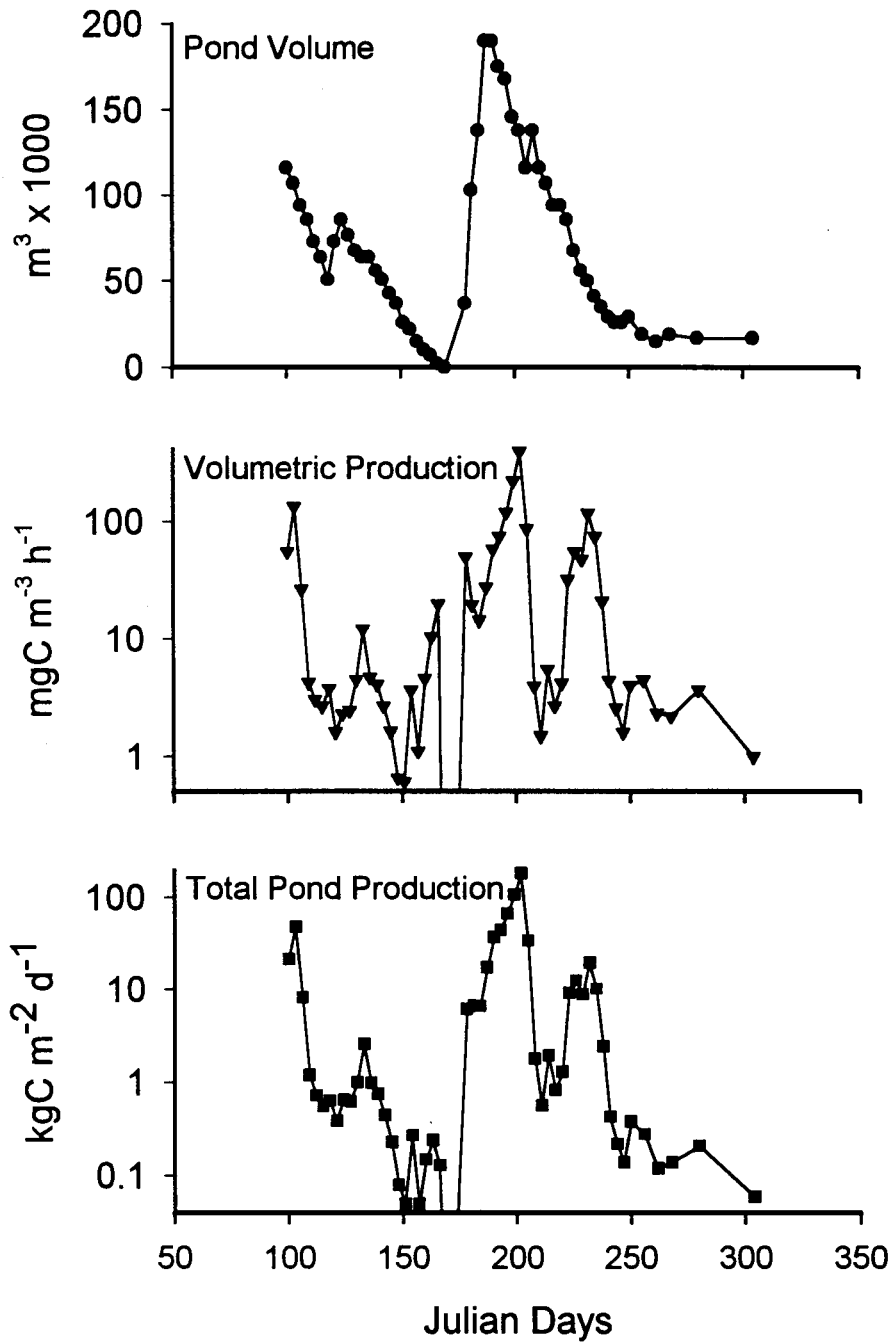
Figure 1. Changes in water volume, phytoplankton volumetric primary production and total phytoplankton pond production for an Alberta pond. Data from Robarts et al. (1995).

primary production in wetlands is difficult because few studies have been sufficiently inclusive to measure all potential producers (Goldsborough and Robinson 1996; Robinson et al. 1997). According to Robinson et al. (1997), there have been few measurements of primary productivity by benthic (periphytic) and planktonic algae in prairie wetlands so their quantitative importance relative to other primary producers is largely unknown. Despite this lack of knowledge, algae may be extremely important to energy flows and food chains in wetlands because: 1) they are available to grazers throughout the ice-free period unlike other foods such as submersed macrophytes and insects, 2) as single or small clusters of cells they are readily assimilated and 3) few aquatic herbivores are able to ingest living macrophyte tissue (Goldsborough and Robinson 1996). In a recent study of Manitoba wetlands, Robinson et al. (1997) determined that algal productivity (sum of phytoplankton, epipelon, epiphyton and metaphyton production) was comparable to that of submerged and emergent macrophytes, which indicated that algae are probably important resources in supporting food webs in prairie wetlands. In fact, they state that the definition of the role that algae play as a base of the wetland food web may necessitate revision of wetland management strategies. Working on billabong food webs in southeastern Australia, Bunn and Boon (1993) concluded from their stable carbon isotope study that food webs in these shallow water bodies were largely driven by a ^{13}C-depleted primary producer, probably a planktonic Chlorophyte. Studies by Hamilton et al. (1992) on the Orinoco flood plain have indicated that algae (planktonic and epiphytic) are the predominant energy source for many aquatic animals in this system even though macrophytes were more abundant. Although phytoplankton production in prairie wetlands is generally thought to be low relative to production by epipelon, epiphyton and metaphyton, it can equal that of epiphyton or metaphyton (Goldsborough and Robinson 1996), especially when nutrient loading from adjacent fertilized, cultivated lands causes large phytoplankton populations.

While climatic warming will affect water levels, macrophyte and phytoplankton production in prairie wetlands, it may also raise wetland water temperatures. Biological process rates are biochemical reactions which have temperature constraints. Therefore, increases in water temperatures resulting from climatic warming could have an impact on wetland microbial physiological processes. Although nothing is known for wetlands in this regard, there is some data available for a shallow prairie saline lake. Primary production per unit chlorophyll in Redberry Lake (Saskatchewan), was temperature dependent and had a Q_{10} (rate of production increase over 10°C)

of 3.3 between 10 and 20°C (Robarts et al. 1992). Although wetland algae
may have a similar relationship with water temperature, there is some indi-
cation they may be fairly resilient to large temperature variations. For ex-
ample, in an Alberta pond the maximum change in water temperature during
the day was from 13.5°C in early morning to 28.5°C in late afternoon, yet
phytoplankton production was not adversely affected by this large tempera-
ture change (Robarts et al. 1995). Therefore, while climatic warming may
increase pond water temperature, it may not have a major impact on algal
production. Of greater concern is the accelerated water loss and the resulting
drying out of wetlands (cf. Poiani and Johnson 1993).

Biogeochemistry

Arid conditions that are predicted as a result of climatic warming may
have an effect on the biogeochemistry of prairie wetlands. Drier conditions
could cause changes not only in the ionic chemistry of these wetlands, but
in the chemistry, production and utilization of dissolved organic carbon. Any
of these changes has the potential to significantly affect overall wetland
carbon cycling.

In Pond 4857, a meso-eutrophic, freshwater wetland located within the
St. Denis National Wildlife Area near Saskatoon, Saskatchewan, DOC con-
centration increased from spring to fall (Fig. 2). Although major precipita-
tion events occurred, there was no noticeable increase in the DOC concentra-
tion associated with these, suggesting that summer precipitation was not
crucial to the concentration, i.e., evaporation and evapotranspiration were
probably more important in the DOC increase. This pond also has extensive
beds of macrophytes and thick organic bottom sediments which would
intuitively seem to be major sources of DOC. Under climate change sce-
narios, therefore, DOC concentrations could increase due to the interacting
effects of evapotranspiration and increased autochthonous DOC production.
The relative importance of autochthonous and allochthonous DOC sources
in wetlands has not been studied.

It is well known that DOC affects the fate and bioavailability of trace
nutrients and contaminants (Curtis and Adams 1995) and so increases in
DOC concentrations could have important implications for nutrient cycles in
prairie wetlands. Waiser and Robarts (1995) have shown that in Redberry
Lake little of the soluble reactive phosphorus (concentration 9-31 μg l^{-1}) was
available for microbial processes and this unavailability was probably linked
to high concentrations of DOC (37 mg l^{-1}), but the mechanism for this is
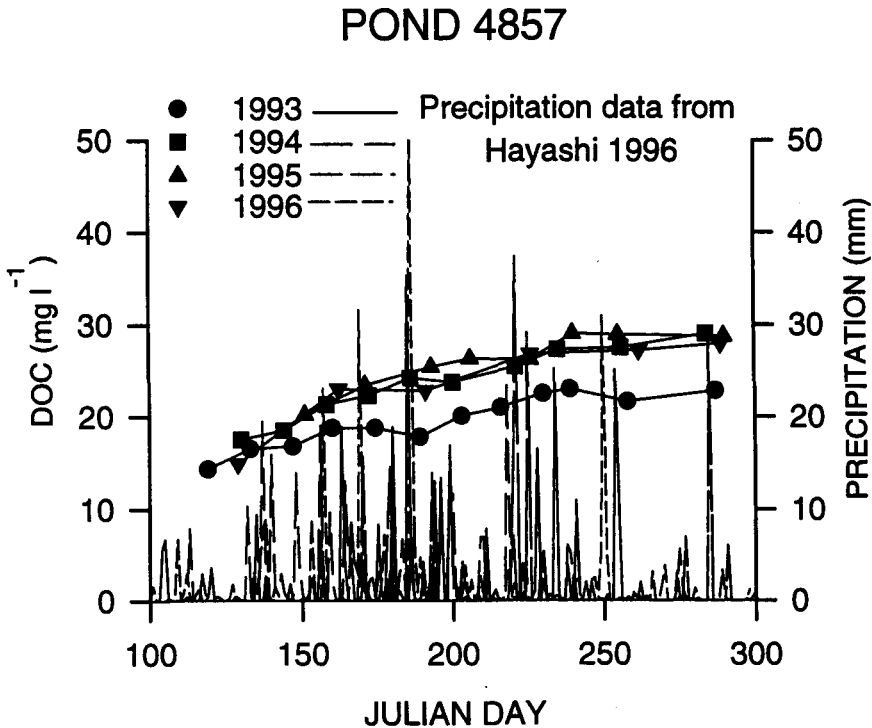
POND 4857

Figure 2. The relationship between the dissolved organic carbon concentration (DOC) in Pond 4857, St. Denis Wildlife Area, Saskatchewan, and precipitation. Precipitation data are from Hayashi (1996) and the DOC are from Environment Canada (unpublished data).

unknown. Although increases in DOC concentrations may arise from climatic warming, the effects on nutrient cycling in prairie wetlands remain unclear.

As noted earlier, prairie wetlands are located in a semi-arid ecosystem where evaporation exceeds precipitation. They are expected to gradually dry out under the warmer, drier scenarios of climatic change and this gradual drying out may increase the number of saline wetlands across the prairies. Many prairie wetlands, however, are naturally saline and as they dry out, salts will be further evapoconcentrated (Curtis and Adams 1995). This increase in salinity could have an effect on wetland DOC concentration and its

molecular weight size distribution. In Alberta surface waters, Curtis and Adams (1995) have shown that concentrations of DOC increased with increasing salinity and concomitantly the percentage of low molecular weight DOC (<1000 Daltons) also increased. Historically low molecular weight DOC has been considered to be most available for bacterial utilization. In the ocean, however, Amon and Benner (1996) have shown that it is actually high molecular weight DOC which is biologically labile. In Redberry Lake (DOC 37 mg l^{-1}) 96% of the DOC was <1000 Daltons and <1% of this was available to bacteria as an energy source, even when phosphorus and nitrogen were added (Waiser and Robarts 1997). Therefore, increases in the amount of low molecular weight DOC arising from increased salinity might negatively affect overall carbon cycling in these systems but this remains speculative. Why DOC in these saline systems is not biologically available is unknown.

Bacteria are generally accepted as the main decomposers of organic carbon and regenerators of minerals in aquatic ecosystems. Further, they directly utilize dissolved organic carbon, incorporating it into their biomass. Bacteria, in turn, are fed upon by various microbial and macro-grazers and in this fashion energy, carbon and nutrients are cycled up food chains to higher trophic levels. Unfortunately, studies of overall carbon cycling, specifically microbial production and the factors that regulate it, have not been done in prairie wetlands. In order to fully appreciate the impacts of climatic warming on prairie wetlands, it is imperative that we acquire a fundamental understanding of the role that bacteria, both planktonic and attached, play in wetland carbon cycling.

Information on planktonic bacterial production in prairie aquatic ecosystems is scarce. There is, however, some data for Humboldt Lake (Robarts et al. 1994), a shallow prairie lake. Bacterial production was determined as the rate of radiolabelled thymidine (TdR) incorporation into bacterial DNA during the ice-free season over a 2-year period. Bacterial production was strongly correlated with water temperature (Fig. 3) and the Q_{10} for this relationship was 3.1 between 10 and 20°C. Between 15 to 25°C, however, the Q_{10} increased to 7.4 as the rate of bacterial production rose rapidly above ~20°C. In this way, elevated water temperatures associated with climatic warming could lead to significant increases in bacterial production in prairie wetlands during summer. Provided that sufficient nutrients were available and the DOC was prone to microbial processing, DOC concentrations could be reduced. The results would be twofold: increased production of CO_2, a greenhouse gas, from bacterial respiration and increased penetration of
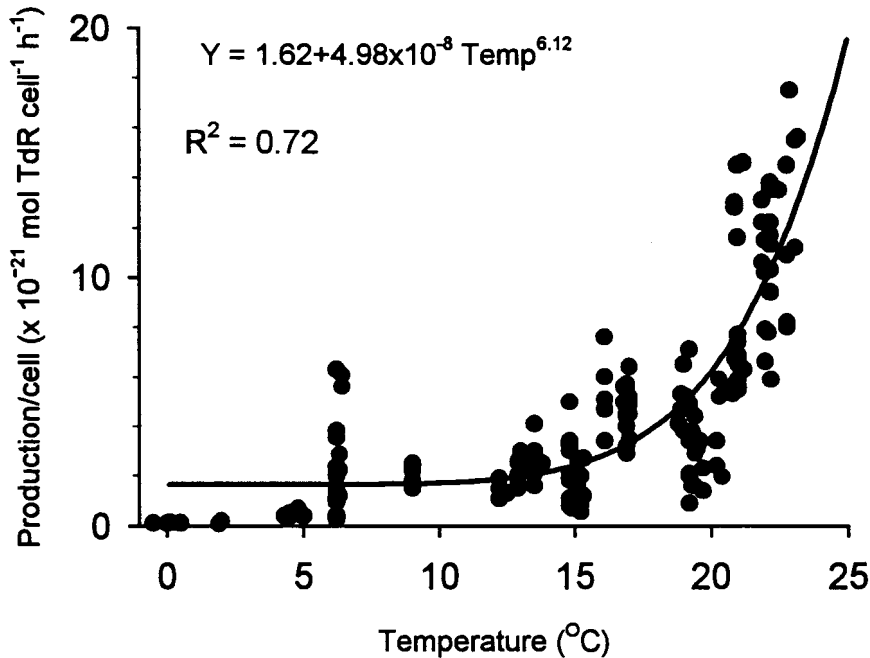
Figure 3. The relationship between bacterial production (rate of thymidine incorporation per cell) and water temperature in Humboldt Lake, Saskatchewan. Data from Robarts et al. (1994).

UV-radiation (see below). Levels of methane, another greenhouse gas with a global warming potential greater than CO_2, might also increase, since its production by methanogenic bacteria is highly temperature sensitive with a Q_{10} of 5.6-16 over a temperature range of 0-35°C (Topp and Pattey 1997).

Although food chains in marine wetlands have been fairly well studied, very little effort has been spent developing an understanding of food chains in prairie wetlands (Murkin 1989). Since primary producers link ecosystem consumers and resources, two critical factors will limit secondary production: net primary production and the efficiency with which energy is transferred between trophic levels. As noted by Murkin, there are two basic pathways for this transfer: the direct consumption of algal and plant material

by herbivores and utilization of plant detritus by detritovores. Although algal production is directly available to many consumers, primary production in wetlands may be dominated by various groups of macrophytes. Microbial biofilm communities (consisting of bacteria, fungi, algae, protistans), which colonize the surface of these living macrophytes may also contribute significantly to primary production in wetlands (Robinson et al. 1997), while at the same time serving as an important food source for herbivores.

Based on studies done largely in rivers and salt marshes, it is generally accepted that the major structure of a wetland ecosystem proceeds from plant detritus, to microorganisms, to a variety of invertebrate consumers and then, in some cases, on to vertebrate predators (Murkin 1989). Microorganisms are the first-level consumers of dead plant material—their activities produce both dissolved organic carbon and nutrients, which may be utilized by other autotrophic and heterotrophic communities, and particulate carbon which has an enhanced nutritional value due to microbial colonization and processing. Mann and Wetzel (1996), for example, have shown that DOC leached from two species of living and dead emergent macrophytes significantly increased bacterial production. As well, temperature has been shown to be a major factor influencing the rates of decomposition and the conversion of particulate matter to DOC (Godshalk and Wetzel 1978).

Fungi may play important roles in biogeochemical cycles and decomposition processes in prairie wetlands, although studies on fungal production in these systems are lacking. For example, Newell et al. (1995) found that fungal production associated with decaying sedge leaves in a freshwater swamp was always much greater (from 5 to >100 times greater) than bacterial production in the same system. Their findings are similar to those of Suberkopp and Weyers (1996) who studied decomposing riparian vegetation leaves in a stream. Fungal production has a Q_{10} of about 2 over the temperature range of 10 to 25°C.

While there are a few studies of herbivory, there are no estimates of detrital consumption and subsequent utilization in prairie wetlands (Murkin 1989). Murkin noted that based on the large amounts of plant litter observed in prairie wetlands and the often high densities of assumed detritivores, it has been assumed that detritivory forms the base of the food chains. Clearly, studies of the production and development of microbial biofilm communities on living and dead macrophytes, and the factors which regulate these, are urgently required for our understanding of how prairie wetlands are influenced by climatic warming.

Increased UV-radiation

While life on earth depends on solar energy, ultraviolet radiation (~100-400 nm) is more likely to damage or kill organisms than higher wavelengths within the visible (400-750 nm) range. Atmospheric layers above the stratosphere absorb the most biologically harmful wavelengths of UV. Ozone in the stratosphere is primarily responsible for UV-B (280-320 nm) attenuation (Karentz et al. 1994). Both UV-B and UV-A (320-400 nm) wavelengths penetrate the stratosphere and are transmitted into aquatic environments. Significant depletion of ozone has been observed over Australia, Antarctica and the Southern Ocean (Jeffrey et al. 1996) largely due to releases of anthropogenically produced halocarbons. Not only have levels of UV-B radiation reaching the earth's surface increased but so too has penetration of UV-B light into aquatic ecosystems. The end result has been increased stress on aquatic organisms. Consequently there is great concern regarding potentially negative impacts of UV-B on aquatic ecosystems (Karentz et al. 1994; Zepp et al. 1995). Studies from marine and freshwater systems have shown UV-radiation can have significant negative effects on autotrophic and heterotrophic organisms (Jeffrey et al. 1996; Zepp et al. 1995; Herndl et al. 1993). No study, however, has involved a prairie wetland. As well, the severe decline of many amphibian species has been linked to increased UV-radiation (Blaustein et al. 1994).

Within aquatic ecosystems, there is an inverse relationship between UV light penetration and DOC concentration (Scully and Lean 1994; Morris et al. 1995): as DOC concentration increases, the depth to which UV-B radiation penetrates decreases. Generally, UV-radiation does not penetrate to great depths in most aquatic systems. For example, in a study of North American lakes (maximum DOC concentration of 10.7 mgC l^{-1}), Williamson et al. (1996) reported that the 1% penetration depth for UV-B radiation was > 4 m in only 25% of lakes studied. In other lakes, 75% had 1% penetration depths <0.5 m.

The Prairie ecozone contains millions of shallow wetlands (<1 m depth). Although UV-radiation is usually completely attenuated over the first meter or so of water, shallow prairie wetlands could potentially be very vulnerable to increased UV-radiation. In addition to being shallow, however, prairie wetlands also tend to have high concentrations of DOC (e.g., from our work in Saskatchewan it is rare to find a wetland with DOC concentrations <10 mg l^{-1}) which should severely limit the penetration of UV-radiation.

Lately Arts et al. (unpublished data) have undertaken a survey of UV-light penetration in Saskatchewan lakes and wetlands using a scanning spectro-radiometer. One of the ponds studied, Pond 4857, is shallow (maximum depth 1 m) and the water humate-stained. DOC concentration is about 25 mgC l^{-1}. This survey found that the attenuation coefficient for UV-B radiation (K_d) for Pond 4857 was 49.7 m^{-1} (depth of 1% penetration = 9 cm). Recently, there have been a number of models developed that predict K_d from ambient DOC concentrations (Scully and Lean 1994; Granéli et al. 1996). Scully and Leans' model was derived using data from freshwater, low DOC (<8 mgC l^{-1}) systems while Granéli et al's model was for more humate stained lakes with DOC concentrations up to 19.4 mgC l^{-1}. According to Scully and Leans' model, the attenuation coefficient (K_d) of UV-B in Pond 4857 would be 165 m^{-1} (depth of 1% penetration = 2.8 cm) while for the Graneli et al. model the predicted K_d was 85.8 m^{-1}, almost twice the measured value. Clearly there is a major discrepancy between measured and predicted attenuation coefficients and therefore these models cannot be utilized to predict attenuation of UV-B light in high DOC prairie wetlands. Moreover, the results from Pond 4857 confirm the suspicions of Williamson et al. (1996) that substantial differences in the optical properties of DOC in different regions might exist.

As noted earlier, the prairies are characterized by low levels of precipitation and high rates of evaporation. As a result, many wetland systems tend to be saline to various degrees. Our research has shown that DOC in saline prairie waters differs from that in other areas of North America. DOC in saline systems is largely low in molecular weight and non-colored (Curtis and Adams 1995). Because of the lack of color, it attenuates UV-radiation much less than DOC in softwater systems. Again, using Sculley and Lean's (1994) model, the UV-B K_d for Redberry Lake with an average DOC of 37 mgC l^{-1} would be 343 m^{-1}. Arts et al. (unpublished data) measured a value of 5 m^{-1}. We anticipate that penetration of UV-B radiation will be greater in saline wetlands than would be predicted from current regression equations and therefore there is an urgent need to generate suitable equations for use in the prairie region.

The above data indicate that prairie wetlands may not be as protected from increased UV-radiation as might be expected from their high DOC concentrations. In Pond 4857 UV-B penetrated to ~10% of the maximum water level. This means that 10% of the water column when the pond is at full volume, and the organisms living within it, are exposed to UV-radiation. Shallow prairie wetlands are also subject to large variations in water level and frequent wind-induced mixing which means that planktonic organisms

would not easily be able to seek refuge from UV-radiation deeper in the water column. If with climatic warming and increased UV-radiation the DOC concentrations in prairie wetlands were to decrease, this could further stress the aquatic organisms in these systems.

The direct effect of UV-radiation on the growth and metabolism of microbial communities in prairie wetlands has not been measured. In a recent study, Ferreyra et al. (1997) found that UV-B had no effect on phytoplankton primary productivity and chlorophyll concentration in Redberry Lake. Bacterial numbers, however, decreased in water samples exposed to UV-B as compared to those that were not exposed. These preliminary results need confirmation not only for saline lakes and wetlands with non-coloured DOC but also for freshwater wetlands with high DOC concentrations and strong humate staining.

DOC is also extremely photoreactive. Long-term exposure of DOC to UV light causes photobleaching (loss of color due to irradiance) which decreases its attenuation characteristics. (Valentine and Zepp 1993; Granéli et al. 1996). Photobleaching of DOC explains the low UV-B attenuation in Redberry Lake. Redberry Lake is located in a hydrologically closed basin with inflows but no outflow. As a result, water residence time is extremely long and DOC entering the lake stays there and is constantly exposed to UV radiation which photobleaches it.

In addition to photobleaching, DOC can be photolysed (breakdown due to light absorption) directly to dissolved inorganic carbon (DIC), which can be used by autotrophic organisms. This has been shown to be a significant DOC loss process in humic lakes (Granéli et al. 1996) but has not been investigated in prairie wetlands. Photolysis may also cleave high-molecular weight DOC into smaller compounds that bacteria can then use, provided that adequate supplies of nitrogen and phosphorus are available for DOC processing (cf. Waiser and Robarts 1997). Kieber et al. (1990) have estimated that the half-life of riverine DOC in the ocean is 5-15 years based on photolysis experiments and subsequent microbial consumption of low molecular weight carbon compounds. Through photolytic processes, DOC concentration would be reduced, bacterial biomass increased for grazers and DIC formed by bacterial respiration.

We have measured the effect of DOC photolysis on bacterial production in Redberry Lake and in Pond 4857. Water samples were passed through a filtration device to remove algae and bacteria. Water was then exposed to sunlight for 1 to 10 days in a number of experiments; control samples were kept in the dark. After this treatment, bacteria were placed back into the

water and bacterial production was measured as the rate of TdR incorpora-tion over time. Photolytic production of labile DOC was concluded to have occurred if there was a significant difference between TdR incorporation rates in the exposed as compared to the control treatments.

Representative results for the two systems are shown in Figure 4. It is clear that photolysis had both negative and positive effects on aquatic bacte-ria from these two systems. For example, photolysis caused significant inhibition of bacterial production in Redberry Lake waters during the initial day of the experiment. This inhibition was probably caused by the produc-tion of free radicals, such as hydrogen peroxide, during photolysis (Sculley et al. 1995). The significance of photolytic production of free radicals from DOC, and its impact on aquatic food chains in prairie wetlands, has not been investigated.

Both Pond 4857 (Fig. 4) and Redberry Lake (data not shown) showed the stimulatory effect that photolytically produced labile carbon could have on bacterial production. These rates were significantly higher in treatments where water had been exposed to total sunlight as compared to controls. These increased rates were seen in both short (1 day) and long (10 day) exposures of Pond 4857 water to natural sunlight. The significance of pho-tolysis and subsequent biological loss of DOC to overall carbon cycling in these aquatic systems is difficult to assess. Currently there is no technology available to measure relatively small changes in DOC concentration in the large DOC pools found in prairie wetlands.

Photolysis of aquatic DOC may also produce carbon monoxide (CO) (Valentine and Zepp 1993). A major part of aquatic DOC is composed of chromophoric compounds which absorb sunlight (Clair and Sayer 1997) and may undergo chemical transformations which result in CO production (Zuo and Jones 1997). While not a greenhouse gas, carbon monoxide has an important effect on the radiative balance of the atmosphere through its enhancement of methane accumulation, ozone and other radiatively impor-tant atmospheric trace gases (Valentine and Zepp 1993). Photochemical carbon monoxide production may also be an important process in the cy-cling of refractory DOC in shallow natural waters (Zuo and Jones 1997). For lakes and wetland waters, Zuo and Jones (1997) estimated a DOC turnover time of 2-10 years based on photochemical formation of CO. As well, if CO is not reduced by in-water biological processes, wetlands could be important sources of carbon monoxide, both on global and regional scales (Valentine and Zepp 1993).
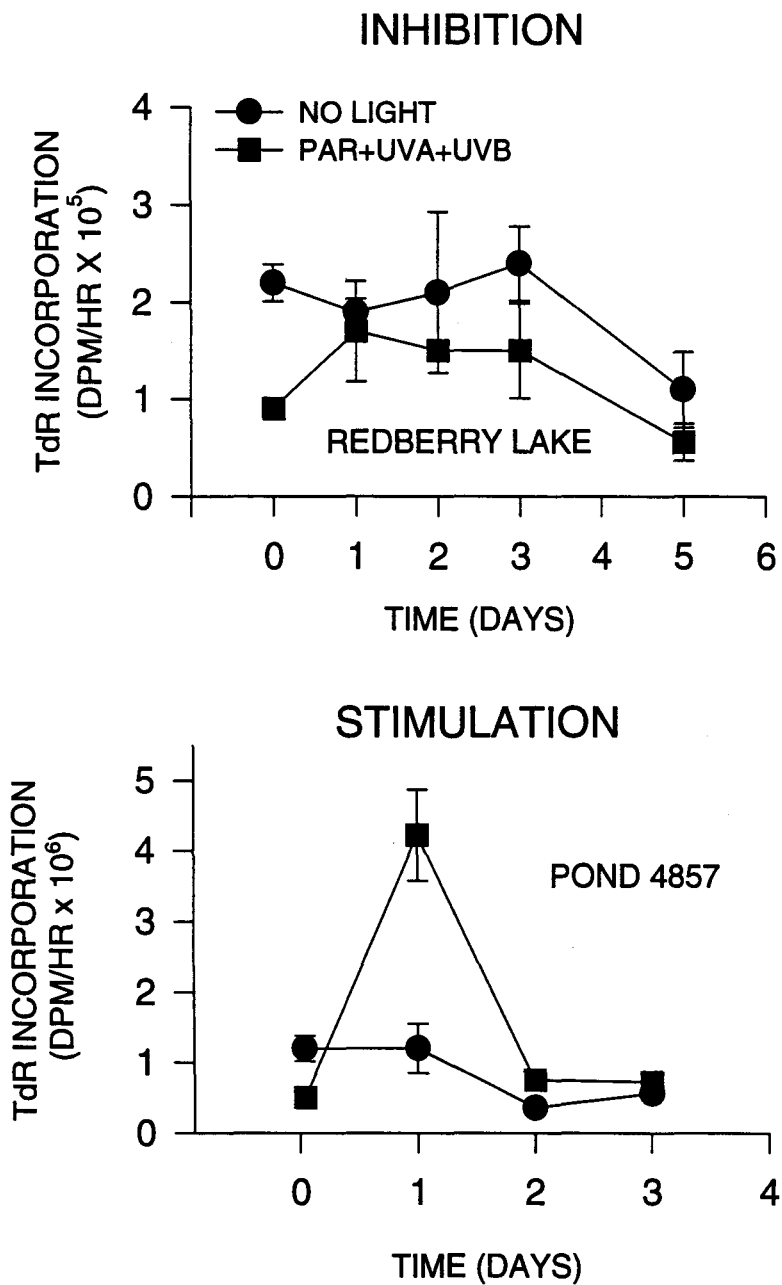
INHIBITION

STIMULATION

Figure 4. The effect of photolysis of DOC on bacterial production in Pond 4857 and Redberry Lake, Saskatchewan. PAR+UVA+UVB = visible plus ultraviolet, natural sunlight. See text for details.

While our preliminary research has focused on the planktonic bacterial populations of these systems, it essential that this type of research be applied to biofilm communities growing on aquatic macrophytes. These biofilms may be extremely productive but it is not known how UV-radiation will affect them. Fungal and bacterial activities associated with terrestrial litter were significantly reduced when exposed to UV-B (Zepp et al. 1995), but no such data exists for biofilms in wetlands. Within aquatic systems, autotrophic and heterotrophic biofilm constituents secrete a polysaccharide exopolymer composed of large-molecular weight compounds (>10,000 Daltons) (Decho 1990). This material is highly adsorptive, sequestering dissolved organic compounds, metals and nutrients. Biofilms subjected to different stimuli produce different amounts of exopolymer. It is possible that these secretions may protect biofilm microorganisms from UV-radiation damage although this has never been studied.

In aquatic studies, it seems that UV-radiation research has almost solely been focused on phytoplankton and bacterial populations and DOC while little, if any, has assessed its effects on fungal populations and particulate organic matter. There is also a need to determine the effect of UV-radiation on the growth, production and decomposition of aquatic macrophyte communities in prairie wetlands. Significant changes in any of these processes could have profound effects on the role of wetlands in the productivity and biodiversity of the prairies.

Agriculture

Prairie wetlands often experience significant contamination by agricultural pollutants such as nutrients (nitrogen and phosphorus) (Crumpton and Goldsborough 1998) and anthropogenic organics (herbicides and insecticides) (Neely and Baker 1989; Goldsborough and Crumpton 1998). These contaminants may enter a wetland from cultivated fields with sediments (Gleason and Euliss 1998), surface runoff, subsurface drainage or as direct inputs from overspraying. The impacts of these additions on algae are largely unknown. Goldsborough and Robinson (1996) noted that there have been few studies of the magnitude of the contamination, the nature of the contaminants and their environmental chemistry in wetlands. In phosphorus dynamics studies of four freshwater, humate-stained Saskatchewan wetlands, we found no evidence of phosphorus limitation of either the phytoplankton, bacterioplankton or epiphyton (unpublished data). Waiser and Robarts (1995, 1997) found that the microbial populations in Redberry Lake were severely

nutrient limited and therefore nutrient additions stimulated phytoplankton and bacterioplankton growth. In addition, the majority of the large DOC pool in this lake was unavailable for bacterial use and consequently the bacteria were carbon limited (Waiser 1995). Experiments that looked at the effect of the herbicide triallate on the microbial community in this lake showed that bacteria were able to utilize triallate as a carbon source but only when nitrogen and phosphorus were added to the incubations. These experiments also demonstrated significant decreases in algal biomass after exposure to triallate but only when the herbicide concentration exceeded 1000 μg l^{-1} (Waiser and Robarts 1997). Other studies of herbicide effects on marsh epiphyton have shown that herbicides can have long-lasting effects on productivity and species composition (Goldsborough and Robinson 1996).

     Another effect of nutrient addition on prairie wetlands includes the enrichment of emergent plant tissues and stimulation of emergent plant production. Such nutrient enrichment of plant tissues will eventually accelerate emergent plant decomposition and these accelerated rates will in turn cause higher release rates of nitrogen, phosphorus (Neely and Baker 1989) and dissolved organic carbon. The effects of such nutrient enrichment on prairie wetland carbon cycling and productivity is not known.

     In addition to indirect agricultural effects on wetlands there may also be significant direct effects. Anderson (1995) has shown that > 50% of soil organic carbon has been lost from prairie soils either by mineralization or by erosion post-cultivation. Moreover, this loss is probably an ongoing process. Our studies on DOC isolated from Redberry Lake indicate that this DOC is terrestrially-derived based on stable carbon isotope analysis. It would appear that at least some of the organic carbon lost from prairie soils post-cultivation has been deposited in prairie wetlands (also see Gleason and Euliss 1998). This organic carbon could not only contribute significantly to wetland DOC, but could increase water color thereby directly affecting the penetration of UV-radiation. It is unknown, however, how much of this terrestrially-derived organic carbon is available to wetland microbial populations. Availability would depend on its chemical composition and the presence of adequate nitrogen and phosphorus supplies to process it (cf. Waiser and Robarts 1997). For terrestrially-derived DOC entering Redberry Lake via the largest inflow, Oscar Creek, we found that 12% is available to bacteria under ambient nutrient conditions. When nutrients (nitrogen and phosphorus) were added, however, the amount of DOC biologically available rose to 19%. Schindler et al. (1992) found that nutrient enrichment of Precambrian shield lakes resulted in a large increase in autochthonous DOC

production and subsequently increased microbial utilization of allochthonous DOC. For prairie wetlands we need to determine the lability of the DOC pools and whether these are affected by nutrient enrichment.

Conclusions

Considering the recognized importance of wetlands in the prairie ecozone it is surprising to find that relatively little is known about in-water biogeochemical processes and the factors which regulate them. As Poiani and Johnson (1993) noted, current climate models cannot accurately predict changes in temperature and precipitation patterns expected with climatic change, particularly with respect to regional estimates. Even if climate models were more precise in their predictions, aquatic ecologists would be hard-pressed to make similar predictions about aquatic biogeochemical changes that would occur in prairie wetlands. Furthermore, the interaction, and often counteracting effects, of climatic warming, increased UV-radiation and agriculture activity make such predictions more difficult.

Assuming that the general prediction of a warmer and drier prairie region is correct, what are the possible consequences for in-water wetland processes? From the few studies that have been undertaken, we have shown that both autotrophic and heterotrophic processes have a temperature dependency. Between 10 and 20°C these rates increase by about a factor of 3 but, in the case of bacteria, these processes might increase more sharply at higher temperatures (Fig. 3). In the presence of adequate supplies of nitrogen and phosphorus this could lead to increased aquatic productivity. An increase in nutrients may be generated by increased decomposition processes in the wetlands and this may compensate for decreased inputs of nitrogen and phosphorus to wetlands in a more arid environment. The increase in bacterial processes, however, combined with increased photo-bleaching, may decrease the concentration of DOC and water color thereby leading to significant increases in the depth to which UV-radiation may penetrate. Such increases could significantly increase the susceptibility of many aquatic organisms (cf. Schindler et al. 1996) in shallow wetlands. Indeed, Williamson et al. (1996) have concluded that changes in DOC concentrations are probably more likely to alter the UV-environment in lakes than are changes in stratospheric ozone. This conclusion is particularly pertinent to prairie wetlands because of their general shallowness.

In studies of long-term changes in prairie wetland chemistry we have reviewed, we found no data on DOC. There is no information regarding

external processes that may affect not only the rate of accrual of DOC to prairie wetlands, but the quantity and quality of DOC as well. This is unfortunate considering the pivotal role DOC plays in aquatic biogeochemical processes. Based on data from the Cottonwood Lake area, LaBaugh et al. (1996) concluded that effects of precipitation extremes are not limited to the season or years in which they occur, as extremes set the stage for subsequent years by their effect on wetland and groundwater levels. They also noted that wetland responses to precipitation extremes have not been considered in attempts to determine controls on chemical composition of prairie wetlands or to determine empirical relations between major ion abundance because few studies have documented what happens in these wetlands when extremes occur. Climatic warming, increased UV-radiation and agricultural activity all have the potential to have extreme effects on the biogeochemistry and food chains of prairie wetlands. It is imperative, therefore, that we obtain an understanding of the major biogeochemical processes in prairie wetlands and how these may be affected by external perturbations related to atmospheric change and agriculture. Construction of a carbon model for a prairie wetland would be an important intial step in this process.

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