Ecology of a peat bog

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Summary
Previous work investigating Canadian peatlands and their ecology has shown the microbial activity responsible for their formation and maintenance, as well as the ease with which this environment can be disturbed, possibly with significant consequences. Research indicates that it is essential that we look very carefully how our actions may destroy these unique ecosystems. A general description of the ombrotrophic peat bog is followed by specific investigations into cellulose degradation, methane production, the hydraulic conductivity of peat and then of a possible methane inhibitor. These demonstrate the potential outcome of bog destruction, whether by physical removal or flooding, either by man or climate.

Key index words: methane, peatlands, acrotelm, catotelm, methanogens

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Introduction
The aim of this paper is to draw attention to the ecology of peatlands, in order to emphasize how this environment may impinge on government and industry, which may not be sufficiently aware of the readily available data, which may affect their policies. Having spent several years over a decade ago working on some thirty Canadian peat bogs to better understand their ecology, and realising the potential of methane ebullition when their structure is destroyed, the author would like to ensure that the consequences are understood.

Bogs are both persistent and complex. Peat is formed by the slow degradation of surface plant biomass, and the differences found in the structure of the peat depend not only on the primary vegetation but also on the amount of degradation that has taken place. Bogs contain two different microbial ecosystems: one at the surface, the aerobic acrotelm, and the other in the body of the bog, the anaerobic catotelm. The oxygenic condition of the acrotelm means the decay is similar to that found on the forest floor, or even in domestic compost heaps, with the production of carbon dioxide. But in the catotelm methane is produced from a much slower anaerobic degradation of the organic matter. The radiative effect of methane is twenty times that of carbon dioxide, so its loss to the atmosphere needs to be avoided.

The growth rate of the vegetation is greater than its microbial degradation so plant detritus builds up as peat. The under-saturated acrotelm, composed of living and partially decayed vegetation, is moderately permeable as it is sufficiently porous to allow meteoric water to flow laterally through the bog and into the surrounding lagg stream, but the catotelm cannot be penetrated readily by water. Since the only input of nutrients is from precipitation a bog is not only oligotrophic, which slows microbial activity, but it also has few cations available to neutralise metabolic acids, creating an acidic environment as well as a reducing one. Also, since bogs do not readily drain, where the climate is favourable they can easily increase in extent and cover complete hillsides to form blanket bogs.

Studies

Cellulose degradation
Peat can be regarded as a soil matrix derived from plant biomass, made up of three polymers, cellulose, hemicellulose and lignin. Cellulose is a linear polymer of glucose, hemicellulose a heteropolymer mainly of xylose, and lignin is a random polymer of phenylpropane units that resist enzymatic degradation, and which tends to make up the inert humus. Cellulose is the component most easily degraded. Aerobic microbes can transform it rapidly to carbon dioxide and water, whilst anaerobic microbial degradation is much slower and requires a consortium where each microbe species performs one step in a series of consecutive reactions. The anaerobic consortium first breaks down the plant cellulose polymers into sugars, and then ferments the sugars to volatile fatty acids, alcohols, carbon dioxide and hydrogen, some of which are then used as substrates by methanogenic bacteria to produce methane. Finally this methane may be reoxidised to carbon dioxide by methanotrophic bacteria in the acrotelm (Brown, 1998).

The most important characteristic of a peat soil is the degree of decomposition, which has been measured in 30 organic soils on the Precambrian rocks of the Canadian Superior Province by comparing the cellulose component, measured as glucose in an acid hydrolysate, with both the aerobic respiration rate and the rubbed fibre content of the soils (Brown *et al.* 1988). The hydrolysate gave a reasonable correlation with the other two methods, and since it is quantitative and less subject to operator error and variability, the glucose hydrolysate is a useful measure to determine peat decomposition.

In three soil types investigated, the glucose content was just over a quarter by weight, which gives an indication of the potential of the soil to be microbially degraded, while the major portion, mainly the phenolic lignin, is acid-insoluble and resistant to degradation. The cellulose content, measured at four stations in Mer Bleue, a raised bog near Ottawa, Canada, was found to decrease with depth with the concomitant increase in the insoluble residue (Brown *et al.*, 1988).

Methane production

To probe the methane content of waterlogged peat we developed a set of stainless steel probes with a retractable inner plunger as described in Dinel *et al.* (1988). Water samples were collected periodically into evacuated bottles from three levels in the peat between 500 mm and 1350 mm. The results showed that the amount of both methane and carbon dioxide increased with depth, and that the amount of methane extracted from the lower depths was greater in amount than could have been dissolved in the extracted water, indicating the methane was trapped, either by occlusion in the peat matrix or by supersaturation in the pore water.

Further investigations in Mer Bleue from 25 stations at three depths between 600 mm and 1200 mm (Brown *et al.*, 1989) showed the methane concentration to vary widely between samples, and that this variation was greater at each individual depth than between the different depths. However, approximately two and a half times as much methane was found in the samples taken at the two greater depths than those in the shallower one. The amount of methane from the deeper samples correlated well with laboratory incubations of the peat, but the incubations of peat from the more surficial samples produced a much greater amount of methane than could be extracted in the field. This may be explained by the absence of oxygen in the laboratory incubations, which would not have been the case in the field where methanotrophs could have utilised (oxidised) some of the methane.

Hydraulic conductivity of peat

The bacterial activity found in Canadian peats, and especially that of Mer Bleue, suggested that in situ methane generation in the strictly anaerobic layers could prevent water flow and hence reduce the hydraulic conductivity in the catotelm. Three 200 mm diameter plastic columns with various measuring probes were packed with Mer Bleue peat, and saturated from the bottom with de-aerated, temperature-equilibrated distilled water, and eluted by direct continuous flow at 20°C. One column was used as a control and sterilised by irradiation and eluted by sterilised de-aerated water. At the end of the first part of the experiment, the active columns were flushed with helium under a head of 400 mm water in order to maintain an anaerobic environment while displacing the methane and carbon dioxide. Resaturation with water removed the remaining helium (Reynolds *et al.*, 1992).

The results are mainly from one of the active columns. The second column gave similar results but was used for technique development and so had a greater margin of error in the final accounting. The first column was eluted for 12 weeks in Run 1, before it was degassed and resaturated with water; it was then eluted for a further 5 weeks in Run 2. Water flow was maintained by stepwise increases of the applied head. In Run 1 the hydraulic conductivity decreased by 1.6 orders of magnitude, and moisture content by 20 percentage points, while concurrently there was a rhythmic, but general, increase to near fifty-fold in the methane concentration. After degassing and resaturation of the peat, all the parameters returned to values similar to those at the beginning of Run 1. In Run 2 the water flow and moisture content decreased similarly to that of Run 1, but there was a faster accumulation of methane. The irradiation of the control column produced a large amount of carbon dioxide through degradation of the organic matter, but all this gas was washed out by the eluting water within 3 weeks. Since this column produced no gas the peat soon became completely water-saturated, with the water flow increasing to a plateau that held for the duration of the experiment (Brown and Overend, 1993).

Data from these experiments show that active growth of methanogens decreases the hydraulic conductivity in the peat through the production of methane. This gas is largely insoluble, hence it forms bubbles in the interstitial pores of the peat, causing the bog to be undersaturated, an effect similar to that of air in unsaturated mineral soils. The amount of methane at the end of each run contained in the columns was was between 1 L and 2 L, corresponding to 7.7 mol methane m^{-3} of peat. A pore diameter of 70 µm was obtained by calculation from the measurement of the pressure needed to break through the gas blockage.

Possible inhibitor

Only small amounts of methane have been measured leaking from peat bogs, in spite of the considerable quantities that have been found within them (Rouse *et al.*, 1995). However, since peat incubations in the laboratory are able to continue to produce methane so long as there is sufficient cellulose substrate, it would appear that there must be some mechanism controlling methane production in the catotelm. This cannot be oxygen as it is in the acrotelm. Incubation of peat taken from the same sites as the extracted gas shows methane production was spatially heterogeneous, but averaged 40 nmol g^{-1} h^{-1}. There was a passable correlation in the catotelm between field extracted methane and that produced from laboratory incubations, but in the acrotelm samples there was none (Brown, 1998). Statistical analysis of the methane production in the field shows that, despite the spatial heterogeneity, there is actually only one methanogenic population in the catotelm. But when results from the catotelm and acrotelm are pooled in the laboratory, two separate populations are found. A cumulative probability curve shows that just under half (45%) of the group are active methane producers, which may suggest that these originate in the acrotelm, while the rest form methane at a much slower rate, more typical of the catotelm (Brown, 1989).

In these laboratory incubations methane is produced by the acrotelm peat at over 100 times the rate of that of the catotelm peat, but when these two peats are mixed together in equal quantities then the joint rate is only twice that of the catotelm peat alone, rather than an average of the two as would be expected. However, if the catotelm peat is first sterilised by autoclaving then part of the inhibition is removed, and the rate rises to 60% of that of the acrotelm peat alone. Thus the catotelm peat not only produces significantly less methane than the acrotelm, but also considerably inhibits methane production in the acrotelm irrespective of the presence of any methanotrophs. What this inhibitor might be is unknown. Since it is only partially removed by autoclaving it is unlikely to be a metabolite. This result is consistent though with what is known of the catotelm. Methane production in the catotelm cannot continue without becoming unstable, for, although methanotrophs in the acrotelm are generally able to prevent the escape to the atmosphere of methane produced at a slow rate in the catotelm, they would not be able to do so if the rate was much greater, as can be seen when bogs are disturbed (Brown, 1998). From the field and laboratory evidence it would seem necessary that some type of inhibitor should be present to maintain a stable equilibrium.

Discussion

Peat bogs are unders-aturated by water due to the considerable content of gaseous methane in the matrix. The flux of this methane is in equilibrium, possibly explained by the presence of an inhibitor in the catotelm. In the natural environment any loss of carbon from the bog is through the escape of carbon dioxide, either through the oxidation of methane by acrotelm methanogens, or directly through diffusion and advection. Except for the occasional 'burp' when atmospheric pressure is low, methane remains within the bog so long as its structure remains intact and the hydraulic pressure remains constant.

Methane is only sparingly soluble in water. The amount present in the catotelm is such that it cannot be wholly dissolved within the pore-waters, so much is present as free gas bubbles. These occlude the interconnecting pores within the peat matrix greatly reducing its permeability whilst increasing the stagnant state of the bog, thus essentially forming a huge sponge that is extremely difficult to drain.

As acrotelm degradation of plant mass is incomplete the catotelm thickens and becomes an overall carbon sink. However, the integrity of the catotelm can be compromised through a breach in the acrotelm, as can happen when bogs are drained for farming, forestry or mining. Once the integrity of the acrotelm is disrupted the catotelm will become oxygenic, methane will no longer be contained within its pores but will escape to the atmosphere, where it has a considerably greater radiative effect than carbon dioxide. Without the interstitial pore-blocking gas bubbles water will be lost, the high water table will fall, and eventually the biomass of the bog will be subjected to aerobic degradation leading to the loss of the carbon sink and the direct production of carbon dioxide. Furthermore, if climate change should significantly reduce the precipitation causing a fall in the water table, the acrotelm will dry out and again there will be degradation of the peat biomass.

The disruption of the acrotelm ecosystem need not only be by physical removal but can also occur during flooding (Rudd *et al.,* 1993). Since peat bogs are not actually fully saturated because of the internal pressure of methane bubbles, when they are flooded, for instance due to construction of hydroelectric dams, there is an increase in hydraulic head, a loosening of the acrotelm structure, and if the water is not static there is an increase in the penetration of oxygenated water, with a concomitant increase in both methane escape and its alteration to carbon dioxide. Similarly, if climate change causes an increase in precipitation leading to the flooding of peat bogs, again there would be a loss of methane.

The peat bog ecosystem is complex and easily compromised. Since there are considerable areas of such bogs world wide, it is our responsibility to take great care that they are not disrupted, and that a secure carbon sink is not turned into a significant factor of climate change.

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