24. *Sphagnum*, the peatland carbon economy, and climate change

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24.1 SUMMARY

Northern peatlands cover about 3% of the Earth's land surface and contain about 600 Gt of carbon — about the same amount as there is in CO_2 in the atmosphere. Species of *Sphagnum* are abundant in most of these peatlands and are amongst the most important fixers of carbon. They decay more slowly than most plants and so come to be over-represented in peat. They are also the main determinants of the porous structure of the surface of most peatlands.

The peat continues to decay anaerobically though very slowly. As the depth of peat increases so the *total* rate of loss increases and the rate of accumulation decreases. Thus the carbon sequestering power declines.

Crudely calculated carbon fluxes into and out from the surface ($\mathrm{mol\,m^{-2}\,a^{-1}}$) are: influx fixed from CO_2 by photosynthesis 5.2; efflux as CO_2 from aerobic decay 1.1–2.7; efflux as CH_4 from anaerobic decay 0.2–0.5; efflux downward to peat proper 2.0; efflux as dissolved organic matter in runoff 0.5. The net effect on the atmosphere is to remove CO_2 at $3.0\,\mathrm{mol\,m^{-2}\,a^{-1}}$ and to replace it with CH_4 at $0.2\text{–}0.5\,\mathrm{mol\,m^{-2}\,a^{-1}}$. This CH_4 has, molecule for molecule, perhaps about 20 times the warming potential that CO_2 has so the net effect is the equivalent of *adding* CO_2 to the atmosphere at $1\text{–}7\,\mathrm{mol\,m^{-2}\,a^{-1}}$.

Both mechanisms tend to contribute to the warming potential of the atmosphere. *Sphagnum* is the only bryophyte abundant enough to be capable of having a significant effect of this kind.

KEYWORDS: Carbon dioxide, carbon sequestering, methane.

24.2 INTRODUCTION

The bogmoss, *Sphagnum*, has gone its own evolutionary way and achieved remarkable success in a limited environmental range as a result of its ability to make its environment acid, its ability to grow well in nutrient-poor conditions, and its resistance to decay (Clymo, 1997). At the Centenary Meeting of the British Bryological Society (BBS) I discussed its potential, through the peatlands of which it is the chief engineer, to affect the climate. Here I try to explain some of the ideas involved but make no attempt to review the rapidly growing literature on this subject.

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24.3 THE AMOUNT OF *SPHAGNUM*

Individual gametophyte plants of *Sphagnum* range from small to robust (as bryophytes go) but all are minute when compared with an average woody tree. At least, they appear to be. We cannot yet tell whether a single genetically distinct patch on a peatland occupies an area a few centimetres across (similar to the typical size of unispecific patches) or interdigitates with other species over many square metres. If the latter were true then one might equate the peat with the mass of structural wood in a tree, and it would become obvious that this single *Sphagnum* plant was similar in mass to a tree. Linked but separate is the question: how old is this individual *Sphagnum* plant? Is it the direct vegetative continuation of a spore that germinated five millennia ago, or did its generating spore begin to grow only a few years or decades ago? By the bicentenary of the BBS the answers to these questions will probably be known. For the time being we can bypass them and try to answer the third of these sorts of question: how much *Sphagnum* is there altogether on the Earth's land surface?

Sphagnum grows in a wide range of habitats and places, avoiding the highly calcareous and the very dry (though a few species essay moderately calcareous and mesohydric conditions). But most species and all the most abundant ones grow best and most commonly in wet acid peatlands, often those dependent on rainwater for their surface water. In such places they may occupy half the surface area or more. The total area of such peatlands is difficult to assess (Clymo, 1996b) because they are difficult to identify by remote sensing and often interdigitate with other types of system or have sufficient trees on them to be categorized as forests. Gorham (1991) estimated that there are about 350 MHa of such peatlands in Boreal and Subarctic North America, Fennoscandinavia and the former USSR. This is 3,500,000 km^2: equivalent to a square of side about 1900 km. These northern peatlands thus occupy about 3% of the Earth's land surface.

Most of the live *Sphagnum* is in the top 3 cm of capitulum and topmost branches (Clymo & Hayward, 1982), and has a dry bulk density of about 0.05 g cm^{-3} (Clymo, 1983). If half (0.5) of this northern peatland is covered by *Sphagnum* the total dry mass of these living plants is about $0.5 \times 350 \times 10^6(\text{Ha}) \times 10^4(\text{m}^2) \times 0.05 \times 3 \times 10^4 (\text{g})/(10^6(\text{t}) \times 10^9(\text{Gt})) = 2.6$ Gt.

The general operation of peatlands is now well-known. New mass is produced at the surface. In the case of *Sphagnum* the capitulum behaves like a factory extruding stem and branches behind it as it grows upwards. Below, the cells die for lack of light. The structure is porous and decay is mainly aerobic producing mostly CO_2. The 5–50 cm thick surface layer is the acrotelm of Ingram (1978). Some plants decay rapidly: *Rubus chamaemorus* is an example. Others, including *Sphagnum*, decay unusually slowly and thus come to be over-represented by the time that collapse and the consequent reduction of hydraulic conductance cause the peat to become permanently waterlogged and thus anoxic, with anaerobically produced CH_4 as a product — the catotelm of Ingram (1978). The proportion of *Sphagnum* in the catotelm is thus likely to be greater than it is at the surface, though we do not know by how much. Here I guess that the peat is 70% *Sphagnum*. Gorham (1991) estimated that the average depth of peat in the Boreal and Subarctic zones is 2.3 m. The mean dry bulk density of the peat is probably about 0.1 g cm^{-3}. The total dry mass of

Sphagnum in peat is then about $0.7 \times 350 \times 10^6$(Ha) $\times 10^4$(m^2) $\times 0.1 \times 230 \times 10^4$ (g)/(10^6(t) $\times 10^9$(Gt)) = 620 Gt. There are several assumptions in this calculation: the true value might be half or double that given.

24.4 CARBON ACCUMULATION IN *SPHAGNUM*-DOMINATED PEATLANDS

As recently as 30 years ago the general view of peatlands was that they fixed carbon at the surface, lost a small fraction of this in decay and accumulated most of what they had fixed in peat where decay was negligible. *Sphagnum* plants grew onward and upward leaving their dead remains below to accumulate. Peatlands could be viewed as a 'permanent' sink for carbon. Alternating layers of highly humified and less humified peat, if synchronous over a large peatland, represented drier and wetter climates. Carbon-14 dating later showed that in many (but not all) cases these layers corresponded with periods of slower and faster peat accumulation. Apart from these changes, covering a few centuries each, there was no reason to think that carbon sequestration would not continue at much the same average rate until some catastrophic change — another ice age for example — removed the peatlands and all their peat. In the context of current concerns about atmospheric CO_2 concentrations and climate change, peatlands as carbon sinks (and *Sphagnum* as their main agent) were a 'Good Thing' in the sense implied by Sellars & Yeatman (1930).

This simple picture has proved to be incomplete. It is now unclear whether peatlands increase or decrease the temperature-changing potential of the atmosphere. The debate hinges on two matters. First, is the picture of indefinite accumulation of peat at much the same average rate correct, or does the rate decline with time *even if the climate and internal peatland processes remain the same*? Secondly, what is the role of CH_4 produced in the anoxic conditions in waterlogged peat?

24.5 RATE OF ACCUMULATION OF PEAT

The key idea here is that the catotelm is the true peat accumulating layer; the living plants in the acrotelm, among which *Sphagnum* is usually conspicuous, fix carbon and decay predominantly aerobically but at different rates. For any one species one may write, for unit area, something like:

$$dM/dt = p - \alpha M,$$

where M is the accumulated dry mass, p is the rate of addition of dry mass (p for productivity), α is the proportional decay rate, and t is time. The solution to this is:

$$M = (p/\alpha) \times (1 - \exp(-\alpha t))$$

(Fig. 1), which rises from zero at first towards the asymptotic limit p/α (Clymo, 1984). At first there is no material for decay to work on, so the slope of the line at $t = 0$ is simply the rate of addition, p: *any* slope on the graph of M *vs* t is a rate (productivity) physically similar to p. As time goes on decay can operate on an increasing accumulated mass, so the rate of loss, αM, increases and rises toward the rate of addition. The true rate of accumulation — the net effect of +p and of

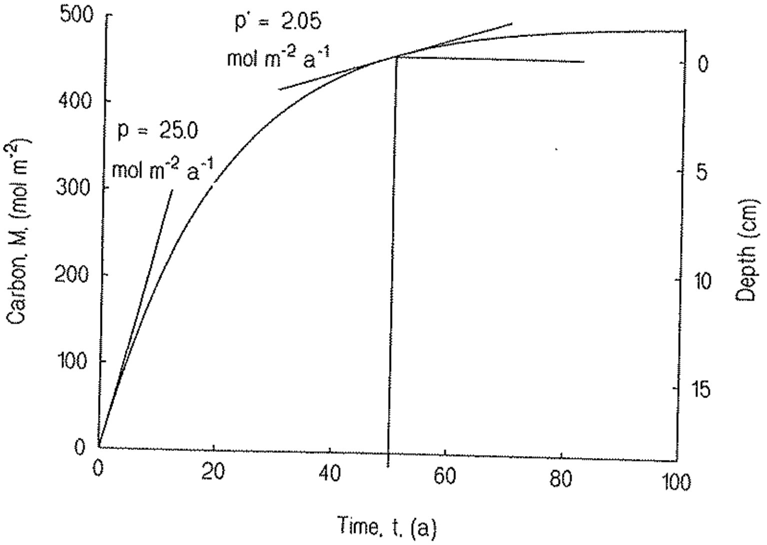

Figure 1. Accumulated dry mass, M, in the acrotelm as a function of time, t, following $M = (p/\alpha)^* (1\text{-exp} (-\alpha\ t))$. The rate of addition, p (productivity) is the slope of the line at the origin. The rate of addition to the catotelm, p′, is the slope at the time of collapse when the peat enters the catotelm, after 50 years in this example. The right scale shows the depth (cm) from the top of the steady-state acrotelm. The left scale shows the temporal course of increasing thickness. $p = 25\ \mathrm{mol\ m^{-2}\ a^{-1}}$, $\alpha = 0.05\ \mathrm{a^{-1}}$.

$-\alpha M$ — is the slope of the curve at any chosen time, and it decreases steadily as time passes. One may argue about the functional form of the decay coefficient, α: is it really constant or does it decrease with time? But it makes little difference to the outcome because within 10 to 100 years structural collapse and the rising water table cut the process short as the catotelm rises to engulf the base of the acrotelm. If p′ is the slope at this time then for the acrotelm one has:

$$dM/dt = p - \alpha M - p' = 0.$$

This formalizes two ideas. First, the acrotelm is of fixed thickness and is not a net accumulator of peat once it has reached this thickness after perhaps 50 yr (Fig. 1). Secondly, the acrotelm is a pre-processor: it fixes carbon, loses much of it differentially (50–90% during passage of *Sphagnum* through it; nearly 100% for *Rubus chamaemorus*) and passes on a small part of it at a rate p′ to the catotelm where the peat accumulates. Another way to put this is that p′/p is typically about 0.5–0.1 for *Sphagnum* and <0.01 for *R. chamaemorus* leaves. Of course there is variation with climate and microtopography (hummock, hollow). In a hollow the acrotelm may be only 5 cm thick, and p′/p for *Sphagnum* might be 0.5 while in a hummock the acrotelm may be 50 cm thick, with correspondingly longer time for decay to operate, and p′/p for *Sphagnum* might be only 0.05. But the general idea that the acrotelm hands on only a part of what it has fixed to the catotelm, where the peat then accumulates, is the same whatever the exact processes, proportions, and rates.

What happens in the catotelm? If there were no decay *at all* then the catotelm would, as was once thought, be a peat accumulator at rate p′ indefinitely. But the mistake was to confuse *no* decay with a very small rate. That decay does continue is shown, for example, by the CH_4 concentration decreasing from the base to the top of the catotelm (Clymo & Pearce, 1995). We can use the same approach as we did for the acrotelm, but (for variety and in the hope that the main ideas have been established) let us suppose that the decay coefficient, α, is not constant but decreases as the proportion of more refractory matter increases because the less refractory matter has already decayed. Two possibilities are mathematically tractable (Clymo, 1992; Clymo, Turunen & Tolonen, 1998): that the decay coefficient decreases linearly with the amount of dry mass left, and that the decrease is quadratic:

$$\alpha' = \hat{a}'_L(M'_T/M'_0) \text{ linear decay;}$$

$$\alpha' = \hat{a}'_Q(M'_T/M'_0)^2 \text{ quadratic decay}$$

where the ′ indicates the catotelm, M'_T is the mass of a notional piece of peat which entered the catotelm with mass M_0. When these (and the constant α' model) are put into $dM'/dT = p'\alpha'M'$ and the equation is solved one gets:

$$M' = (p'/\hat{a}'_C) \times (1 - \exp(-\hat{a}'_C T)) \text{ constant decay;}$$

$$M' = (p'/\hat{a}'_L) \times \ln\,(1 + \hat{a}'_L T) \text{ linear decay;}$$

$$M' = (p'/\hat{a}'_Q) \times ((1 + 2\hat{a}'_Q T)^{1/2} - 1) \text{ quadratic decay.}$$

The first is a curve with an asymptote at $p'/\hat{a}'_C$ (similar to Fig. 1). The other two resemble it but have no asymptote: each continues to rise but ever more slowly. To test these one may fit, for several depths at one site, measured cumulative mass (derived from a profile of dry bulk density) to age, derived from C-14 dates converted to dendrochronological age (Clymo, 1992). Or one may use, for the base only of numerous different sites, the measured cumulative dry mass and the corresponding dendrochronological age (Clymo *et al.*, 1998). In the majority of suitable cases there is a fairly good fit, and no difference in the exactness of fit among the three models. Here we are concerned mainly with the fact that all three models curve over, so that the true rate of accumulation, dM'/dT, decreases steadily. This means that the peatland is becoming steadily less effective at sequestering carbon. The sequestering ability of the catotelm, S', may be defined by the rate of accumulation now as a proportion of p' which it was originally: $S' = (dM'/dT)/p'$. For the three models of decay this gives:

$$S' = \exp(-\hat{a}_C T) \text{ constant decay}$$

$$S' = 1/(1 + \hat{a}_L T) \text{ linear decay}$$

$$S' = 1/(1 + 2\hat{a}_Q T)^{1/2} \text{ quadratic decay}$$

For those cases calculated so far (Clymo *et al.*, 1998) one gets values of S' of about 0.7: peatlands now are only 70% as effective at sequestering carbon as they were when they began growth several millennia ago. Of course they may have spread since they began growth and that will counteract the diminishing effectiveness of unit area by increasing the total area. There are too few data yet to be able to make sensible calculations.

24.6 CARBON DIOXIDE AND METHANE

The two main carbon-containing gases that exchange with the peatland surface are CO_2 and CH_4. Photosynthesis, fixing CO_2, seems to be the only carbon influx process, but there are several sources and routes of efflux, indicated in Fig. 2. There is no single site (yet) where all these components have been measured so I have taken plausible values for fluxes from several sites. The units are for carbon and are $mol\ m^{-2}\ a^{-1}$.

First is the transfer of peat from the acrotelm to the catotelm. The value 2.0 is the best estimate (Clymo *et al.*, 1998) of this rate for peatlands in the concentric bog region of southern Finland. This carbon has been fixed and removed 'permanently' from the atmosphere.

The sideways arrow represents losses as soluble carbon in runoff through the acrotelm. The 0.5 value is the mean for about a dozen peatlands in southern Finland (Kortelainen & Saukkonen, 1996). It is not clear how rapidly this carbon returns to the atmosphere: here I assume that it does so within a few years.

Methane, produced by decay in the catotelm, diffuses up to the acrotelm (Clymo & Pearce, 1995) but the flux is small compared with that of CH_4 produced just below the watertable. Some of this now combined upward flux is oxidized by methanotrophic bacteria to CO_2, but some escapes. And some moves much more rapidly in the low-resistance path of the gas spaces inside the roots of plants. The median value

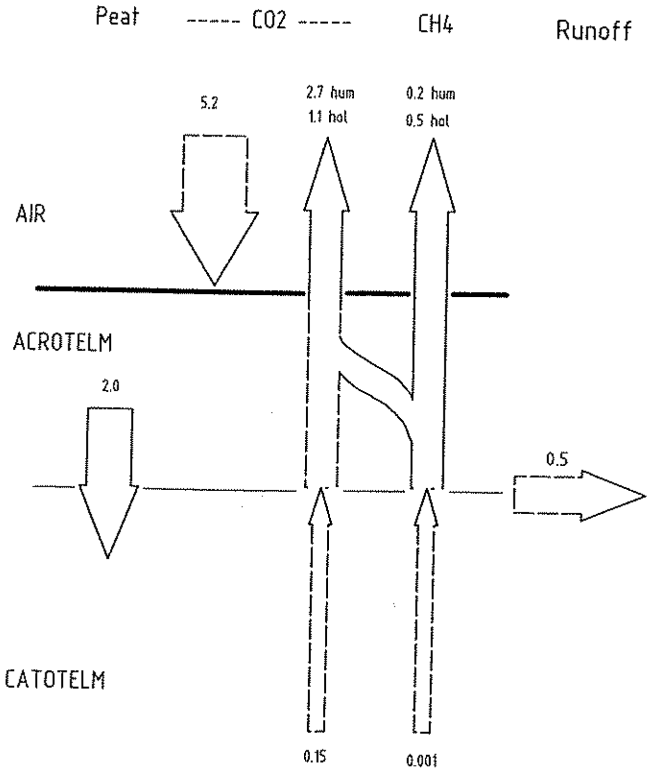

Figure 2. Pathways and approximate fluxes ($mol\ m^{-2}\ a^{-1}$) of peatland carbon. Dashed lines show the main sites of production. Efflux of CO_2 is shown separately for hummocks and hollows.

of this combined efflux from ombrogenous peatland in southern Finland recorded by Nykänen *et al.* (1996a) was about 0.35. This agrees well with the values for *Sphagnum*-dominated microhabitats in a peatland in south-west Scotland: 0.5 (hollows) and 0.2 (hummocks) (Clymo & Pearce, 1995).

Some CO_2 is produced in the catotelm but the upward flux is small compared with that of CO_2 produced in the acrotelm. Together their upward flux in the same *Sphagnum*-dominated peatland was about 1.1 (hollows) and 2.7 (hummocks) $mol\ m^{-2}\ a^{-1}$.

The most uncertain quantity is the gross input into plant mass. The value $5.2\ mol\ m^{-2}\ a^{-1}$ ($150\ g\ m^{-2}\ a^{-1}$) is similar to that reported for northern Sweden by Svensson & Rosswall (1980) and for *Sphagnum* in northern England (Clymo & Reddaway, 1971). But it gives a value for net CO_2 influx of about $5.2\text{-}(2.7+1.1)/2 = 3.3\ mol\ m^{-2}\ a^{-1}$ while Nykänen *et al.* (1996b) measured a value for net CO_2 flux in a southern Finnish bog of about 2.0 for the six growing months. On the other hand the transfer to the catotelm (p′) is $2.0/5.2 \approx 40\%$, which may be a bit high.

For the values given above the net influx of carbon in CO_2 is 3.3 from which must be subtracted the 0.3 which is organic matter in solution on its way back to the atmosphere, i.e. a total of $3.0\ mol\ m^{-2}\ a^{-1}$. The efflux of CH_4 is about $(0.2+0.5)/2 = 0.35\ mol\ m^{-2}\ a^{-1}$. But every molecule of CH_4 has about 20 times the atmospheric warming potential of a CO_2 molecule and $20 * 0.35 = 7.0$, which is greater than the 3.1 removed. If these values are typical then peatlands, particularly those with a large proportion of wet hollows, may already be contributing to climate warming.

24.7 Conclusion

It has long been known that peat stratigraphy can be used to infer something about past climate, because the peat accumulating process reflects, to some extent, the climate. Now we can see that there is sufficient peat for it to be possible that peatland processes might affect the climate-changing potential of the atmosphere: the sequestering ability of peatlands diminishes with time though perhaps countered by an increase in area; and it is not clear whether the ordinary processes fixing carbon are more important or less so than the effective conversion of CO_2 to CH_4. In the worst case peatlands are already contributing to the temperature-raising potential of the atmosphere, and almost any alteration, except starting new peatlands, would increase this potential. The truth is probably less dramatic than the worst case, but we lack the data to be sure. Here is a worthwhile problem for the next century.

The bog moss, *Sphagnum*, is the most important constituent of the surface vegetation of northern peatlands and decays unusually slowly so it becomes even more important in peat. *Sphagnum* is thus at the centre of any discussion of peat accumulation. In quantitative terms it is the *only* bryophyte of any importance whatever, but (like the diarist Pepys, who became the first Secretary and main creator of the British Navy) its obscure family, were it able, might well be proud that one of their number had reached such absolute, as well as relative, eminence.

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