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The future of cool temperate bogs

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SUMMARY

The temperate peatlands are extensive, covering around 3.5 million km^2 of land. They contain about 455 Gt of carbon, almost equivalent to the carbon stored in all of the living things on the surface of the planet, and representing around 25% of all the soil carbon on earth. These bogs are a sink for atmospheric carbon and their carbon uptake accounts for about 12% of current human emissions. They vary considerably in their form and structure and are an important resource for scientific research, including the study of past environments and climate change, and they are also valuable in environmental education. They are low in biodiversity, but their fauna and flora are distinctive and many groups are confined to this habitat. For all these reasons, the future conservation of peatlands is a matter for concern. Threats to peatlands come from direct human exploitation in the form of peat harvesting for energy and horticulture, and drainage for forestry. Rising environmental awareness should control both of these processes in the western world, but continued northern peatland losses are likely locally, especially in Asia. Peatland drainage for forestry or agriculture will result in losses of carbon to the atmosphere, adding to the greenhouse effect. Human population pressures, industrialization and urbanization are unlikely to have an important direct and immediate influence in the boreal zone. Fragmentation of the habitat is not an important consideration because bogs are by their very nature 'island' habitats. Acidification by aerial pollution may be a local problem close to sources, but the habitat is naturally acid and should not be severely affected. The input of aerial nutrients, however, particularly nitrogen, could have widespread impact on bogs, enhancing their productivity and altering their vegetation composition. The physical rehabilitation of bogs damaged by human activities presents many problems, particularly relating to the re-establishment of peat structure and vegetation, but the process can result in the re-formation of a carbon sink so it is worth the effort. Climate change is the most important consideration in its impact on bogs. Higher temperature (especially if accompanied by raised atmospheric carbon dioxide levels and increased nitrate deposition) will enhance productivity, but will also result in faster decomposition rates. The outcome of these opposing factors for peat formation will ultimately depend on the future pattern of precipitation. If, as seems most likely, summer conditions become warmer and drier in continental regions and winters become milder and wetter, the summer drought could cause peat loss and bog contraction. An excess of decomposition will lead to bogs becoming a carbon source and thus a positive feedback in global warming. Emissions of methane and nitrous oxide would add to the greenhouse gas problem, but likely oxidation of methane and low N_2O production may well mean that this impact will not prove to be significant. Tree invasion of bogs as a consequence of summer drought could locally lead to increased water loss through transpiration, and higher heat absorption through albedo change. This will enhance the drying effect on the bog surface. Oceanic mires will be less severely affected if the expected increase in precipitation takes place in these regions. The most important overall factor in determining the future of the northern bogs is likely to be the quantity and pattern (both spatially and temporally) of future precipitation in the zone.

Keywords: wetlands, bogs, mires, climate change, human impact

INTRODUCTION

About 3% of the world's land surface is covered with wetlands (Dahl & Zoltai 1997), of which some 60% are forested. Peatlands are a type of wetland in which an organic soil of at least 30 cm depth has developed, and various calculations have been made concerning their global area (e.g. Gorham 1990). O'Neill (2000) comes to the conclusion that there are 353.4 Mha of peatland worldwide (see Table 1). Most peatlands (86.4%) are found in the temperate zone and of these 99.4% are located in the northern hemisphere. Gorham (1991) calculated that there are 346 Mha of northern peatland, having a mean depth of about 2.5 m (Clymo *et al.* 1998). O'Neill (2000) arrives at a very similar figure of 351 Mha (approximately 3.5 million km^2) of northern peatland. If

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Table 1 Global distribution of peatland areas. Based on O'Neill (2000).

	Area (Mha)	*% of global peat area*
Eurasia	180.2	44.1
North America	171.1	41.9
South Asia	43.6	10.7
South America	6.2	1.5
Africa	4.9	1.1
Central America	2.6	0.6
Australasia and Pacific	0.3	0.1
Total	408.9	100.0

all of these peatlands were brought together they could cover a square with a side of 1900 km. Most of these peatlands lie in the cool temperate zone, between latitudes 50°N and 70°N in Russia, Fennoscandia and north-west Europe, Canada and the United States of America, especially Alaska (Fig. 1). Canada alone is reckoned to contain 25% of the world's wetlands (Dahl & Zoltai 1997), almost 70% of which are forested. In the Southern Hemisphere, temperate peatlands are located in the lowlands of western Chile (up to 600 m altitude) (Pisano 1983) and scattered through Tasmania, south-eastern Australia, and New Zealand (Campbell 1983). There are also isolated peatlands on some islands, such as the Falkland Islands.

Peat-accumulating wetlands are conventionally divided into fens and bogs, or, more strictly, rheotrophic (flow-fed) and ombrotrophic (rain-fed) mires (Moore & Bellamy 1973). The word 'bog' comes from the Irish language and means 'soft' (O'Connell 1997). The scientific term 'bog' is normally confined to those peatlands that receive all their water supply directly from the rainfall and with no contribution from drainage water. In common parlance, however, the term is often used to describe acidic, nutrient poor peatlands that receive some through-flow of ground water. Wheeler and Proctor (2000) have proposed that acidity and low nutrient content is a more natural definition of bogs (as opposed to fens). It is easier to recognize the distinction on the basis of both chemistry of the waters and the composition of vegetation, whereas hydrological differences are often difficult to determine. Hydrological questions have also been raised concerning the possibility that some peat domes may receive water inputs from upwelling and capillarity, leading to an occult supply of nutrients to surface vegetation (Glaser *et al.* 1997; Moore 1997; Lamers *et al.* 1999). This leads to further difficulties in the recognition of true ombrotrophy that complicates the use of conventional terminology. It is convenient, therefore, to use the term bog here to encompass all acidic, low-nutrient, peat-forming ecosystems (mires). According to Masing *et al.* (1990) almost 60% of the northern peatlands are oligotrophic and could, in this broader sense, be regarded as bogs.

The considerable extent of the world's bogs and their range of specialist wildlife make them an important natural ecosystem that is valuable for the conservation of biodiversity. Their accumulations of organic materials, some of which may date back several millennia, and their properties of water retention result in their having global impacts on the cycling of carbon and of water. It has been claimed that the bog mosses (*Sphagnum* spp.) alone contain more carbon in their living and dead tissues than any other genus of plants, including trees (Clymo & Hayward 1982). It is vital, therefore, that we understand the nature and function of peatlands so that we can approach their conservation and management in an informed way, and so that we can predict the future outcomes of human exploitation, changing climate or management policies.

Peatlands are unique in that their gross ecosystem productivity exceeds the sum of their respiration, decomposition and biomass growth. The net surplus of carbon compounds becomes stored within the ecosystem as peat, so the growing peatland acts as a carbon sink in relation to the atmosphere. The excess of organic material within the ecosystem is a consequence of slow decomposition rather than unusually rapid productivity. The accumulation of dead organic matter in the 'soil' system has a number of implications. It creates structural modifications within the ecosystem, elevating the soil surface in relation to ground water. It modifies the hydrological relations of the surface vegetation. It leaves behind a sequential record of its own history in the plant and animal fossils within the stratified layers. Being sensitive to those factors (in part climatic) that influence decomposition rates, the peat stratigraphy can also act as a proxy for past climatic reconstruction. This unique type of ecosystem, therefore, presents important research opportunities in a variety of fields. The future of peatlands will depend on many varying factors. Increasing human exploitation for peat, drainage and afforestation, the impact of both water-borne and air-borne pollution, the effects of raised global temperatures on productivity and decomposition rates, the influence of changing patterns of precipitation, will all impact upon the cool temperate peatlands. The main aim of this paper is to examine the processes at work in peatlands, and to use this knowledge as a basis for predicting the likely outcomes of global changes in the coming two decades and assessing the likely state of the world's temperate bogs in the year 2025.

TYPES OF PEATLAND

The cool temperate peatlands fall into a number of different types (Moore & Bellamy 1973, Lindsay 1995). Ombrotrophic mires include raised bogs (including both forested and treeless varieties), some quaking bogs, and blanket bogs. Rheotrophic mires include fens and string 'bogs', the latter being strictly fens that may have ombrotrophic, acidic 'bog islands' within them (see Table 2).

Where the cool temperate zone abuts onto the Arctic, a range of tundra mires can be found. The patterned *polygon mires* of the high latitudes are mainly rheotrophic, with angular, polygonal pools surrounding flat mire expanses. They arise only within regions of permafrost and are mainly

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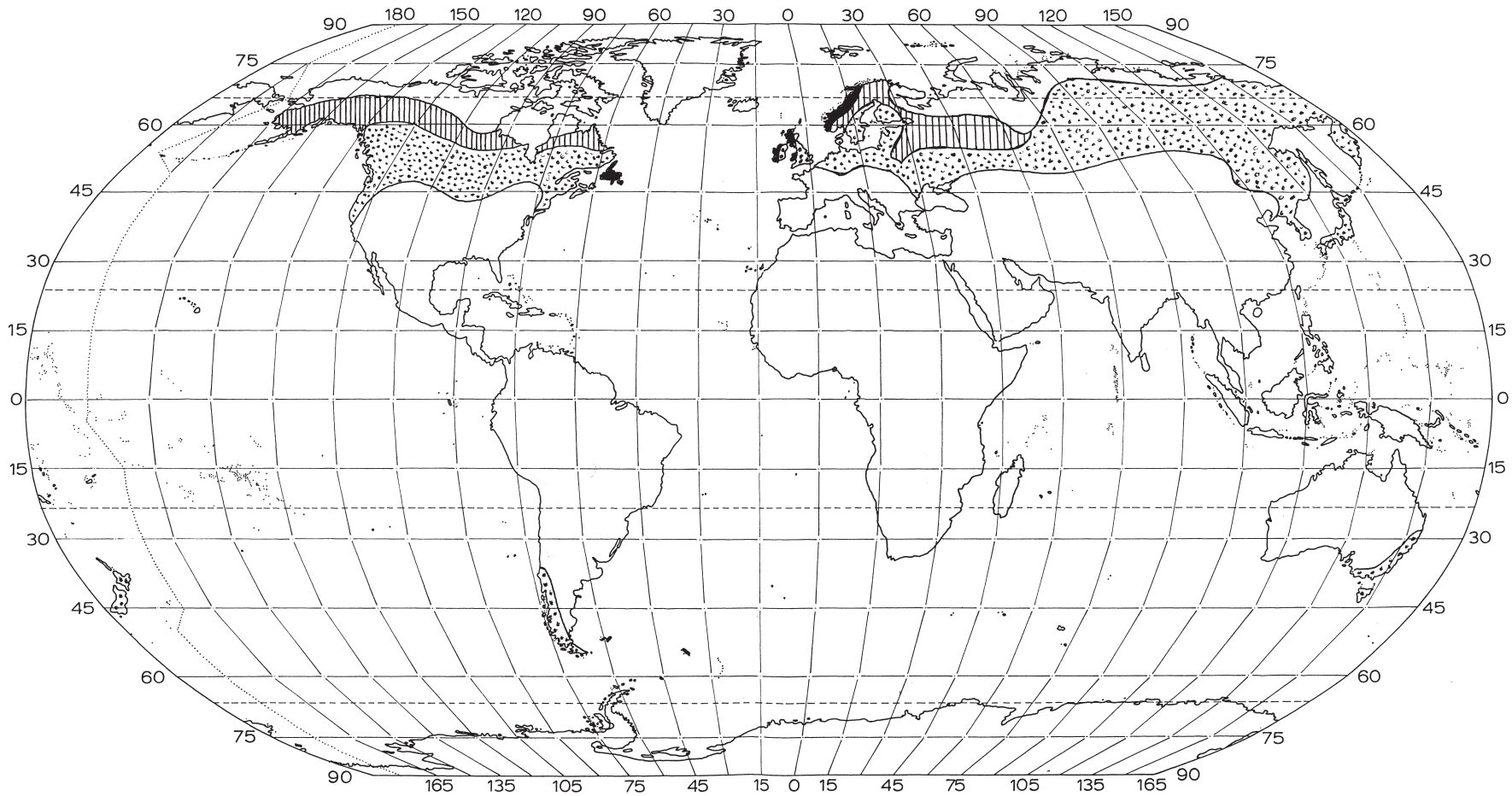


Figure 1 Distribution map of cool temperate mires. The major zones shown are as follows: Black = zone dominated by oceanic blanket mires; vertical hatching = zone dominated by aapa mires/ string bogs; stippled = zone containing a range of temperate mires with raised mires dominating in the oceanic regions and fens in the more continental regions. The area to the north of these zones contains tundra and palsa mires. Based on Moore and Bellamy (1973), Botch and Masing (1983), Gore (1983), and Masing *et al.* (1990).

Table 2 Types of cool temperate mires: their distributions and characteristic features.

Mire type	*Hydrology*	*Distribution*	*Features*
Tundra mires	Rheotrophic	Arctic and boreal permafrost areas	Polygon patterns
Palsa mires	Rheotrophic/ locally ombrotrophic	Northern boreal and Arctic	Elevated peat masses with ice cores
Aapa mires/ string bogs	Rheotrophic	Boreal regions	Linear strings and hollows aligned at right angles to slope and water flow
Raised mires	Ombrotrophic	Most frequent in the oceanic regions	Elevated peat domes, often several km in diameter
Blanket mires	Ombrotrophic	Only found in the extremely oceanic regions	Peat deposits clothe the landscape, even over gentle slopes
Valley mires	Rheotrophic	Throughout	Central streams or soaks have richest nutrient supply; lateral parts are poor in nutrients
Fens	Rheotrophic	Throughout	Topography-determined mires; nutrient chemistry supply depends on catchment and water flow
Quaking mires/ Schwingmoore	Rheotrophic/ ombrotrophic	In kettle-hole areas on edge of former ice sheets	Floating carpet of vegetation that eventually develops into ombrotrophic peat mound

found north of the Arctic Circle, as well as in parts of Siberia south of their normal limits (see Fig. 1). A further high latitude mire type is the *palsa mire*. These have an irregular surface consisting of elevated mounds of peat (up to 50 m in diameter and several metres high) with permanently frozen cores interspersed with areas of open water and sedge marshes. These are known to undergo cycles of formation and decay as the ice cores expand and collapse, leading to the creation of the pool systems. Palsa mires occur in European Russia, northern Scandinavia, and locally in the Labrador Peninsula in eastern North America. The elevated portions of the peat surface are well above ground-water influence and are essentially ombrotrophic in nature.

Aapa mires and '*string bogs*' form on gently sloping ground to the south of the palsa zone (Tolonen 1967). They are characterized by raised ridges running along the contours of the mire (at right angles to the slope), alternating with elongate pools. These patterns are most distinctive from the air, and there has been much discussion concerning the physical and biological causes of the patterns (Wright & Glaser 1983; Foster *et al.* 1983). They vary greatly in their degree of oligotrophy, depending on the geology of their catchments and the speed of flow of water. The aapa fens of western Russia and Finnish Karelia are relatively eutrophic, whereas the patterned mires of western Siberia and the continental region of boreal North America are more oligotrophic (Botch & Masing 1983; Masing *et al.* 1990).

Raised bogs consist of extensive domes of peat, elevated to a height of several metres above ground water influence. Their nature varies geographically across the continental land masses of the cool temperate zone. The bogs of the continental interiors often have summits of forest, sometimes radiating in lines (Glaser & Janssens 1986). The more northern continental raised bogs bear conifer forests, but a deciduous component becomes more important in the more southern regions, such as in the Great Lakes area of North America. Masing *et al.* (1990) calculate that the mixed deciduous/coniferous forested mires comprise 0.12 million km^2 of which 62% are oligotrophic. A further 0.14 million km^2 of mires in western Europe, North America, New Zealand, Chile and Tierra del Fuego carry deciduous forest, of which 19% are oligotrophic. The bogs of maritime, oceanic regions, such as the eastern part of North America, the Pacific Northwest and Alaska, and the western regions of Europe, are not forested, but are open plateaux and domes, usually covered with dwarf evergreen shrubs and with a ground layer of *Sphagnum* mosses. Non-forested bogs are also found in higher latitudes (generally above 51° N in the Hudson Bay region). Here the lack of trees is probably climatically determined.

These raised bogs are often of great antiquity. Surveys of large numbers of bogs in western Canada (Halsey *et al.* 1998; Campbell *et al.* 2000) indicate that the majority began by the paludification of forest approximately 7000–8000 years ago. Many of the raised bogs of oceanic western Europe have a similar age. In the case of the North American maritime bogs, the lack of trees is generally associated with greater age (Glaser & Janssens 1986). The forested condition of the more continental bogs may be an earlier successional stage that eventually leads to the treeless state, for these forested mires are generally younger than the maritime bogs. The ombrotrophic, forested mires of Minnesota, for example, are relatively recent in their origin, dating back only 2000–2500 years (Glaser & Janssens 1986). Raised bogs are also found in the southern hemisphere, in western Chile (Pisano 1983). They are dominated by *Sphagnum magellanicum*, but become increasingly forested to the north.

Blanket mires are ombrotrophic peatlands that develop only in highly oceanic areas where a combination of high precipitation and generally low summer temperature lead to

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an excess of soil moisture. The mires are treeless and cover plateaux, valleys and all but the steepest slopes. Most of the plateau blanket mires began forming between 3100 and 5100 years ago (Tallis 1998). Their initiation and development is often associated with evidence of human activity, particularly burning and grazing, and it is likely that prehistoric human activities contributed substantially to their development and spread within the appropriate climatic regions (Moore 1993). In very oceanic regions, such as western Ireland, western Norway and the Falkland Islands, blanket bog develops even at sea level.

Valley mire is a term applied to a range of topogenous (topography determined) mire types in which water supply is enhanced by catchment and accumulation on a valley floor. The expression is usually restricted to sites that are characterized by a central valley stream with lateral poor fens (Rose 1953) that may even become isolated from groundwater flow as a result of local elevation of the peat surface. In areas where the geology results in drainage water being of poor nutrient status, the rate of flow of water in valley mires is critical in determining the local nutrient supply. Hence, the central stream (fast flow) confers a relatively rich nutrient status, while the lateral fens (slow flow) have low nutrient provisions. The central steam area may become forested with wet-tolerant trees, such as alders and willows, while the lateral areas are usually herbaceous and often *Sphagnum* dominated, depending on water chemistry and flow rate. Topogenous mires of this type are found throughout the cool temperate and even into the warm temperate regions, especially at high elevation. Their initiation has occasionally been linked to human modification of valley soils, usually as a result of burning vegetation, erosion and the blocking of soil drainage properties by transported small carbon particles (Moore 1987). Topogenous mires are also found in the southern hemisphere, such as the buttongrass plains of Tasmania and the Restionaceae-dominated bogs of New Zealand (Campbell 1983).

Quaking bogs, or '*Schwingmoore*', are found in parts of Europe and, more frequently, in eastern North America. They are usually developed over steep-sided kettle-holes, formed by the melting of blocks of ice buried by till. They are initiated as oligotrophic lakes and, because of slow sedimentation, may continue in that state for millennia. They are eventually colonized by floating carpets of vegetation developing from the sides of the basin, which coalesce in the centre. This floating carpet can develop into a peat layer, several metres in thickness, and can even support the growth of trees. The centre of the mire may become sufficiently elevated to be effectively ombrotrophic in its hydrology and nutrient supply. The development of these mires seems to have taken place largely in historic times (Waterman 1926). Studies in Wales (French & Moore 1986) and in eastern North America (Warner *et al.* 1989; Warner 1993), indicate that a phase of agricultural eutrophication as a result of catchment cultivation may act as a stimulus for the development of the floating carpet.

The cool temperate 'bogs' are thus varied in their nature and their relationship with both the natural environment and the land management activities of human beings. It might be expected, therefore, that their response to environmental change will be equally varied. On the other hand, they have certain features in common, particularly their peat accumulation processes, and in this respect some general patterns of environmental response can be discerned.

ENVIRONMENTAL FORCING FACTORS

Sensitivity to physical environmental change

Peat-forming ecosystems are essentially unbalanced in their carbon budgets, having a net surplus that accumulates as peat. Whereas most terrestrial ecosystems have a carbon output (ecosystem respiration, *sensu* Odum 1969), that is equal to their gross production (unless the ecosystem is in a state of succession leading to biomass growth), peatlands have a rate of carbon accumulation that exceeds carbon output. Gross production is higher than ecosystem respiration (including decomposition) and the excess is stored in organic detritus, peat. The cool temperate peatlands are not notable for their high primary productivity (see below). Peat accumulation, therefore, is not so much a consequence of high rates of productivity, but rather of low rates of decomposition. But environmental change that alters the rate of either productivity or decomposition can be anticipated to influence the overall function of a peatland ecosystem.

In order to appreciate the impact of environmental change on either of these processes, it is necessary to consider the nature of the peat itself, and how its architecture, particularly in the upper layers where plants are rooted and most microbial activity is found, affects production and decomposition. It has long been recognized that the upper layer of organic deposit (often around 20–30 cm depth) of a mire is more frequently aerated than lower layers (Clymo 1965). A silver wire inserted into the peat becomes rapidly oxidized in the upper layer, but remains bright below. PVC tape inserted into a mire for 15 months becomes discoloured and also indicates the position of the oxidizing/reducing boundary (Belyea 1999). The upper zone has been termed the 'acrotelm' and the lower zone the 'catotelm' (Ivanov 1981). Living plant roots are generally more abundant in the acrotelm, and this is also the site of most microbial activity (especially fungi). Although anaerobic decomposition continues within the catotelm, the overall rate of decomposition is much slower than in the acrotelm.

The different properties of acrotelm and catotelm are a consequence of the architecture of the peat. The upper layers of growing mosses, living roots and uncompacted dead material are loose in structure and permit the free movement of water, both vertically and horizontally. Their hydraulic conductivity is high. Lower layers of peat consist largely of dead, compacted organic material (mainly plant-derived matter), which is permanently saturated with water and has a

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very low hydraulic conductivity. It is possible that the occlusion of interstitial pore spaces by bubbles of methane gas also contribute to this low hydraulic conductivity (Reynolds *et al.* 1992; Brown & Overend 1993). The hydraulic conductivity of the catotelm is generally around 1000–10 000 times lower than that of the acrotelm (Ivanov 1981). Lateral water movement, therefore, takes place largely through the acrotelm, and vertical drainage from the acrotelm is impeded by the low permeability of the catotelm

Obviously, low water supply, either through low precipitation or reduced catchment input to the mire, results in a lowering of the water table and hence of the boundary between acrotelm and catotelm. Such reduced water supply, however, can also result in the contraction of the acrotelm, leading to a smaller acrotelm in depth terms (Ivanov 1981). This permits the survival of surface vegetation during drought. *Sphagnum* is particularly important in this process because its elastic properties allow expansion and contraction with water availability. Essentially, the contraction of whole peat masses, particularly the acrotelm, is a mechanism that permits bog persistence in drought.

Changes in water table influence oxygen availability. Oxygen dissolves readily in water, but its diffusion rate in water is roughly 10 000 times slower than in the atmosphere. As a result, oxygen availability in a permanently waterlogged environment (such as the catotelm) is much lower than in a location with a fluctuating water table (such as the acrotelm). Not only is oxygen in short supply for root respiration, but the low redox results in the generation of phytotoxins such as Fe^{2+}, Mn^{2+} and S^{2-}. Wetland plants may also suffer from the byproducts of anaerobic respiration, such as ethanol, and must be metabolically adapted to cope with such stresses (Wheeler 1999). But plants also generate oxygen through photosynthesis and in some cases their tubular structures may carry oxygen to lower layers and enhance local oxygen supply. Even some mosses, such as *Scorpidium scorpioides*, may facilitate the growth of more waterlogging-sensitive plant species as a consequence of oxygen generation (Giller & Wheeler 1986).

Many wetland plants, however, although able to cope with excess water, are drought sensitive. They have inefficient control of water loss through stomata, higher rates of cuticular water loss through the leaves, poor vascularization, and often have poor root systems. So drought can reduce productivity and even cause death in wetland species if the water table is lowered too far. What constitutes a fatal lowering of the water table varies considerably with species, with timing, with associated temperature, and with the dependence of the plant on seedling recruitment, which may be particularly strongly affected (Wheeler 1999). *Sphagnum* species, with their sponge-like structure, have good water retention and survive surprisingly well through drought periods (Clymo 1997). This is particularly true of hummock-dwelling species, which often have fine leaves and a high degree of capillarity and water retention (e.g. *S. capillifolium*), while pool species (e.g. *S. auriculatum*) have poorer water-retention properties (Clymo 1973).

Factors affecting primary productivity

Primary productivity in boreal peatlands is generally measured by harvest methods, and root production is normally neglected. Figures for productivity from such methods usually range between 250 and 450 $g\,m^{-2}$ dry matter per year (Moore & Bellamy 1973; Thormann & Bayley 1997). The value varies with site factors and with vegetation, particularly depending on the presence or absence of forest. A study of black spruce (*Picea mariana*) productivity on the forested bogs of northern Minnesota (Grigal *et al.* 1985) showed that productivity of the trees on fully ombrotrophic raised bogs was 100 $g\,m^{-2}\,yr^{-1}$, while that on the partially rheotrophic 'perched bogs' was 310 $g\,m^{-2}\,yr^{-1}$. The trees were evidently favoured by additional nutrient influxes. In part, however, this effect was compensated for by the growth of shrubs (*Ledum* and *Chamaedaphne*), leading to overall productivity figures of 750 $g\,m^{-2}\,yr^{-1}$ on the perched bogs and 630 $g\,m^{-2}\,yr^{-2}$ on the raised bogs (Grigal *et al.* 1985).

Above ground biomass in boreal peatlands is generally variable, often ranging from 400 to 4000 $g\,m^{-2}$ (Moore & Bellamy 1973). Biomass is often related to water table, larger biomass being associated with lower water table. Root biomass has rarely been measured, but the value of 2000 $g\,m^{-2}$ may be fairly typical. High biomass peatlands generally have a higher productivity.

Productivity measurements using gas exchange methods in the field range between 0.15 and 0.35 mg CO_2 $m^{-2}\,s^{-1}$ (Frolking *et al.* 1998). Such measurements, however, are usually carried out in optimal conditions for photosynthesis (bright sunlight and relatively high temperature) so must be regarded as considerable overestimates of the potential of the ecosystem for overall carbon fixation.

The rate of productivity in a mire is often limited by the availability of carbon dioxide, (when light and temperature are not limiting) and experimental elevations of atmospheric CO_2 (usually in conjunction with raised temperature to simulate future climatic conditions), have usually resulted in enhanced productivity. For example, when sample plots of an *Eriophorum vaginatum* bog in Alaska were supplied with CO_2 levels of 680ppm (roughly double the natural level) together with a 4°C rise in temperature, carbon fixation by the ecosystem was enhanced in the first year (Oechel *et al.* 1994). However fixation subsequently declined, the likely explanation being that enhanced vegetation growth swiftly resulted in nutrient limitation to the system.

Nutrient availability in bogs, therefore, particularly nitrogen and phosphorus, may also limit primary productivity. Most plants in oligotrophic habitats are well adapted to low nutrient conditions. They often have efficient systems for the mobilization and recycling of elements prior to leaf fall, and many are able to take up nitrogen in the form of ammonium ions or even as organic nitrogen (Nasholm *et al.* 1998). This effectively short-cuts the nitrification process (which is oxygen demanding and is often slow in mires). Northern ecosystem productivity is generally considered to

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be nitrogen limited (Melillo *et al.* 1993), so the impact of raised atmospheric CO_2 levels in enhancing productivity may be less than expected.

Factors affecting decomposition

Factors that enhance decomposition rates are likely to result in the decline of peat deposits and the ecosystems that produce them. In general, decomposition is slower in *Sphagnum* bogs than it is in fens (Scheffer & Aerts 2000). Low oxygen availability as a consequence of waterlogging is an important factor in reducing decomposition rates. Most fungi are aerobes and their activities are therefore restricted to the acrotelm. Lowering the water table, therefore, would be expected to favour fungal activity and therefore to increase decomposition rates, as reflected in soil respiration. Experimental lowering of the water table in a bog by 15 cm led to losses of carbon from the peat that ranged from 4–157 $gC\,m^{-2}\,yr^{-1}$, being greatest in the hummocks and least in the hollow areas of the mire surface (Alm *et al.* 1999). Methane emissions from the deeper layers also increased by 4–7 times, especially in the lawns and hollows. On average, the total annual loss of carbon over the bog surface was 90 $gC\,m^{-2}yr^{-1}$ (Alm *et al.* 1999). Lowering the water table thus converted an atmospheric carbon sink into a carbon source.

An additional factor that contributes to the low decomposition rates of peatlands is the inhibition of the activities of many microbes by the phenolic compounds that are particularly abundant in peatlands. In aerobic conditions, phenol oxidase can operate to break down the cyclic carbon compounds; once the phenols (including polyphenols) are degraded in this way, their inhibitory effect on microbes is nullified and decomposition is enhanced. This enzyme does not operate under anaerobic conditions, however, and its activation may be the most important impact of increased oxygenation of peat masses when their water tables are lowered (Freeman *et al.* 2001).

Low temperature affects the rate of chemical, including enzyme-controlled reactions. Different enzymes have their various temperature optima and when temperature falls below these optima the rates of reactions will be slowed. Decomposition rates, therefore, will generally become slower as a result of any climatic cooling and enhanced by warming.

Low nutrient concentrations also contribute to reduced decomposition rates. Nitrogen limitation, in particular, can result in reduced decomposition (Hu *et al.* 2001), while elevation of nutrient inputs (particularly of nitrogen) is likely to stimulate decomposition.

Carbon balance

It is the degree of balance or imbalance between carbon sequestration via photosynthesis and its loss through respiration and decomposition that determines whether a mire is a source or a sink for atmospheric carbon. While peat is being accumulated in a bog, then, the balance clearly lies on the side of the sink role. In addition to the transfer of carbon from acrotelm to catotelm by litter burial, the downward movement of dissolved organic carbon in water seepage (see Fig. 2) may play an important role (Charman *et al.* 1994).

Peatlands generally sequester carbon at a rate of 19–30 $gC\,m^{-2}\,yr^{-1}$ (Gorham 1991: Vitt *et al.* 2000). Based on a study of 795 peatlands in Finland, Clymo *et al.* (1998) adopted a figure of 21 $gC\,m^{-2}\,yr^{-1}$ for the northern peatlands, and extrapolated from this to obtain a value of 0.7 $GtC\,yr^{-1}$ for the rate of sequestering carbon from the atmosphere by the peatlands. The size of this peatland sink for carbon is relatively small when compared with the 6Gt of carbon released into the atmosphere each year by human activities (Schimel 1995), particularly fossil fuel burning, but it is nevertheless a significant contributor to carbon sequestration from the atmosphere. As much as 12% of the human output of carbon into the atmosphere may find its way into the boreal peatlands and any environmental change that results in the decline of peatlands can thus have an impact on the global carbon balance.

Release of carbon from peat as a result of enhanced decomposition may not be in the form of carbon dioxide. Under conditions of low oxygen availability, especially in the presence of hydrogen carbonate ions, methane may be formed.

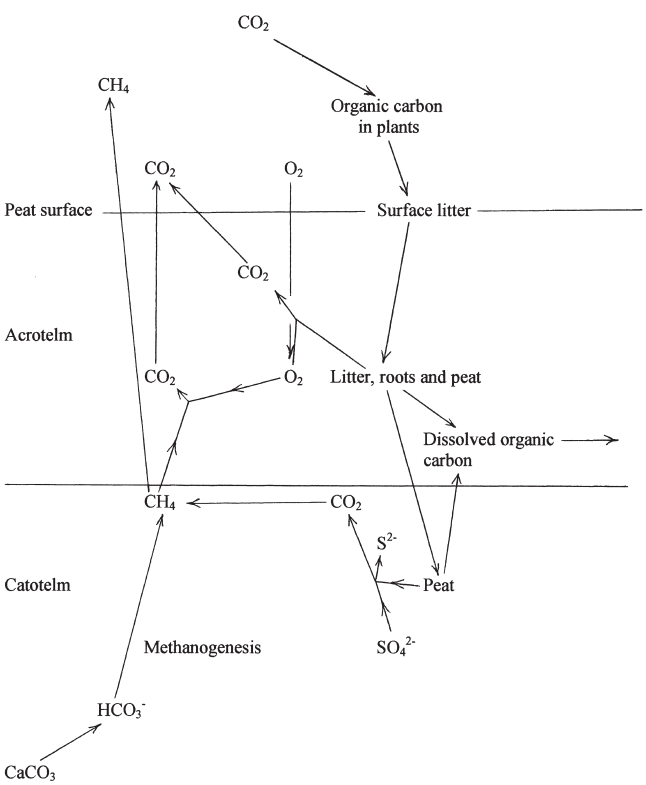


Figure 2 The paths of movement of carbon between the atmosphere, the acrotelm and the catotelm in mires. Calcium carbonate may be available from groundwater flow in the case of rheotrophic mires, and from sub-peat sediments in the case of ombrotrophic mires. The pattern of methanogenesis is based on Lamers *et al.* (1999).

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Masing *et al.* (1990) estimated that the peatlands north of latitude 40°N currently emit a total of 72×10^{12} g methane per year. If this is correct, then it represents about 15% of the total global release of methane to the atmosphere, including the various human sources, such as landfill, rice paddies, and natural gas leakage. Since methane is a greenhouse gas with approximately 30 times the efficiency for infrared absorption compared with carbon dioxide, this emission is a significant one for the global environment (Ashmore 1990). Even more important is the fact that atmospheric methane levels could rise strongly in the event of peatlands becoming drier (Alm *et al.* 1999), depending on oxidation rates. Experimental studies with isolated peat cores suggest that raised atmospheric carbon dioxide levels could lead to a doubling of methane emissions from a mire (Hutchin *et al.* 1995). Methane emissions from an intact, undisturbed mire, however, are likely to remain low because the gas becomes oxidized during its passage through the acrotelm. Methane output is actually greater from flooded surfaces such as beaver ponds (Brown 1997) rather than from dry sites. Lower water tables would likely result in more carbon dioxide production, but a reduced water table is not likely to increase methane output because this would enhance oxygen penetration and hence methane oxidation. There is, however, a possibility that the gaseous methane formed and stored (Brown *et al.* 1989) in deeper peats could leak from a mire in a dissolved form (Charman *et al.* 1994; Lamers *et al.* 1999).

Apart from being a sink for atmospheric carbon, the boreal peatlands are also a major terrestrial store of carbon. The northern peatlands have accumulated a total of 455 Gt of carbon over the past 10 000 years (Gorham 1991) amounting to an accumulation of $0.94\ \mathrm{GtC\,yr^{-1}}$, which is of the same order of magnitude as the $0.7\ \mathrm{GtC\,yr^{-1}}$ arrived at by Clymo *et al.* (1998) and using different methods of calculation. The carbon reservoir of the northern peatlands is similar to that found in all of the remaining living things of the earth, about 510 GtC (Schimel 1995). It is also equivalent to approximately 25% of the total carbon stored in the soils of the world. It is a significant carbon reservoir, therefore, and any factor that might result in the release of such quantities of carbon back into the atmosphere must be viewed very seriously.

Present human impacts

Human beings have had a generally negative impact on peatlands globally, at least in historic times. Also, while open water has the compensation of fisheries and a means of transport and communication, peatlands offer few attractions to human beings, so have often been regarded as wasteland. A widespread fear of peatlands in the human mind (Moore 2001) has often led to their wilful destruction, especially by burning. The most important human impacts on peatlands, however, are drainage for forestry and agriculture, harvesting peat, atmospheric pollution, and recreation and education. These impacts will now be reviewed.

Drainage for forestry and agriculture

Trees growing in wetlands, even those most typically associated with wet habitats, such as black spruce (*Picea mariana*) and tamarack (*Larix laricina*), generally extend their roots in the surface layers (often the upper few centimetres) of the soil where oxygen is more easily available for respiration. Lowering the water table in a peatland can result in faster growth and more timber production in these wetland trees (Macdonald & Yin 1999). In drainage experiments at Slave Lake, Alberta, there was an increase in growth, especially in black spruce, following drainage (Macdonald & Yin 1999). This fact of tree physiology is widely appreciated by foresters, who often resort to drainage of peatlands prior to their exploitation for timber or afforestation with timber trees (Paavilainen & Paivanen 1995).

Fifteen million hectares of peatlands have been drained for timber production in the boreal and temperate zones, more than 90% of which has taken place in Fennoscandia and Russia (Paivanen 1997). This is still common practice in some Baltic States, but in Finland and in Britain there has been a shift in emphasis from the extended drainage of virgin peatland to the maintenance of productivity of currently drained and forested sites (Paivanen 1997). Even so, less than 10% of Finland's original peatlands remain in a relatively natural state.

In Canada, drainage of peatlands for forestry is generally less common than in Eurasia and only 25 000 ha of peatlands have been drained for this purpose (Jeglum 1990). Canada also has a policy of harvesting only in winter and removing only boles of trees, but the latter policy is directed more at the conservation of nutrients within the ecosystem than the protection of habitats and wildlife (Jeglum 1990). Timber extraction inevitably causes damage to other vegetation and especially to peat soils, which become compacted and consequently have a lower hydraulic conductivity, especially if the acrotelm has been removed during afforestation (Brooks & Stoneman 1997). The outcome is often waterlogging, sometimes initiating wetland succession once again. The emphasis of forest managers in Canada and in Europe is generally away from pure forestry and towards multi-purpose use of forests, including hunting, fishing and recreation (Jeglum 1990). In this respect, the peatland forests may prove particularly valuable. Young forest growth and the borders of forests on peatlands are particularly favoured habitats for a range of bird species (Avery & Leslie 1990).

In Britain, planting policy for trees is moving away from the use of peatlands and 'low quality' agricultural land because such areas of low fertility are often of high conservation value. Instead, foresters are being encouraged to use better quality land (Anderson 1997). The argument that peatland drainage results in an increase in the atmospheric carbon load is also one that weighs heavily in this policy decision. It is in the oceanic regions, where trees are not a 'natural' feature of bog landscapes, that concern is most acute regarding the conservation implications of forestry. The rehabilitation of such originally treeless bogs by the removal

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of planted trees has been attempted, but the recovery of vegetation, peat structure and hydrological systems can be slow (Brooks & Stoneman 1997). The drainage and afforestation of blanket bogs can permanently affect the hydrology of soils so that subsequent waterlogging is impeded and recovery of the wetland is rendered very difficult (Anderson *et al.* 1995).

Drainage and use of cool temperate bogs for agriculture normally involve the stripping of peat prior to use, so are effectively an offshoot of the harvesting process considered below. Peatland agriculture has been concentrated on the southern fringes of the northern mire zone, as in western Europe and in the Great Lakes area of the USA and Canada. In the latter, for example, around 6.7 million hectares of peatland has been drained and used for agriculture (Williams 1990).

The structure and chemistry of peat has made it a valuable commodity in horticulture as a soil conditioner. The spongy structure, particularly of *Sphagnum* peat, provides good water-holding capacity and adds to the structural complexity of the soil. Its organic content, when mixed with soil, encourages the activity of soil invertebrates, such as earthworms, and also bacteria that encourage nutrient cycling processes. In addition, the chemical structure of peat, with its high content of polyphenolic compounds, gives to the soil extra cation exchange capacity that supplements clay minerals in retaining plant nutrients in the soil (Moore & Bellamy 1973). These valuable properties have led to the mining of peat deposits (Maltby 1986; Prince 1997; Moss 2001).

Harvesting peat

The peat produced by cool temperate bogs is of value as a horticultural resource, but also as an energy reserve. Consisting largely of organic plant material, it has a relatively high energy content and can therefore be used as a source of energy when combusted. Peat harvesting has been in operation throughout history, and the traditional method of hand cutting turf and stacking blocks to dry, is still used in many remote areas of Ireland, Scotland and Norway. The commercial application of the same principle is operated in several locations in western Europe, such as England and Germany. The more frequent commercial method in current use, however, is milling. In this process, the surface vegetation is removed, effectively taking away the acrotelm of the peatland ecosystem. The peat is then harrowed, after which it is allowed to dry before being sucked up by vacuum collectors. Catotelmic peat is then harvested until either silt or fossil wood becomes frequent and interferes with the quality of the product. The harvested site may then be reclaimed for agriculture or can be rehabilitated as a wetland, but the peat forming structure contained in the acrotelm has been lost by this stage, so rehabilitation is essentially the flooding of remnant, fossil catotelmic peat.

The harvesting of peat from cool temperate bogs has been particularly significant in Russia, Canada, northern Europe and especially Ireland. In Britain, around 94% of the lowland raised bogs have been severely damaged or destroyed by drainage and peat harvesting in the past century (Gosselink & Maltby 1990). In the Republic of Ireland, the government-sponsored *Bord na Mona* harvests peat at a rate of approximately 5 $Mt\,yr^{-1}$ for use as an energy resource in its peat-fired power stations (McNally 1997). In 1991, 14% of Ireland's energy requirement was supplied by peat, falling to around 7% in 2001 and expected to fall to 4% by 2011 (McNally 1997). Oil and gas are becoming proportionally more important energy sources. The non-renewable nature of peat as a power source limits its potential for future development, but it is still expected to provide as much power for Ireland as the combined renewable sources of wind and water.

The use of peat in horticulture is extensive. In the UK alone, approximately $1.5 \times 10^6\,m^3$ are used each year by gardeners, about 60% of which is supplied by the rapidly disappearing lowland raised bogs of Britain, most of the remainder being imported from Ireland (Doar 1997). The use of alternative soil conditioners and surface mulches, such as chopped tree bark from the forestry industry, and cocoa fibres from the chocolate industry may relieve the pressure on peat consumption (Pryce 1991). Bracken litter, which is available in abundance in many parts of the world, is a further possible alternative to peat as a mulch (Pitman 1994).

Atmospheric pollution

Ombrotrophic mires obtain their nutrient inputs from the atmosphere and from precipitation. *Sphagnum* mosses are generally dependent on nitrate deposition from the atmosphere for the supply of this element (Proctor 1995). But the plant species associated with ombrotrophic habitats are not by nature nutrient-demanding and can easily become ousted by more competitive species if the supply of nutrients is increased (Chambers *et al.* 1999). Atmospheric eutrophication as a result of human activities will inevitably result in subtle changes to peatland vegetation that may prove difficult to monitor and even more difficult to control or reverse.

A further source of pollution that has been implicated in the decline of some bogs is the injection of sulphur dioxide into the atmosphere as a result of industrial combustion of fossil fuels. In parts of the world where pollution is particularly heavy, such as the southern part of the Pennine Mountain chain in northern England, *Sphagnum* mosses have been practically eliminated from the landscape. It has been suggested that this effect has resulted from sulphur dioxide pollution, and field experiments with *Sphagnum* have shown that it quickly succumbs to the application of SO_2 in solution (Ferguson & Lee 1979). This effect is much more pronounced in oligotrophic conditions; plants with a more abundant mineral supply may rely upon transition metals to detoxify the impact of the dissolved bisulphite ions, oxidizing them to sulphate (Lee 1998). Increased sulphur content and decreased pH in precipitation, however, can influence nitrogen availability in the acrotelm (Sanger *et al.* 1996), thus

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complicating the observed response of mire vegetation to atmospheric pollution.

Recreation and education

The recreational opportunities provided by cool temperate peatlands are limited. In eastern Europe, the gathering of food resources such as berries (*Vaccinium* and *Rubus* spp.) and fungi attract some recreational attention. The use of peat in balneotherapy, which is reputed to be a tonic for the skin and complexion (presumably by suppressing bacterial and fungal activity), puts some local pressure on peatlands. The use of peatlands as a medium for ecological education is expanding because peatlands have much to offer as a source of ecological and conservation information and inspiration. In many respects they provide an ideal ecosystem in which to teach principles of ecology and conservation management. O'Connell (1997) stresses that environmental education involves not only the transfer of information from tutor to student, but also the modification of lifestyle and behaviour. In this respect, peatlands provide salutary subjects for education, for their history of exploitation at human hands is well documented and the outcome is clearly visible.

One of the major problems, however, in the use of peatlands either for recreation or education is the fragility of the habitat. The delicate structure of the peat surface, which is so necessary for the hydrological and gaseous exchange processes that interact to ensure the functioning of peatland vegetation, is easily damaged by physical pressure. A single footprint may not have fully recovered from the initial impact even 18 months after its formation (Slater and Agnew 1977). Although cosmetic recovery takes place within this time, the surface vegetation is modified by the experience for a much longer period. The use of peatlands for education or amenity, therefore, requires careful planning and management to reduce physical impact and the consequent destruction of the habitat.

Rehabilitation

The influence of humans on the cool temperate bogs is not entirely negative. In recent times, awareness of the rapidity with which such habitats have been disappearing from the landscape, particularly in western Europe, southern Canada and the northern USA, has led to much effort in the sphere of rehabilitation (Wheeler *et al.* 1995). The process of rehabilitation requires the restoration of a high water table (following drainage), removal of trees (following afforestation), and the restoration of the peat-forming vegetation (following peat harvesting and the loss of peat surfaces).

The simplest method of restoring high water tables is to dam discharge channels. Peat itself is effective as a tool for this operation, especially catotelmic peat that has a low hydraulic conductivity. Recovery following the damming of drainage channels in cut-over raised bogs is slow (Mawby 1995). Cut-over bogs have a greater amplitude of water-table fluctuation than undisturbed bogs, and this condition persists even when damming has taken place. Seepage of water from dammed drainage ditches is also a problem, and has led to a failure to maintain high water tables in some rehabilitated bogs (Heathwaite 1995).

Rehabilitation also demands the re-establishment of former vegetation, and this can be a problem in cut-over bogs, partly because there may be little of this left surviving and partly because the residual peat surface (being catotelmic) has a very different physical nature from the original surface. Replacement of conserved surface layers of vegetation meets with limited success. The survival of plant fragments or seeds in the peat is unlikely if any great depth of peat has been cut. It is likely to be the rarer species, especially those with limited powers of dispersal, which are lost. The use of *Sphagnum* fragments as an 'inoculum' in cut-over sites does improve recovery prospects (Money 1995).

An alternative approach is to flood the cut-over surface and recommence the succession process from an open water stage. This is more likely to meet with success if the leakage problems can be overcome, but the time needed to recover an ombrotrophic mire will run into millennia, since this is the length of time they have taken to form in the past (Godwin 1981). There is also the problem that such flooded ecosystems tend to become sources of methane.

IDENTIFIED LONG-TERM TRENDS

Peatlands have some advantages over other ecosystems when attempts are made to identify long-term trends. In the deposits that underlie them, peatlands record their own histories in the form of stratified sediments. Organic materials, in particular the fossil remains of plants, provide a record of successional development (e.g. Godwin 1981), changing hydrological conditions (e.g. Succow & Lange 1984), changing nutrient status (e.g. Moore *et al.* 1984) and even climatic shifts (e.g. Barber 1981). The study of stratigraphy, therefore, provides a solid source of historical information on the basis of which projections into the future can be made.

Care must be exercised, however, in the interpretation of observed changes, particularly in hydrology, because a variety of factors can operate and interact in the underlying causes. The initiation of peat deposition, for example, can be interpreted in terms of increasing wetness, but the hydrological shift in a groundwater-fed system may in fact be due to a variety of factors (Moore 1993). Changing drainage patterns may bring more water to a site; changing land use in the catchment (such as forest clearance) can have the same effect; and changing climate can also be involved.

It is known from palaeoecological studies that there have been shifts in biome boundaries and in peatland types over the past 10 000 years (Tallis 1991). The fact that so many raised bogs in North America and Europe developed from a rheotrophic to an ombrotrophic state around 7000 to 8000 years ago suggests a widespread and general cause rather than a local one (Godwin 1981). On the basis of palaeoecological data, considerable climatic changes have been taking place in

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the last 20 000 years and continue to take place. Climate models have been developed from fossil data for selected dates in the geologically recent past (18, 12, 9 and 6 thousand years ago and present) (COHMAP Members 1988). Between 6000 and 8000 years ago conditions in the boreal zone are considered to have been warmer and wetter than at present (Beck 1998). The situation at 6000 years ago represents the warmest set of global conditions experienced since the last glaciation (Cwynar & Spear 1991), with temperatures between 2°C and 4°C higher than at present in the continental interiors of North America and Eurasia. Subsequently temperatures have fallen, and this has had a marked positive effect on the cool temperate peatlands. It is during this time that most of these peatlands have developed and spread.

Blanket mires in western Europe have extended southwards during the past 6000 years, which is likely to be in part due to climatic shifts, but is made more complex by the impact of human activities in forest clearance during that time (Moore 1993). The loss of tree cover, especially in oceanic environments, leads to increased groundwater and can result in the initiation of peat growth where the ratio of precipitation potential evaporation is sufficiently high. Such has been the case in Wales and parts of Scotland, Ireland and lowland western Norway (Kaland 1986). In Minnesota, ombrotrophic peatlands have an origin dating only to the past 2000 to 2500 years (Glaser & Janssens 1986), so the development of these peatlands has taken place relatively late in the Holocene and since the post-glacial climatic 'optimum'.

The boreal peatlands, therefore, have mainly developed in the last few millennia and much of their success must be regarded as a consequence of the lower temperature and higher precipitation experienced in these recent times. Based on the thesis that a higher index of precipitation to potential evaporation will result in faster bog growth, and supported by models of bog architecture (Ingram 1982) and peat accumulation (Clymo 1984), attempts to study the relationship between bog growth and climate have proliferated recently, usually with a view to reconstructing palaeoclimate (e.g. Chambers 1997; Ellis & Tallis 2000). Ombrotrophic mires are clearly the most suitable for this type of study as they may be expected to respond directly to climate and not to changes in groundwater movements that can have local causes. Such studies can, however, be confused by small-scale patterns of hydrology on bog surfaces, such as pools and hummocks (Barber 1981). Nevertheless, a pattern of evidence for climatic shifts is emerging, particularly in European studies, which generally ties in well with other evidence for past climate changes.

It is clear, therefore, that the cool temperate bogs have changed in their extent and in their nature as a consequence of the climatic changes of the past few thousand years. The fact that these long-term trends in response to changing climate are now documented provides an appropriate base for the development of predictions regarding the future of these bogs in the coming decades. An alternative technique for prediction lies in the modelling of current mire distribution in relation to known climate variables and to extrapolate from such data. For example, a model has been developed that is based on the difference between precipitation (P) and potential evapotranspiration (PET) that is almost 90% accurate in predicting the current geographical distribution of *Sphagnum*-dominated mires in western Canada (Gignac *et al.* 2000). Where P minus PET fell below 6 cm, no peatlands were found. This finding provides a sound basis for predicting peatland extent in any given future scenario.

A further topic that requires attention is the response of bogs to additional aerial nutrient inputs. Industrial and agricultural activities, together with land and air transport, are all contributing to an increasing load of nitrogenous compounds in the atmosphere, both oxides of nitrogen and ammonium ions (Lee 1998). Ammonia and nitrates are highly soluble and are washed out of the atmosphere by rainfall, thus enriching the nutrient supply to terrestrial vegetation. Such inputs are of particular significance to ecosystems dependent on rainfall for their nutrient supply (such as epiphyte communities as well as ombrotrophic mires). Bogs are low in nitrate, mainly because of the high level of denitrification associated with such an anaerobic environment, so the additional input can have a strong impact both on the vegetation of such mires and their microbial populations (Lee 1998). The increase in the grass *Molinia caerulea* in blanket mires to the west of Britain, for example, is a feature of very recent origin and appears to be correlated with industrial growth and nitrogenous air pollution (Chambers *et al.* 1999). The decline of heather, *Calluna vulgaris*, and of *Sphagnum* species, in such regions as the British southern Pennine Mountains, are also influenced by nitrate deposition, but here pollution with sulphur is a further cause of vegetation degradation (Ferguson & Lee 1979).

Just as bogs may act as a sink for air-borne nutrients, so they can serve as a reservoir and a possible source of such elements. Although peats are relatively poor in nitrogen, peat decomposition resulting from drying and aeration can lead to the release of this element into the atmosphere. Often this release takes place in the form of nitrous oxide (N_2O), which is a significant greenhouse gas. Martikainen *et al.* (1993) compared the nitrous oxide emissions of virgin and partially drained peatlands in Finland, however, and came to the conclusion that the rate of emission resulting would not be significant on a global scale (about 1% of total global output).

POTENTIAL STATUS OF BOGS IN 2025

Predicting the future state of the cool temperate bogs demands information concerning how this habitat has responded to change in the past, how the future global environment will develop, and how the habitat will respond to such change. The first of these is perhaps better known in the case of bogs than in most other habitats because of the stratigraphic record they leave behind. Such information should assist in the third process, estimating the response to future change. The remaining unknown, the future state of

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the global environment can only be estimated by extrapolation from current trends.

The global population by 2025 may well be 25% higher than at present (United Nations 1998). But, in the areas of the world where the northern peatlands are found, the population density may not be very different from the present day. Population growth in Canada, northern USA, northern Europe and Siberia is relatively stable compared with that in lower latitudes (United Nations 1998). The likelihood is, therefore, that there will be little loss of temperate peatland simply as a direct consequence of human population pressures on space. Urbanization is not very likely except in centres where oil exploration may become more significant, or where the forestry industry is centred. The boreal zone as a whole has little attraction for industrial and hence urban development.

Human demands for resources other than space, however, may well place pressures on the temperate bogs. The demand for peat in horticulture will undoubtedly continue for some years, but public pressure from conservation groups will undoubtedly lead to an increasing demand for peat substitutes. Commercial horticulture is already turning from the use of peat as more appropriate (and sometimes cheaper) alternatives come onto the market, and it is likely that gardening interests will follow suit (Pryce 1991). Peat extraction for these purposes will be limited to some extent by economics, including transport costs when the extraction of peat from remote regions of Siberia and Canada is considered. The bogs most at risk are those on the southern fringe of their distribution, particularly in southern Canada and the northern USA, plus Europe (Maltby 1986).

Peat supplies for power will come under pressure when sources of other fossil fuels are either exhausted or so expensive that the peat alternative is economically viable. In North America, this is unlikely to occur in the next 25 years because of the continuing availability of conventional fossil fuels and the expense that would be involved in the draining, mining and transportation of peat from the boreal zone of Canada. There will, however, be local pressures on peatlands south of the boreal zone, as in Minnesota and in North Carolina (Maltby 1986). Projections in northern Europe, such as in Ireland, suggest that the proportion of energy derived from peat is likely to fall rather than grow in the coming years. Fourteen per cent of the electricity generated in Ireland in 1991 came from peat combustion and this is likely to fall to 4% by 2011 (McNally 1997). Russia constitutes a major area of temperate bogs in which peat exploitation for power is likely to be a significant threat to this habitat. There are already over 70 peat-fuelled power stations operating in Russia and the transport costs of alternative fossil energy are likely to be so great that peat exploitation remains economically viable in the north, perhaps even attractive (Moore & Bellamy 1973). The use of biomass fuel based on tree growth in Siberia is the most reasonable alternative, and this will undoubtedly develop, despite the possibility that the global atmospheric carbon balance could be modified by any overall loss in forest biomass (Denning *et al*. 1995). There is no technical reason, however, why peat exploitation and forestry should not proceed in concert, since cut-over bog could provide an appropriate base for the cultivation of fast-growing biomass crops. The Russian bogs are therefore at risk from this form of exploitation and development.

The loss of peatlands as a result of peat harvesting or drainage for reclamation will affect the general distribution pattern of this habitat. In some types of habitat, such as forest, piecemeal destruction can result in fragmentation and this in turn can lead to problems of species movements between sites (Collingham & Huntley 2000), genetic isolation, and often to genetic impoverishment as a result of the accumulation of harmful mutations. In the case of peatlands, however, fragmentation is already a part of the system in which species have evolved (Moore 1990). Raised bogs, in particular, develop largely in isolation from one another and the species that inhabit raised bogs must be able to colonize new locations from afar (Moore 1982). In the case of plants, this generally means that the seeds must be small and either wind-dispersed or carried in the gut of a mobile animal, usually a bird. Rheotrophic wetlands have no problems of isolation because they are usually linked by water-flow systems, so their plants generally have large, water-borne fruits and seeds (Moore 1990). The consequence of these geographical features is that fragmentation and subsequent recolonization in isolated locations is unlikely to be a serious problem. Perhaps more serious is the fact that cut-over sites have such different physical conditions associated with them that colonization and establishment becomes difficult for adventive propagules of dispersed plants (Money 1995).

The rehabilitation of damaged mires, although fraught with problems, can be effective in the re-establishment of a carbon sink. In southern Finland, the restoration of *Eriophorum vaginatum* at a drained ombrotrophic site led to its becoming a carbon sink with the capacity to absorb 54–101gC m^{-2} yr^{-1} (Koulainen *et al*. 1999). At untreated sites, carbon uptake was close to zero. This should encourage conservationists to make the effort to recover damaged and even destroyed peatlands.

Air pollution, including acidification, sulphur enhancement and nitrate enrichment, is likely to continue and will influence the development and survival of the cool temperate bogs. Acidification will lead to poor fens becoming more oligotrophic; even rich fens may become acidified (Beltman *et al*. 1995), despite being buffered by ground water sources of calcium carbonate. It is possible that there will be a more marked contrast in vegetation with microtopography even in rich fens, for even a few centimetres in elevation could cause a considerable change in local pH and hence in vegetation (Bellamy & Rieley 1967). Patterned fens, therefore, particularly in areas most influenced by industrial aerial acidification (such as Fennoscandia and eastern Canada) could develop yet more contrasting vegetation patterns as strings and hummocks become further acidified (Eurola *et al*. 1984).

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Ombrotrophic mires are already acidic in reaction and, unless sulphur deposition becomes extremely heavy, are not likely to be affected. While the pH of the soil surface remains above 3, the sphagna are unlikely to suffer damage from acid rain: nitric acid deposition, however can create problems for *Sphagnum* (Lee 1998).

Climatic changes in the next two decades are very likely (IPCC [Intergovernmental Panel on Climate Change] 1996), but the precise set of conditions that can be expected in the cool temperate zone in 2025 is difficult to predict and will undoubtedly vary geographically around the zone. Warming is to be expected, and this is likely to be higher within the latitudes 40°N to 70°N than at other latitudes, if current trends continue (IPCC 1996). The rise in temperature could be as much as 1.5°C greater than at present, but is more likely to be around 0.5°C by the year 2025. The observed rise in temperature in recent years appears to be tracking the lower projected temperature rise rather than the upper one (Wigley 1989), possibly because sulphate aerosols are acting as a brake upon global temperature rise (IPPC 1996). The implications for bogs of such a temperature rise in the higher latitudes, however, can be fully appreciated only if the precipitation picture is known (Hilbert *et al.* 2000).

A rise in temperature alone would be expected to increase both productivity and decomposition rates, because any such rise would increase the rate of enzyme activity in high latitudes. It could also result in a poleward movement of some species. Deciduous trees would become more common in the zone of mixed forested mires, and conifers would move further north into the tundra zone. Trees generally might be expected to increase in abundance on mire surfaces, which could affect the evapotranspiration rate, leading to the drying of surface layers (Chambers 1997), but this possible impact is in dispute. The overall effect of these events, however, depends upon the future of precipitation in the cool temperate zone, which has proved difficult to predict (Rind *et al.* 1992). Precipitation is the vital factor in determining the rate and the pattern of peat formation in these ecosystems (Hilbert *et al*. 2000).

The trend over the past 13 years has been one of higher precipitation over the higher latitudes, especially during winter (IPCC 1996). Combined with higher temperatures, this has led to less snow cover, meaning a longer growing season for the vegetation. Again, the implications of this scenario, if the trend should continue into the future, are difficult to predict unless certain assumptions are made about the seasonal pattern of precipitation. Perhaps the most likely detailed scenario, particularly for the continental interiors, is that summers will become warmer and drier, while winters will become milder and wetter (see Moore *et al.* 1996).

In general, the warmer spring and summer should lead to an increase in growing-season length and, in particular, to an earlier spring start to plant growth. This in turn should lead to elevated primary production. A rise in plant productivity could be further enhanced by the raised carbon dioxide levels in the atmosphere, although other limiting factors such as nitrate or phosphate availability could intrude and set a ceiling on any rise in productivity. A longer growing season, however, especially if accompanied by spring rain, could be harmful to vegetation. Rain falling on frozen ground leads to ice encasement that can damage early growth in plants (Crawford 2000). This would be particularly important in the continental mires. It is possible that higher temperature would also result in faster decomposition, leading to less rapid movement of carbon from the acrotelm to the catotelm for more permanent storage. This means that a bog would be a less efficient sink than had formerly been the case, but the balance of productivity to decomposition is the critical factor, and this would be dependent on moisture levels as well as temperature (Hilbert *et al.* 2000).

Perhaps the most critical set of conditions to affect the status of cool temperate bogs would be that of a combination of higher summer temperature and lower rainfall. Summer drought would certainly have a profound effect on bog growth; low water tables in summer would not only reduce carbon movement from acrotelm to catotelm, they could result in the movement of carbon in the opposite direction (Warner *et al.* 1993). Bogs could be transformed from a sink for atmospheric carbon into a source of carbon. Methane production under such circumstances would be a particularly serious feedback mechanism because of the high infrared absorption capacity of this gas. Bogs contain a reservoir of methane gas in the catotelm (Brown & Overend 1993) that can be released when the peat is disturbed. Increased CO_2 levels in the atmosphere can also stimulate the production of methane (Hutchin *et al.* 1995). But increased methane production may be counteracted by enhanced oxidation both in the catotelm (see Fig. 2), where interaction with sulphate ions could result in oxidation to CO_2 (DeLong 2000), and in the acrotelm (Lamers *et al.* 1999). Whatever the resulting balance in methane production and oxidation, carbon loss to the ecosystem is likely to be greater under a combination of warmer and drier conditions (Carroll & Crill 1997; Alm *et al.* 1999). The release of all the 455 Gt of carbon held in the terrestrial peat deposits (Gorham 1991) would raise atmospheric levels of CO_2 by about 60%, thus adding significantly to the overall greenhouse effect. This, however, would take a long time to achieve, and is an unlikely, extreme scenario. Any release of CO_2, however, particularly if accompanied by methane and nitrous oxide, would add to the greenhouse effect.

It is salutary to look back in time to seek patterns against which such a scenario could be tested. The situation 6000 years ago could be helpful in this respect (COHMAP Members 1988). Boreal mires were much scarcer at that time and more confined in their distribution. If the conditions of 6000 years ago, including higher temperature (around 2°C), and lower summer precipitation, were to be restored, then a reversion of the northern peatlands to their former scarcity is to be anticipated. Any move in the direction of raised temperature and lower summer precipitation would cause such decline to commence. The positive feedback caused by

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carbon emissions into the atmosphere would enhance the climatic shift and accelerate the decline.

Drier summers would also encourage the growth of trees on the mire surface, possibly leading to faster water loss from those mires, but the increase in the overall biomass of the ecosystem as a result of enhanced tree growth would compensate to some extent for the loss of the carbon reservoir in the peat. This uptake of atmospheric carbon, however, would occur only while the afforestation of the mire surface was in progress. There is an additional consideration in the case of tree cover becoming established in formerly treeless environments, and that is change in albedo. The development of forest over land that has formerly been devoid of trees leads to a decrease in albedo, especially where snow-lie is frequent (Betts 2000). On the basis of a 2°C temperature rise, albedo changes associated with tree invasion of boreal mires could result in heat absorption equivalent to a further 4°C in spring and 1°C at other seasons (Foley *et al*. 1994). Since black spruce and other trees could respond rapidly to new conditions (Pastor 1993), this feedback effect could enhance the changes associated with temperature rise.

The oceanic mires of western Europe might be expected to behave differently from the more continental regions. Over the past 30 years there has been an increase in the index for the North Atlantic Oscillation, associated with increased precipitation to western Europe (Bianchi & McCave 1999; Crawford 2000). If this continues, then the blanket bogs of the west may escape significant change despite any rise in temperature. On the other hand, the location of blanket bogs, on slopes and plateaux where drainage is most effective, leaves them very sensitive to climate change (Ellis & Tallis 2000). Much also depends on the maintenance of pastoral regimes and a change in grazing patterns could lead to bracken or scrub invasion of some areas (Chambers 1997).

Drying of mire surfaces in both the continental and in the oceanic regions will render them more susceptible to fire (Tallis 1987). This can have a marked influence on species composition and on the growth of bogs, reducing their efficiency as carbon sinks. In the case of blanket mires it can also contribute to erosion and large-scale peat loss and oxidation (Tallis 1985)

CONCLUSIONS

There are many unknowns involved in the prediction of the future of the cool temperate bogs, some related to the precise nature of future conditions and others related to the ecology of the peat-forming process itself, or to future patterns of precipitation.

More efficient modelling of peat-forming ecosystems is also required if the future of bogs is to be adequately predicted. Current models (Clymo 1984; Clymo *et al*. 1998) have been developed and largely tested on oceanic raised bogs and need to be expanded to cope with continental bogs and also to deal with more minerotrophic peatlands. Basic to any modelling or understanding of bog function is a more thorough knowledge of the decomposition processes of peatlands and, in particular, the interactions in the acrotelm and the movement of carbon into the catotelm. This is currently poorly understood. Associated with this is the behaviour of methane in these layers and the extent to which it may escape from the bog surface or become oxidized in its passage through the acrotelm. Until such detailed processes are understood at the micro-scale, predictions at the macro-scale are bound to lack precision.

Threats to the cool temperate mires over the next 25 years can be regarded as human induced, either directly in terms of habitat destruction and exploitation, or indirectly as a consequence of climate change. The direct impacts are likely to be geographically localized, concentrated in northern Europe, parts of Russia, southern Canada, and in parts of the northern USA. Climatic impacts will be more general, but are likely to be most severe in the continental interiors of Canada and Siberia.

Destruction of peatlands for horticultural and energy-extractive purposes will continue, but pressures are already being placed upon governments in North America and Europe to limit and reduce the rate at which such activities continue (Foss 1997). Much damage has already been done, especially in Europe, but sites now enjoying protection should survive.

The draining and use of peatlands for forestry is largely confined to Europe, and this practice is already declining. Again, much peatland has already been lost in this way, but the situation should not get much worse. The issue of carbon controls now has sufficient prominence to encourage governments to avoid unnecessary transfers of carbon from soil to atmosphere.

The recreational and educational use of peatlands will not cause excessive damage to the surviving bogs, but needs to be managed in a sensitive manner. The gains from such activities in terms of public awareness and sympathy are worth the risks of localized disturbance and damage involved (O'Connell 1997).

Air pollution, especially the aerial deposition of sulphur and nitrates, will continue and, in the case of nitrates, probably increase. Where such impact is greatest, that is close to emission sources, not only will the vegetation of bogs become modified, but the loss of key species, such as the *Sphagnum* mosses, may result in degradation and erosion (Lee 1998). Over more extensive areas the deposition of nitrates will add to the productivity of bogs, enhancing the effect of rising atmospheric carbon dioxide.

Higher levels of fertilization and hence primary productivity will encourage vegetation changes, favouring competitor species over species tolerant of stresses (Grime 2001) such as low nutrient conditions, waterlogging, and anoxia. Higher productivity will not necessarily mean higher rates of peat formation and therefore carbon sequestration. Higher biomass species will become increasingly important, including tussock-forming grasses and sedges (Chambers *et al*. 1999), together with water-tolerant trees. Sensitive

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species, particularly those that do not tolerate shade will decline and may be lost in this process. Birds, mammals and insects are likely to find appropriate breeding and feeding sites in other locations further north (Hill *et al*. 1999).

The anticipated global rise in temperature will impact upon mires largely via (and in conjunction with) associated changes in precipitation. If continental interiors become both warmer and wetter, then peat formation may well continue, but if the summers are dry, then decomposition rates will rise and peat loss will commence. In such a scenario, the bogs will become a source rather than a sink of atmospheric carbon. The picture with respect to methane production is unclear, but if oxidation processes in the soil are adequate, then methane output may not become a threat. Oceanic regions are less likely to suffer summer drought, indeed, summer rainfall may increase, in which case the bogs of these regions should not suffer damage.

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