Sphagnum peatland distribution in North America and Eurasia during the past 21,000 years

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Abstract. The distribution and abundance of Sphagnum spores in North America and Eurasia are mapped for the past 21 ka. The present-day distribution of abundant Sphagnum spores corresponds closely to areas with peatland development, with maximum Sphagnum abundance between 630 and 1300 mm annual precipitation and between −2° and 6°C mean annual air temperature. During the Wisconsin glaciation, there were apparently large areas of peatland in North America, except in Alaska. High Sphagnum spore percentages were found in eastern North America during deglaciation. Major peatland development occurred in boreal North America after 9 ka and there was a southward movement of high Sphagnum spore abundance after 5 ka in the western Great Lakes region. Major peatland development began after 9 ka in Europe and Asia. On the basis of maps of the area supporting peatlands, carbon accumulation in peatlands is estimated to be low prior to 11 ka, increased slightly between 11 and 5 ka, and greatly increased during the past 5 ka.

1. Introduction

Since the last glacial maximum (LGM), there have been many biogeographic changes on the Earth’s surface. The migration of the major tree species has been analyzed in some detail, especially in North America and Europe where there are extensive networks of pollen data [e.g., Webb et al., 1998; Prentice et al., 1998]. These studies emphasize the development of upland vegetation, but less is known about the development of wetlands and peatlands. Understanding the development of the lowland vegetation is important because peatlands are important components of the carbon cycle [e.g., Gorham, 1991]. Sphagnum is a characteristic taxon of peat bogs, and the rests of this moss make up much of the biomass of a bog. In the boreal zone, bogs and fens store large amounts of carbon in peat deposits that have accumulated up to 5–6 m or more during the postglacial.

A number of attempts have been made to reconstruct variations in carbon storage since the last glacial maximum. However, estimates have varied considerably [Crowley, 1995], and this is due in part to assumptions about the distribution and nature of the vegetation at full glacial. These studies typically reconstruct ecosystem classes defined by some criterion. Carbon estimates are then assigned to the classes to compute changes in storage (reviewed by Peng et al. [1998]). However, boreal peatlands are a major source or sink of carbon. Peatlands have not been rigorously included in previous reconstructions of biomes [e.g., Peng et al., 1994, 1998; Prentice and Fung, 1990], probably due to lack of quantitative data on peatland distribution through time. Acknowledging this uncertainty, Adams et al. [1990] assumed there were few peatlands at full glacial because of the cooler and drier climate, a conclusion questioned by Crowley [1995].

In this paper, we investigate one aspect of the biogeographic changes through the glacial-interglacial transition, the distribution of Sphagnum peatlands. We present maps of the spatial patterns of Sphagnum spores for several time intervals to indicate the distribution of peatland limits through time. Although the emphasis of this study is North America, we present some results from the entire Northern Hemisphere. Peatlands are ecosystems that sequester carbon through peat accumulation, owing to greater rates of biomass production than decomposition [Kubry and Vitt, 1996]. Because oxygen supply is low in these water-saturated organic soils, decomposition is very slow [Moore and Bellamy, 1974]. Boreal and subarctic peatlands store an estimated 455 Pg of carbon, which is approximately one third of the global soil carbon pool, and remove an estimated 0.076 Pg of carbon from the atmosphere annually [Gorham, 1991].

Peatlands can be classified as either bogs or fens. Bogs are ombrotrophic systems that receive water and nutrients solely from precipitation and dry fall and are therefore poor in solutes. Fens are minerotrophic systems, which are fed by groundwater and are therefore usually richer in solutes, notably Ca²⁺ [Gignac and Vitt, 1990; van Breezen, 1995]. Fens may be alkaline or acidic and range from mesotrophic to oligotrophic, whereas bogs are acidic and oligotrophic [Vitt et al., 1994]. These peatlands can be further subdivided on the basis of vegetation cover and the presence of local peat landforms [Vitt et al., 1994; Halsey et al., 1997].

Peatland development is strongly linked to climate, with bogs and fens occurring in areas where precipitation exceeds evapotranspiration and where total annual precipitation is typically greater than 500 mm [Gignac and Vitt, 1994]. Climate also plays an important role in the regional distribution of peatland types [Moore and Bellamy, 1974; Gignac and Vitt, 1990, 1994; Gignac et al., 1998]. The extent of peatlands also depends on topography, and flat terrain provides an ideal setting for vast expanses of peatlands [Zoltai and Pollett, 1983].

Sphagnum is by far the dominant component of bogs and poor fen peat. No other group of mosses is as ecologically dominant on a worldwide basis [Andrus, 1986]. Calculations suggest that there is more carbon locked up in Sphagnum (dead and living) than is fixed by all terrestrial vegetation in one year [Clymo and Hayward, 1982]. The extensive carpet-like growth and slow rate of decay of Sphagnum are two of the primary reasons for its large volume in bogs. The low pH and low dissolved solute concentration of bogs are conducive to Sphagnum growth [Gignac and Vitt, 1990]. However, the general restriction of Sphagnum to these sites is only partly determined by the environment, with Sphagnum playing a considerable role in creating these conditions [Andrus, 1986]. The success of Sphagnum is due to its ability to create a
2. Methods

Spores of Sphagnum are preserved along with pollen grains in lake and bog sediments. They are easily identified and routinely counted along with other pollen grains. Pollen grains and spores have similar dispersal and preservation properties and data on their presence in sediments are available in public databases. Sphagnum data were extracted from sites available in the North American Pollen Database (NAPD) [Grimm, 2000b], European Pollen Database (EPD) [Cheddadi, 2000], and Global Pollen Database (GPD) [Grimm, 2004a] furnished by the National Oceanic and Atmospheric Administration (NOAA) Paleoclimatology Data Center. All available data for North America, Europe, and Siberia were used to make the maps.

Sphagnum percentages were computed within a sum based on all upland plants, pollen, and Bryophyte spores. Radiocarbon chronologies were obtained from the database. The radiocarbon equivalents of target calendar years spanning 0–21 ka by 2 ka intervals were determined using CALIB version 4.2 [Stuiver and Reimer, 1993; M. Stuiver and P. Reimer, Quaternary Isotope Laboratory HTML CALIB 4.2 manual, available at http://depts.washington.edu/qil/calib]. Sphagnum percentages were then linearly interpolated to these radiocarbon equivalents to produce our maps.

Maps were then drawn of the abundance of Sphagnum spores at 2000-year intervals. Geodetic coordinates of sample sites were projected using the forward spherical solution for the Albers Equal-Area Conic projection [Snyder, 1987], and Sphagnum percentages were interpolated using a standard inverse-distance squared algorithm [Lam, 1983] with a grid resolution of 50 km². In order to limit any further extrapolation within and outside the sampling space, we used a search radius of 750 km in North America and 250 km in Europe. Grid cells with Sphagnum proportions greater than or equal to 0.5% were selected if they fell within modern-day continental boundaries and outside of ice sheet boundaries for each time slice. The extent of the ice sheets was taken from Peltier [1993, 1994]. However, the modern sea level and coastline were retained for simplicity.

Response surfaces [Bartlein et al., 1986; Gignac et al., 1991] were computed to determine the modern climatic range in which Sphagnum occurs and is most abundant in North America. Mean annual temperature and total annual precipitation were extracted from Leemans and Cramer [1991] for the locations of 3005 core tops (age <100 yr B.P.) and surface sediment samples in the GPD. These variables were chosen because they are easily available and can be compared to known patterns of the modern climate. Spore percentages at sites with identical climate values were averaged since they would add no information to the response pattern. The response of Sphagnum percentages to the climate variables was estimated using kernel density interpolation [Cressey, 1995]. The quartic kernel function used Euclidean distance within a 100 x 100 unit grid defined by climate axes scaled to unity. Scaling was necessary because of the large differences in the ranges of the two environmental variables [Gignac et al., 1991]. The scaled axes provided an equivalent resolution of 0.46°C by 19.7 mm, and the bandwidth was set at 3 times these values. This bandwidth and grid resolution limit extrapolation to 59.1 mm and 1.38°C. The resultant surface was smoothed using a 5 x 5 inverse-distance squared center-weighted moving average filter.

Local overrepresentation of Sphagnum percentages in bogs might affect the estimated climatic optimum of the response surface, but we found that the position of the optimum changed relatively little when surfaces were derived using only samples from lakes. The position of the abundance center is robust, but the absolute percentages of Sphagnum are elevated when bogs are included, which is of little concern since our purpose was to estimate the climatic range of the genus. Only the surface based on all samples is shown in this paper. In order to assess the degree to which our response surface represents the possible climates in North America where Sphagnum can occur, we compared plots of North American climate space with the subset of climates sampled by our sites used in the response surface. Finally, sampling intensity surfaces were constructed using all nonzero data in order to determine the extent to which sampling biases in climate space where Sphagnum spores occur could have affected the estimated Sphagnum response optimum.

The pollen databases are made up of contributions from many people over a long period of time, and we thus wanted to assess the reliability of our maps. Palynologists collect cores from both lakes and bogs. Although in the past, paleoecologists frequently cored bogs for pollen studies, the preference today is to use lake sediments. Spores of Sphagnum are present in bog sediments and vary from a few percent, even in Sphagnum peat, to significant amounts [e.g., Gajewski, 1987; Hu and Davis, 1995]. If we were to use bog samples only, the resultant maps would depend on the distribution of bogs that have been studied, which is not an extensive sample set. Bog stratigraphies are dominated by the local presence of spores in the wetland, but it is difficult to interpret the regional distribution of peatlands from these studies. However, spores are also present in lake sediments. These occasional spores do not necessarily indicate the presence of Sphagnum in the immediate area of the deposition site (local pollen and spores) because spores can be transported varying distances by the wind. However, as has been demonstrated with pollen maps [e.g., Anderson et al., 1991], Sphagnum spores are more abundant in the region where the plants are found, with trace amounts found away from the source. Thus the distribution of Sphagnum spores from lake sediments can be used to indicate regions where Sphagnum peatlands are present, in the same way that the distribution of pollen of upland taxa can be used to indicate the distribution of trees. We plot the modern distribution of Sphagnum spore percentages to illustrate the clear relation between spores and peatland extent.

One potential problem became apparent in performing queries on these databases. Because Sphagnum is semi-aquatic, it is not certain that it is routinely recorded or subsequently entered into the database thus allowing some discrepancies in the distribution of this taxon. That is, while a positive value indicates that Sphagnum was deposited at that time within the sediment core, a zero value may not indicate absence of deposition but only that it was not entered into the database. Of course, a zero means only that Sphagnum spores were not recorded for the site and does not necessarily indicate the absence of the plant in the region. We therefore queried the database to determine the extent of this problem. We first identified all sites where a Sphagnum spore was counted at least once during the entire core sequence. For these sites, we then assumed that a zero at one level implied that no Sphagnum spores were observed for that time period (Figure 1). However, within a core where Sphagnum counts were zero for all levels, it is also possible that no spores were deposited at the site throughout the entire period of record, as might occur in the southwest United States. We therefore queried the database to determine those sites where Sphagnum was absent from the record but where the author has been known to enter Sphagnum at other sites. If an author counted and entered Sphagnum spores for other sites in the database, it is likely that one of their cores that have zero Sphagnum spores throughout actually signifies the absence of the spore at that site in question. The remaining sites are more ambiguous, and a zero count may be interpreted as a lack of
Figure 1. Location of core sites from the North American Pollen Database (NAPD) and European Pollen Database (EPD). Grey circles are sites where Sphagnum was recorded at least once during the period of the core. Open circles are sites where no Sphagnum spores were recorded. Open circles with a black dot are sites where Sphagnum is absent throughout the core but the author had recorded Sphagnum in at least one of their entries in the NAPD EPD.
Sphagnum spores or simply that the data were not entered. Although we used all sites for the mapping, these categories can be used in the interpretation of the reliability of a particular zero Sphagnum value (Figure 1).

Estimates of area of peatland and total carbon (TC) stored in peatlands were made for every 2000-year time slice between 21 and 1 ka. To estimate the area of peatland extent in North America and Europe, the number of grid cells within the 0.5% Sphagnum isopoll was counted and multiplied by the grid resolution. Grid cells within the Canadian Arctic Archipelago were excluded from area calculations since most of these spores are probably transported from the boreal region to the south and percentages are inflated due to local underrepresentation of the tundra pollen [Bourgeois, 2000] (see below). The Arctic is too cold and dry to support extensive paludification, although small local peatlands have been recorded.

There are too few data from Asia to compute the area of peatlands for this continent directly. To arrive at a first approximation of the global peatland area for the different time periods, we assumed the total proportion of the world’s peatland area in Asia has remained constant through time. We therefore computed the area of Asian peatlands as 0.765 times the sum of North American and European peatland area and added this to the areas we computed from our maps to arrive at the global total.

The carbon content of peatlands for time period t was estimated using $TC(t) = A_t \times D_t \times p \times C$, where $A_t$ is the total area of peatland at time $t$ (m$^2$), $D_t$ is the peat thickness (m) at time $t$, $p$ is the bulk density of the peat (g m$^{-2}$), and $C$ is the carbon content of the peat (%). The land within the 0.5% isopoll consists of both upland and peatland vegetation. We used ranges of the modern ratio of peatland area to total area (0.1–0.2 for North America and 0.1–0.3 for Europe) [Kivinen and Pakarinen, 1981; Vitt et al., 2000] to scale the total area within the 0.5% isopoll to $A_t$. Average modern peat thickness was estimated as 2.3 m in North America and 1.1 m in Europe [Gorham, 1991]. Values for mean bulk density ($112 \times 10^2$ g m$^{-3}$) and carbon content (51.7%) were also taken from Gorham [1991] and were kept constant for all time periods.

Estimates of peat accumulation rates were needed to generate peat thickness values, $D_t$, for all time periods before the modern. We used an exponential curve ($be^{ct}$) to model the accumulation rate through time (m yr$^{-1}$), where $t$ is in thousands of years (ka). This model reflects the low rates of accumulation in the full glacial and early Holocene [Vitt et al., 2000]. The accumulation rate constant $b$ was set to the modern value of 0.005 m yr$^{-1}$ [Gorham, 1991]. The constant $c$, was set at 0.0002 for North America and 0.0004 for Europe in order to obtain carbon values that are negligible at full glacial and 455 Pg at present [Gorham, 1991]. Modifying the accumulation rate curve tested the sensitivity of total carbon estimates to the accumulation rate. Altering the rates did not significantly change the shape of the resulting carbon estimates unless a very high accumulation was introduced in the early Holocene, which is unreasonable.

There are very few data from which peatland extent in Asia may be accurately estimated. For this reason, carbon accumulation for Asia was roughly estimated using the ratio of its modern carbon total to the carbon total for North America and Europe (0.765).

3. Results

Crum [1984] reports Sphagnum plants from nearly every state of the United States and all of Canada. Although the northern range limit of many species coincides with tree line, several species are found in the low arctic, and others are found on Baffin Island. From the rest of the Arctic Islands, Crum [1986] reports only a few species from eastern Devon, southeast Ellesmere and southern Victoria Islands, although Kuc [1973] suggests a more widespread distribution.

The major area of peatland distribution in North America is in the boreal zone of Canada and Alaska (Figure 2) [Hofstetter, 1983; Zoltai and Pollett, 1983] and most sites across Alaska, Canada, and northeastern and northcentral United States have positive values of Sphagnum spores. The southern, modern-day distribution of positive values of Sphagnum spores corresponds closely to the distribution of peatlands (Figure 2) but not to the distribution of Sphagnum plants. The zone with maximum Sphagnum percentages is found in a band from north of the Great Lakes through to the Gaspé Peninsula. Although there are some sites in western Canada (e.g., Manitoba and Keewatin) with no Sphagnum spores reported, these come from older studies, and spores, although present, were probably not entered into the database. Not only are the percentages elevated in the area with maximum peatland extent, but also nearly all sites contain Sphagnum spores. In contrast, both the values of the Sphagnum spore percentages and the number of sites reporting spores decrease in the southeastern United States. Smaller bogs are located along the Atlantic Seaboard to Florida and at altitude in the Appalachians (Hofstetter, 1983; Weider et al., 1981), and the scattered distribution of positive Sphagnum spore percentages reflects this less extensive presence of peatlands.

Relatively high values of Sphagnum are also found in some arctic island samples. This is due to the low local pollen productivity that inflates the percentages of the Sphagnum, as there are not presently extensive peatlands in these regions. Much of this is presumably transported from the boreal peatlands to the south [Bourgeois, 2000].

The center of Sphagnum abundance ranges from ~630 to 1300 mm annual precipitation and between −2° and 6°C mean annual temperature (Figure 3a). The sites responsible for the Sphagnum percentage maximum are mainly from northern Ontario, meridional Québec, the Maritime Provinces, and the New England states (Figure 3c). Our Sphagnum response surface would suggest that peatlands can be found in areas of low annual temperature and precipitation in the Canadian Arctic Archipelago, but as discussed above, these percentages are inflated. Small clusters of positive values in areas with temperatures greater than 12°C and precipitation around 1200 mm (Figure 3a) represent samples from the southeastern United States (Figure 3c). In this region, the less extensive bogs are nevertheless recorded. Another cluster of high Sphagnum values is found at −3°C and above 1440 mm, which represents a few sample sites in Labrador and Newfoundland (Figures 3a and 3c), areas with extensive bog development but few sample points. Although Sphagnum can occur along a wide range of precipitation and temperature, it is most abundant where precipitation is in excess of 500 mm yr$^{-1}$ in cool to moderately cool temperatures [Halsey et al., 1998].

The reliability of the response surface depends on how well our samples represent the possible climates in North America where Sphagnum can occur and whether limited sampling at those sites with nonzero Sphagnum percentages bias the response surface overall. The convex hull on Sphagnum spore in climate space overlaps 55% of the total area of the convex hull defined by North American climate space (Figure 3d). The 45% not accounted for represents eastern coastal Alaska to Oregon, which is a geographically restricted area. Within the Sphagnum convex hull (Figure 3d), few samples occur where mean annual temperatures exceed 11°C and precipitation is less than 1000 mm yr$^{-1}$ which delimit climates of the American southwest. The aridity of this area prevents widespread bog development, and all of our samples have no recorded Sphagnum spores. We then used a sampling intensity surface to assess the degree to which
Figure 2. Modern Sphagnum spore distribution in North America, based on 3005 sites in the Global Pollen Database. Spore percentages from sites with identical geographic coordinates were averaged.

Sampling biases may have affected the estimated response of the Sphagnum optimum (Figure 3b). Those sites with nonzero, non-missing values (Figure 3d) will have the greatest influence on our estimated center of Sphagnum abundance. The estimated peak abundance of Sphagnum (Figure 3a) coincides with an area of strong sampling intensity (Figure 3b) that is nevertheless found between three regions with stronger sample intensity. None of these other regions produce strong peaks in the response surface, suggesting that the response optimum is not due to limited sampling of areas with positive Sphagnum percentages. Consequently, the samples used in constructing our surface sufficiently represent the areas of climate space where Sphagnum occurs and where it is most abundant.

We depicted Sphagnum spore distribution at 2000-year intervals for North America and Europe. On the basis of the modern distribution of peatland and Sphagnum percentages, the 0.5% isopoll most closely corresponds to the modern limit of peatland.

There was little Sphagnum at 21 ka south of the ice sheet in North America (Figure 4). Scattered sites in eastern North America record a few spores indicating some Sphagnum presence, perhaps in small bogs. Almost all sites in Alaska had Sphagnum spores, and there were high percentages in a few of these. Around 15 ka the number of sites recording Sphagnum increased, especially around the edge of the retreating ice. In the Atlantic provinces of Canada there were large values in many sites. By 13 ka, the number of available sites in eastern Canada and the United States increased, and Sphagnum was recorded in many of these sites. In western Canada, Sphagnum spread eastward on land made available as the ice sheet retreated. During the Holocene, Sphagnum spread eastward from Alaska and westward from the northeastern United States to cover all of boreal Canada by 5 ka. In the late Holocene, Sphagnum spread slightly southward, as more sites in the western Great Lakes region recorded large values.

Although our primary emphasis is on North America, we were also able to map the area of peatland in Europe for the same time period based on data from the EPD [Cheddadi, 2000]. The more complex geography of Europe makes contouring more difficult. Today, extensive peatlands are found in northern Europe, and there are fewer to the south of the Alps [Moore and Bellamy, 1974]. Again there is no Sphagnum recorded in the few sites available at 21 ka (Figure 5). By 17 ka, Sphagnum is recorded in northeastern
Figure 3. (a) Response surface of modern Sphagnum spore percentages plotted as a function of total annual precipitation and mean annual temperature. (b) Sampling intensity surface of sites with nonzero Sphagnum percentages. Contours represent number of sites per 0.46°C by 19.66 mm. (c) Geographic partitioning of Sphagnum spore distribution along climatic axes. (d) Degree of overlap between Sphagnum spore sampling and climate space. Solid outer line is the convex hull containing North American climate; the dotted line is the convex hull for Sphagnum sampling sites in North America. Small dots are individual grid points from Leemans and Cramer [1991] between 25°–83°N and 49.5°–168°W. Black diamonds are sediment sample locations with positive Sphagnum percentages, and small crosses are sites with zero Sphagnum.

Ukraine and Poland and shortly thereafter in Scandinavia and Great Britain. By 11 ka, many sites record Sphagnum in eastern Europe, with occasional reports in western Europe. By 9 ka, there is extensive Sphagnum bog development across Europe, except for sites in the Mediterranean region. This pattern continues until the present.

There are few data available in the Global Pollen Database for Russia and Siberia, although much of central Siberia has extensive peatland development, in a band from around 50° to 65°N, with major peat basins in this zone from 60° to 90°E [Kivinen and Pakarinen, 1981; Neustadt, 1984]. The available cores do not extend to the full glacial. The few pollen diagrams available (Figure 6) suggest little peatland until around 10 ka and most peatland development after 8 ka [Neustadt, 1984]. Values for total area of Sphagnum-dominated peatlands and carbon stored in Sphagnum peatland areas remain low through the Early and Middle Holocene and rise rapidly in the Late Holocene (Figure 7). The Late Holocene increase is due to both
Figure 4. Map of Sphagnum distribution for the past 21,000 ka at 2000-year intervals for North America. Open circles represent zero Sphagnum percentages for that time period, small closed circles are positive values less than 5%, and large closed circles are values greater than 5%. Area within the 0.5% contour is shaded. Ice sheet location is hatched. Projection central meridian is 100°W (North America), 0°W (Europe); origin latitude 50°N; standard lines 35° and 80°N.
Figure 4. (continued)
Figure 5. Map of Sphagnum distribution for the past 21,000 ka at 2000-year intervals for Europe. Symbols are the same as in Figure 4.
Figure 5.  (continued)
an increase in peatland area and to increasing mean peatland depth. Uncertainty in the ratio of peatland area to total area within the 0.5% isopoll was represented as an error bar on the results of our calculations. Calculations were constrained such that total peatland carbon matched the modern value of 455 Pg [Gorham, 1991].

4. Discussion

The response surfaces and maps of the modern distribution show that Sphagnum spores in sediments can be used to illustrate regions of peatland presence that are consistent with their modern geographic and climatic ranges (Figures 1 and 2). Accounting for long-distance transport, the area with abundant spores at most sites corresponds to the boreal region with extensive peatlands. Eastern United States, with smaller and less extensive peatlands, had smaller amounts of spores at some but not all sites and this reflects the smaller amounts of Sphagnum plants in less extensive bogs and moist areas. In the arid southwest, there are no Sphagnum spores reported in the modern data. The southern limit of the 0.5% isopoll corresponds to the southern limit of Sphagnum peatlands (Figure 3). The northern limit of Sphagnum peatlands on the landscape is not well captured by the 0.5% isopoll due to efficient long-distance transport of spores and low local production of pollen, which inflates the Sphagnum percentages. This effect is evident in all of the maps. Our response surface concords with previous work based on plant distribution [Gignac et al., 1998; Halsey et al., 1998].

The maps presented here illustrate the extent of peatlands during the past 21 ka. Sphagnum peatland extent was restricted during full glacial in North America and Europe. Although spruce and other boreal species were found far to the south of the Laurentide ice sheet, this vegetation was not a boreal forest in the sense that we consider it today. Today, much of the boreal zone is underlain by peatlands, in both North America and Eurasia [Moore and Bellamy, 1974; Gorham, 1991; Neustadt, 1984], but this has not always been the case. Models simulating conditions at full glacial should account for this difference in carbon storage. With the exception of Alaska, there is little evidence of extensive Sphag-
num at this time. Little peat was accumulating in Europe. The interpretation of Neustad [1984] only extends to the late glacial, and our results from Siberia cannot ascertain the extent of peatlands in Asia.

Sphagnum peatlands developed shortly after deglaciation (15–11 ka) in eastern North America. The area of peatland initiation and development moved eastward from Alaska and westward from the St. Lawrence region. This spread was related partly to the availability of land after deglaciation, but initial establishment at any site also depended on climate changes. Several studies have illustrated the importance of climate changes in initiating peat formation or in causing a transition from marsh to fen or fen to bog [Vitt, 1994; Zoltai, 1995; Zoltai and Vitt, 1990; Winkler, 1988; Janssens et al., 1992; Kuhlry et al., 1993; Vardy et al., 1998].

In this paper we interpret the closed Sphagnum contour as the area having Sphagnum peatlands present, that is, bogs and poor fens. Rich fens are dominated by other mosses, and their spores are not routinely identified in pollen preparations. However, the distinction between different wetland types in boreal zones depends on the relative influence of groundwater and rainwater (minerotrophic versus ombrotrophic) to the growing surface, and this is influenced by the wetland location in relation to the regional topography. The presence or absence of peat accumulation in peatlands is under the influence of the macroclimate, and this is what can be interpreted in this study. There may be a lag between initial peat formation and the establishment of Sphagnum in a particular peatland, and this time is longer in continental peatlands than in coastal ones [Vitt et al., 1994]. Our estimates of peatland extent are thus conservative. However, if poor fens were accumulating peat during the full glacial, there should have been some trace of this left in the form of peat deposits, but there is little evidence of this accumulation, and our estimates should not have excessive error.

These reconstructions agree broadly with previous local and regional studies. Halsey et al. [1998] show calibrated radiocarbon dates from 90 locations across continental western Canada that indicate peat formation began ~8000–9000 years BP in nucleation zones along the upper elevations of the Montane region of Alberta and in northern Alberta. From 6 to 8 ka, peat formation expanded eastward into Manitoba, and after 6 ka the trend of southeasterly peatland expansion continued. Our results put this into a large-scale context and illustrate that the peatland development in this region is part of the larger-scale movement from west to east from the full glacial onward. In the western Great Lakes region, the Red Lake Peatlands [Heinselman, 1970; Griffen, 1977; Janssens et al., 1992] and smaller bogs [Winkler, 1988] developed later, as the climate became cooler and moister in the middle to Late Holocene. The maps of Halsey et al. [2000], based on presence or absence of spores at a selected subset of North American sites, also agree broadly with our results.

Huntley and Birks [1983] presented maps of Sphagnum spore percentages at 9000, 4000, and 2000 13C years BP for Europe. Since they only mapped isopolls greater than 10%, they were recording the local presence of abundant Sphagnum or sample sites that happened to be bogs or peatlands. Our area of peatland extent is therefore much greater than these earlier results. In the British Isles, characteristic peat basal dates range between 8500 and 7500 years BP in Scotland to 6000 years BP in Wales and Ireland [Taylor, 1983]. There was accelerated peat development in blanket bogs after 2800 years BP. In Sweden, paludification occurred extensively in the Early and Middle Holocene and had almost ceased by 2000 years BP [Sjors, 1983].

Interestingly, there is some suggestion from the literature that Sphagnum reproduces essentially vegetatively and that capsules are rarely observed [Andrus, 1986; Clymo and Duckett, 1986; Cronberg, 1991]. The presence of numerous spores in lake sediments occasionally transported far from the source [Bourgeois, 2000] suggests that considerable numbers of spores are being produced and that these are well transported in the atmosphere. This work provides at least two kinds of information. First, since the distribution of Sphagnum as well as peatlands is related to climate (Figure 3) [Moore and Bellamy, 1974; Vitt et al., 1994], these maps indicate that portion of the Northern Hemisphere that supports Sphagnum growth and how this region has changed through time. Because of the transport of Sphagnum spores beyond the immediate source, the limits indicated here are more extensive than the actual limit of the plant. However, at the scale and resolution of global climate models (GCMS), these maps could be useful for paleoclimate verification.

Studies of CO2 variations through time need to account for major sources and sinks of carbon, and there are great uncertainties in these estimates. Previous work has been forced to ignore or estimate carbon storage in peatlands due to lack of data on peatland extent [Crowley, 1995]. Our work is a contribution to the goal of better understanding carbon dynamics by presenting estimates of Sphagnum peatland extent through time. When rough estimates of the carbon stored in peatlands are made, the results indicate three periods. Before ~11 ka, there was little carbon stored in Sphagnum peatlands. In the Early Holocene, carbon gradually accumulated as the area of land supporting peatlands increased. In the Late Holocene, the carbon stored in these ecosystems increased more rapidly as the depth of the peatlands increased.

These maps only indicate where there was bog and/or poor fen development but not other wetland classes, including rich fen. In some regions, there is a delay between initiation of wetlands and the transition to Sphagnum bog, and peat can be accumulating during this period. For more precise estimates of carbon storage in peatlands, regional-scale models of peat growth [e.g., Gignac et al., 1998] could be combined with reconstructions or simulations of past climates and tested against these maps.

The reduced abundance of Sphagnum peatlands through much of the past 21 ka illustrates significant ecosystem-level changes in boreal and temperate biomes. The hydrological balance and carbon storage were significantly different from the present, as illustrated by a relative lack of peatlands through much of the past 21 ka. These maps indicate changes in the major biomes through time, and the importance of using functional-type climatic models [e.g., Prentice et al., 1998; Williams et al., 1998] in preference to static biomes [e.g., Prentice and Fung, 1998; Adams et al., 1990] when reconstructing vegetation changes through time.

5. Summary

Maps based on Sphagnum spores in lake and bog sediments can be used to reconstruct changes in peatland extent in boreal and temperate biomes. The present-day distribution of abundant Sphagnum spores corresponds closely to areas with peatland development. In North America, maximum peatland development is in the boreal zone and, to a lesser extent, southward along the eastern coastal region. In Europe, the most extensive peatland development is found to the north of the Alps, and in Asia, central Siberia has extensive peatland development. Today maximum Sphagnum spore abundance is found between 630 and 1300 mm annual precipitation and between ~2° and 6°C mean annual temperature in North America. During the Wisconsin glaciation, there were apparently not large amounts of carbon stored in peatlands. Peatlands were growing in Alaska and began developing in eastern North America during deglaciation. Major peatland development occurred in North America after 9 ka, and there was southward movement of high Sphagnum spore abundance after 5 ka in the western Great Lakes region. The major period of peatland development began after 9 ka in Europe and Asia.


Zoltai, S., Regional variations in peatland ecosystems of west-central Canada through time, Gunneria, 70, 35–42, 1995.


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