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## INVITED ESSAY

### New Frontiers in Bryology and Lichenology

#### Bryophytes as Indicators of Climate Change

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Interest in climate change has increased tremendously in the past 10 to 15 yr, both within and outside the scientific community. The reason for this interest is directly related to the anticipated global warming that will result from increased concentrations of greenhouse gases in the atmosphere. As a result of this interest, several questions have been raised relative to climate warming. For example, how can we predict long term climatic change? How accurate are the predictions? What will be the severity and extent of the changes? How will biodiversity, ecosystems, and habitats be affected if climate change occurs as predicted? How long will it take for species and ecosystems to react to climate change? This essay will focus on the utilization of bryophytes to answer those questions.

Bryophytes grow in almost all terrestrial and freshwater environments where plants can be found. These environments have a global distribution and are found in all climatic regimes with the exception of those on permanent ice. The success of bryophytes is largely due to their unique and very effective physiological water relation system that permits them to survive in the wide variety of climates in which they are found. This poikilohydric system permits them to grow during periods when water is available and to suspend their metabolism when water is lacking. Most genera are ectohydric and take up water through the whole surface of the plant and therefore do not need a root system to draw water from the soil. Also, nutrients are taken up through all surfaces from solutes in water that is in contact with the plants. As a result, bryophytes can grow on such very hard surfaces as rocks and tree trunks where higher plants cannot because their roots cannot penetrate the surface.

Although most bryophytes have the same water relation system, there are very few truly cosmopolitan species that can be found under all climatic conditions. Most species have evolved relatively narrow variations in physiological tolerances to drought, insolation, and temperature extremes that

limit their growth to geographically restricted areas or to specific habitats (see Proctor 2000 for a review). Some species, for example those found in tropical montane rain forests, are limited to constantly moist and shady habitats and are sensitive to desiccation. At the other extreme, some species are found on sun baked and bare rock surfaces and can survive long periods even years without any water.

Bryophytes have evolved several characters to limit water loss that include hair points, papillae, lamellae, dead hyaline leaves to protect the photosynthetic leaves, thick cell walls, and the ability to change the orientation of their leaves. These adaptations produce substantial variations in each species ability to withstand desiccation and also affect the time necessary to metabolically recover from drought conditions after rewetting. For example, forest floor species that experience relatively long wet periods recover relatively slowly from long dry periods. Conversely, species found on dry exposed rocks recover rapidly. Also, there is a variation in growth form that is related to water availability. For example, in polar climates, small acrocarpous species are found in arid areas, mat forming pleurocarps are found in wetter environments, whereas cushions are often found in the wettest habitats (Longton 1988). Thus, some species survive better at low than at high humidity and vice-versa.

Most bryophyte species have a relatively wide tolerance range to temperature. This tolerance to temperature is largely due to their water relations since they can withstand greater temperature extremes when dry than when they are wet. Therefore, humidity of the air, total annual rainfall, and length of dry periods are much more important parameters of climate than temperature. Although each species has an optimum photosynthetic range, there is no correlation between temperature optima and the geographic distribution in mosses. Although most studies indicate that the temperature component of the macroclimate is not a controlling factor in species distribution, there is some evi-

dence that this may not be entirely true. For example, areas surrounding hot springs in Iceland and Greenland support species that are not found in the surrounding colder areas. Since water is available in both areas, it must be temperature that is limiting the distribution of those species (Longton 1988). Indirect evidence that may also demonstrate that temperature is a limiting factor can also be found in the relatively narrow climatic distribution of many species (see Schofield 1992 for a review). For example, *Plagiothecium berggrenianum* Frisvoll is a species that has a circumpolar arctic distribution while *Lepidozia reptans* (L.) Dum. is limited to boreal climates (Tan & Pocs 2000). *Lophocolea maritima* Nees is restricted to tropical lowlands in both Africa and South America. All of these taxa are predisposed to long-distance transport thus dispersal does not appear to be a limiting factor.

Species that are limited by relatively narrow moisture or temperature ranges are potential indicators of climate and climatic change. However, in general, bryophytes make uncertain indicators of macroclimate because they are much more attuned to the microclimate that can be widely different from the gross climatic characteristics for a region (Longton 1982). These differences produce disjunct occurrences of both microclimates and habitats that tend to nullify many species usefulness as indicators of the climate. But, there are other possibilities that make bryophytes useful to detect climate change.

The distribution of many species is limited to habitats that have relatively narrow climate tolerances and thus species that are indicative of those habitats become by extension indicators of the climate. Since these habitats migrate on the landscape as a result of climate change, species that are indicative of these habitats will also migrate and thus become indicators of those changes. One such habitat that have been used in climate and climate change studies are bogs and poor fens that are dominated by *Sphagnum* species. Only relatively cold areas with annual moisture balance less than zero can produce *Sphagnum*-dominated bogs (see Gignac 1993 for a review). The annual moisture balance is determined by the ratio between mean annual total precipitation and the amount of evapotranspiration that is directly related to the mean annual temperature. A positive moisture balance occurs when there is more precipitation than evapotranspiration. The distribution of bogs is particularly sensitive to the moisture balance since their moisture is entirely derived from precipitation. In fact, not only is the distribution of these ecosystems sensitive to the moisture balance, but also their shape and the height they reach above the mineral soil surface. Since the water table in poor fens can

also be fed by ground water, they can occasionally form in areas where the annual moisture balance is slightly below zero and where local hydrological conditions are favorable. As a result, bogs and poor fens are almost exclusively restricted to the boreal, sub-arctic, cool temperate, and cool oceanic areas.

Although peatlands have often been used as indicators of climate change they are not the only habitats that are sensitive to the climate. In fact, all major vegetation zones are correlated with mean annual temperature and precipitation (Gates 1993). As either or both of those climatic variables change, the zones will migrate. For example, boreal and temperate forest dieback in the past has been clearly correlated to climate change and extreme weather events.

Before becoming too involved in describing the utilization of bryophytes as indicators of climate change, a brief description of past climates and future climate change would be in order. Also, a brief description of the factors that affect the climate is necessary in order to understand the causes of the anticipated global warming.

#### CLIMATE CHANGE

Bryophytes evolved at some time between the lower Silurian and the lower Carboniferous, approximately 350 million years before the present (myBP). Since that period, continents have drifted together and then separated again, meteorites have struck the earth, sea levels have changed repeatedly, and volcanoes have erupted, all of which have brought about several major extinctions. Throughout this time frame, the climate has continually changed and bryophytes have continued to evolve and diversify.

The first bryophytes began to appear during a period when the climate was much warmer than it is today. This warm period was followed by a long period between approximately 200 and 340 myBP when the Earth was colder, perhaps even colder than it is today. During that time, there were relatively short periods where large areas of the earth's surface were covered by glaciers. These glacial episodes were interspersed with relatively brief interglacial periods. This cold period was again followed by a long period up to 50 myBP when conditions became much warmer. Since the Quaternary began, the Earth's surface has again cooled producing several glacial events interspersed with interglacial episodes reminiscent of conditions that occurred 300 myBP.

Within the last 22 thousand years (kyBP), the climate has gone from full glacial to full interglacial (Gates 1993). Between 22 and 18 kyBP, the ice sheet that surrounded the North Pole and covered

large areas of the Northern Hemisphere had reached its maximum extent. The ice sheet retreated rapidly between 15 and 12 kyBP and had mostly disappeared within 9,000 yr. Recent glacial and interglacial events may have been caused by changes in solar irradiance caused by sun-earth orbital motions. These changes result from three variations: differences in the shape of the earth's orbit around the sun from elliptical to more circular (eccentricity); changes in the tilt angle of the earth in relation to the sun (obliquity); and the conical spinning motion of the earth's rotational axis (precession). These orbital changes, the obliquity and eccentricity in particular, are thought to affect the climate enough to cause cyclical ice ages and interglacial periods every 100,000 yr. Concentrations of such greenhouse gases as CO<sub>2</sub> and methane are also closely associated with past glacial and interglacial episodes. Greenhouse gas concentrations were highest during the interglacial and lowest during the full glacial. Effects of greenhouse gases are thought to accentuate the effects of the sun-earth orbitals on the climate.

Between 13 and 11 kyBP, the climate fluctuated rapidly and suddenly several times within a relatively short time in the North Atlantic, Greenland, and northern Europe. This period, known as the Younger Dryas Event, began with a 4°C warming, followed by a sudden drop of approximately 6°C within a few hundred years that caused a return to partial glacial conditions. This period was again followed by an incredible temperature increase of 7°C within 50 yr. Although not well understood, ocean currents are thought to have been an important contributor to these dramatic changes in the climate. Decreases in the salt concentration as a result of ice melting in waters of the North Atlantic during this period are thought to have produced the collapse of the ocean current creating a rapid drop in temperature. The re-establishment of the thermohaline gradient rerouted the ocean current in a more northerly direction thus creating a rapid temperature increase in the North Atlantic.

Changes in the sun-earth orbitals during the mid-Holocene, between 10 and 6 kyBP, produced a warmer and drier climate than the present in the northern mid latitudes. This was followed by a gradual cooling that achieved its peak during the Little Ice Age between 1,430 and 1,800 AD when there was an increase in the extent of snow and ice greater than at any time since the last major ice sheet. Volcanic eruptions and the dust that was spewed into the atmosphere are thought to have caused this period of global cooling. Aerosols, sulfuric acid in particular, injected into the upper atmosphere reflect sunlight and produce a decrease in global air temperature. The most important ef-

fects are felt in the second and third years after the eruption since it usually requires a year for the aerosols to be distributed over the surface of the globe. Since the Little Ice Age, the global climate has become progressively warmer.

Global climate models attempt to predict climate changes that will result from the doubling of atmospheric concentrations of CO<sub>2</sub> (2× CO<sub>2</sub>). Although each climate model may produce different results there is a consensus that the following changes will occur: global mean surface temperature increase; polar winter surface warming; reduction of sea ice; global mean precipitation increase; summer continental warming and dryness; and a rise in global sea level. The greatest changes are expected to occur in terrestrial continental mid to high latitudes. These changes are expected to happen relatively rapidly (<100 yr) and only the poorly understood Younger Dryas Event offers comparable changes in the past.

#### BRYOPHYTES AS INDICATORS OF PAST CLIMATE CHANGE

Paleoreconstructions of past climates fall into two main categories depending on the source of the data – geological reconstructions, and – reconstructions based on the geographic distribution of plant indicator species, communities, or ecosystems. The latter method quantifies responses of individual plant species or plant assemblages to modern climate. Then, the past geographic distribution of those species and assemblages are reconstructed from the macrofossil, pollen, or spore record found in cores taken from ocean, lake, or river sediments or peatlands. The past climate and subsequent climate change is inferred for a region or locality based on the distribution of the vegetation and the relationship between the vegetation and climatic variables (see Webb et al. 1987 for an example). This method assumes that the relationship between species and climate has not changed during the intervening years.

Two types of bryophyte remains are used to reconstruct past environments: macrofossils and spores. Macrofossils are remains of gametophytes (rarely sporophytes) that are preserved in peat deposits and in lake or river sediments (see Miller 1984 for a review). These remains are identified in much the same manner as living bryophyte samples are today. Macrofossils can be deposited in situ, for example in peat or on occasion in streams or lakes, or in lakes after short distance transport from the surrounding basin. Thus, macrofossil remains are usually used to reconstruct environmental changes for a site or for a small region. Macrofossil reconstructions are almost exclusively restricted to anal-

yses of mosses since hepatics are rarely preserved in peat or sediments. Also, analyses rely largely on the presence of species rather than their abundance.

Several types of analyses of macrofossils can be used to reconstruct past environmental conditions. Single species can be used to make inferences about past climates and subsequent climate change based on their present affinities to the macroclimate. For example, *Polytrichum norvegicum* Hedw. that is an obligate indicator of late lying snow beds in Europe, was found in lake sediments in areas where it does not occur today (Birks 1982). The presence of this species was used to reconstruct the Younger Dryas Event and the Little Ice Age in Britain. *Polytrichum alpinum* Hedw., a species that is absent from areas with mean summer temperatures above 16°C, was also used to reconstruct the climate in the same area.

Another approach to using bryophyte remains to reconstruct past climate is to use their growth form. Moss growth forms are related to such microclimatic variables as the amount of insolation and relative humidity, as well as the macroclimate and thus can be used to reconstruct climate change. This approach is restricted to remains that were deposited in situ since the size of the fossil necessary for this type of analysis cannot withstand even short distance transport (Miller 1980). For example, *Tomenthypnum nitens* (Hedw.) Loeske has an arctic-alpine expression that differs from the more common type by its pattern of branching. Its recovery in peat deposits was indicative of tundra environments in Sweden during the interglacial, conditions that are not found in those localities today (Miller 1980).

A third approach to paleoecological climate interpretations based on macrofossils and certainly the most effective, are those derived from moss assemblages rather than single species because they have a broader base of analysis. For example, climate change was inferred from moss assemblages obtained from late glacial sediment cores in northern Britain. The original assemblage was indicative of snow bed communities and pioneer species. This assemblage was replaced by tundra species that was in turn replaced by open rich fen species and late snow bed communities. The latter series is no longer found in the area and was thought to be an indicator of the climate change that occurred during the younger Dryas Event (Birks 1982).

Another technique involves the analysis of bryophyte macrofossils to determine peatland initiation. Initiation can be easily determined since the vegetation will switch from marsh species to peatland bryophyte species in the case of terrestrialization or from forest species to peatland bryophytes in the case of palludification (Vitt & Kuhry 1992). The

boundary between marsh or forest vegetation and peatland bryophyte species can be radiocarbon dated and mapped for different time slices. Since peatland initiation is a function of climate, inferences can then be made relative to past climatic changes.

Although effective, methods involving the paleoreconstructions of the climate from macrofossil bryophyte indicator species or assemblages have limitations. Among these, analyses of peat macrofossils are mostly limited to areas where peatlands are present today. Also, the time frame is relatively narrow and in most cases only extends between 10 to 14 kyBP. There are some exceptions that may extend as far back as 60,000 yr, but they are few and geographically isolated. Finally, once peatlands are initiated, it is difficult to determine further changes to the climate since it is almost impossible to determine the cause of subsequent vegetation changes. Autogenic factors and such allogenic factors as fire, flooding, and anthropogenic disturbances that are not necessarily related to the climate cause most of the changes in peatland bryophyte assemblages (Vitt & Kuhry 1992). Finally, because macrofossils are produced in situ or transported over relatively small distances in basins, they can only be used to reconstruct local climates. For these reasons, reconstructions using macrofossil indicator species and assemblages are best used to corroborate climatic interpretations that were quantified by other methods.

The vast majority of large scale regional paleoreconstructions using the distribution of plant species and assemblages are based on the distribution of vascular plant pollen rather than the distribution of bryophyte spores. There are several reasons for this discrepancy. With a few exceptions, spores are often produced only in small quantities and close to the ground and are thus not very abundant in sediment cores and as a result are often overlooked during analysis. Also, it appears that it is relatively difficult to identify spores from bryophytes to the species level when compared the identification of pollen. To my knowledge, the only large-scale paleoreconstructions of past climates using bryophyte spores are based solely on the distribution of *Sphagnum* spores in lake sediments.

There are three main reasons why *Sphagnum* spores are a valuable asset in the paleoreconstruction of past climate changes. Firstly, they have a characteristic morphology that is easily identifiable. Secondly, the spores are often concentrated in lake sediments and are therefore included in most pollen/spore keys that leads to their inclusion in many pollen diagrams. Thirdly, they are only found in abundance on two climatically sensitive ecosystems, bogs and poor fens.

*Sphagnum* spores are usually released under dry

and often windy conditions that are the most favorable for dispersal. The number of spores contained in a capsule varies by at least one order of magnitude depending on their size and the size of the capsule and appears to be species specific. For example, *Sphagnum lindbergii* Schimp. in Lindb. produces a mean of 128,256 spores per capsule while *Sphagnum fuscum* (Schimp.) Klinggr. only produces 83,411 spores per capsule. Spore dispersal distance from the parent plant is leptokurtic. Approximately 30 to 40% of the spores released from the capsule land within a few meters from the parent plant. The remaining 60 to 70% are caught in air currents and are dispersed over longer distances. Deposition in lakes is assumed to be random and, once on the lake bottom, spores are assumed not to move within the sediment column. Thus, a core through a lake's sediments would reveal the presence or absence and the number of spores at successive depths that can be then radiocarbon dated to determine their age.

Halsey et al. (2000) found that the presence of spores in the modern profile of a sediment core was related to the presence of a *Sphagnum*-dominated peatland in a  $0.5^\circ$  latitude  $\times$   $0.5^\circ$  longitude grid cell in which the core was taken. The relationship between the number of spores present in the modern spore rain and the presence or absence of peatlands was elucidated to be  $>1\%$ . If spore counts were  $>1\%$  then peatlands were present in a cell, while  $<1\%$ , peatlands were absent. That relationship was then applied to spore counts from different time slices in the past. The distribution of *Sphagnum*-dominated peatlands could thus be determined for 2000-yr intervals from 22 kyBP to current times across North America. Since the presence of *Sphagnum*-dominated peatlands is directly related to mean annual temperature, mean annual total precipitation, and summer drought conditions, values for those variables can be inferred from the reconstructed distribution.

#### VALIDATING CLIMATE MODELS

The interest in global warming has sparked one of the most significant scientific pursuits in relation to climate change: to accurately predict the climate that will result from increases in greenhouse gas concentrations. The ability to accurately predict the climate on a global scale for a longer time frame than weeks or months requires a model. General Circulation Models (GCMs) are mathematical reconstructions of the climate on a global scale consistent with such physical and chemical interactions in the atmosphere as the amount of insolation, greenhouse gas concentrations, and feedbacks from the oceans, ice, land, and biota (McFarlane et al.

1992). They divide the surface of the globe into grid cells of varying sizes from crude,  $4.5^\circ$  latitude  $\times$   $7.5^\circ$  longitude scale, to high resolution,  $100 \text{ km}^2$ , depending on the GCM. They then predict such climatic variables as mean monthly temperature, precipitation, insolation, evapotranspiration, etc. for each grid cell. Thus GCM outputs contain geographic data that are matched with climatic information. Along with predictions for current conditions (control), GCMs produce climates for different time slices in the past for example the mid-Holocene (6 kyBP) and the Last Glacial Maximum (21 kyBP) as well as in the future when  $\text{CO}_2$  concentrations are doubled. Thus, GCM outputs attempt to reconstruct past and future climate change.

There exist several different GCMs of varying sophistication, all of which use different values for climate forcing factors and feedback mechanisms and thus produce different results. A comparison between 10 different GCM outputs for modern zonally averaged Northern Hemisphere ground temperatures over land and observed temperatures for the same area revealed a wide discrepancy between models (MacFarlane, unpubl. data). For example, at  $45^\circ\text{N}$  latitude, the Canadian Climate Center model (CCCMA GCM2) projected a temperature of approximately  $19^\circ\text{C}$ , very close to the observed temperature of  $20^\circ\text{C}$ , whereas the General Fluid Dynamics Laboratory (GFDL) model and the BMRC model projected temperatures of approximately  $30^\circ\text{C}$  and  $33^\circ\text{C}$ , respectively. The remaining models predicted temperatures between  $20^\circ\text{C}$  and  $30^\circ\text{C}$ . These large variations between models are also reflected in their predictions for past and future climate changes and shed doubt on their accuracy and validity. Therefore, validating GCM outputs would be a valuable exercise and would help determine which of the many GCMs provides the most accurate results.

The preceding analysis by MacFarlane is an example of an evaluation GCM modern (control) outputs and is based on direct comparisons with climatic variables obtained from global databases for current meteorological conditions. Those databases divide the earth's land surface on a relatively fine scale grid ( $0.5^\circ \times 0.5^\circ$  lat.  $\times$  long.) and reconstruct the climate in each grid cell based on data from meteorological stations (see Leemans & Cramer 1991 for an example). Evaluating control outputs is a relatively simple procedure since there are meteorological data available for comparison. However, evaluating past climate change scenarios is much more complex since there are not any meteorological data for those time frames.

For past climates, two GCM outputs are usually evaluated 1) a direct evaluation of climatic variables and 2) evaluation of the differences between

past climate and control (past climate – control = anomalies) to determine if the projected differences are accurate. A frequently used evaluation method compares the paleoreconstruction of the distribution of plant species and assemblages with the GCM predictions for the same period and localities. Although effective, this method does not directly verify GCM outputs because there is no link between the climatic data produced by the GCM for individual grid cells and the paleoreconstructed climate. A more powerful and effective evaluation method couples climatic variables produced by GCMs and species or ecosystem responses to those variables and then compares the responses estimated by the GCM data with the reconstructed distributions. This method of evaluation requires that the modern responses of climatically sensitive indicator species or ecosystems are defined by climatic variables that can also be generated by GCM scenarios. The climatic data obtained from GCM outputs for past climates would then be merged with the climatic data used to quantify indicator species and ecosystem responses to the climate. Since the GCM data is matched to geographic grid cells the projected distribution of the indicator species or ecosystem is then mapped for different time slices in the past. The projected distribution is then compared to the paleoreconstruction of the species or ecosystem and the accuracy of the GCM predictions are statistically analyzed.

The indicator value of the distribution of *Sphagnum* is particularly useful in validating GCM outputs. Figure one demonstrates the sequence of steps used to validate GCM predictions for the end of the mid-Holocene (6 kyBP) using *Sphagnum*-dominated peatland responses (SPR) to the climate. The first step is to determine the modern distribution of *Sphagnum*-dominated peatlands based on the presence of *Sphagnum* spores in lake sediments along two climatic gradients: mean annual temperature (Temp) and mean annual total precipitation (Precip).

The second step is to determine the accuracy of the response by rounding values for precipitation and temperature and merging them with a global database for current climatic conditions (Leemans & Cramer 1991). Since this database is arranged on  $0.5 \times 0.5$  latitude by longitude grid, the projected modern distribution of *Sphagnum*-dominated peatlands can be plotted. This distribution is then compared to the actual distribution of *Sphagnum*-dominated peatlands that was determined from ground analyses. A comparison between the predicted and actual distributions in North America revealed that the SPR had an accuracy of 90% (Gignac et al. 2000).

The next three steps validate GCM outputs. The

method is essentially the same as the one used to quantify the predicted SPR error and involves rounding climatic values and match merging them to each GCM output. Since the GCM data are organized in the same format as the global climate database, projected distributions can be plotted in the same manner. The projected distribution generated by merging the GCM control output with the SPR is compared to the current distribution. This produces a total error from which errors produced by the SPR, as determined in step two, are subtracted to produce an accuracy value for the GCM control output.

The last two steps verify two types of GCM outputs for 6 kyBP. The first directly measures the climate generated for this time slice while the second measures climate change projections by adding the anomalies to the global database. In both cases, the projected 6 kyBP distribution is compared to the paleoreconstructed distribution as determined by the analysis of *Sphagnum* spores in lake sediments. Thus, the accuracy of both types of outputs can be quantified. A preliminary analysis of the control and 6 kyBP outputs for two GCMs for North America indicated that this method not only effectively distinguished between each GCM but also indicated areas where each GCM was found to be lacking (Gignac, unpubl. data).

The preceding analysis was generated for the late mid-holocene, but could be used to validate outputs for data from any time slice generated by a GCM since the Last Glacial Maximum. The method is only limited by the time frame for which the geographic distribution of paleoreconstructed peatlands has been generated. Of particular interest would be an analysis of data for the Younger Dryas Event in Northern Europe, since the climate change in that area for that period most closely resembles the projected climate change that will be produced by global warming.

#### BRYOPHYTES AS INDICATORS OF GLOBAL WARMING

The predicted relatively short term (<100 yr) increases in global temperature that will result from increased concentrations of greenhouse gases in the atmosphere will have important effects on the vegetation zones particularly in mid and high latitude continental regions. Past climate changes have clearly shown that ecosystems and species will migrate when climatic conditions change. An important utilization of bryophyte indicator species would be to predict the migration of climatically sensitive ecosystems.

Gignac et al. (1998a) used an empirical model to project the northward migration of peatlands in the Mackenzie River Basin, northern Canada at  $2 \times$

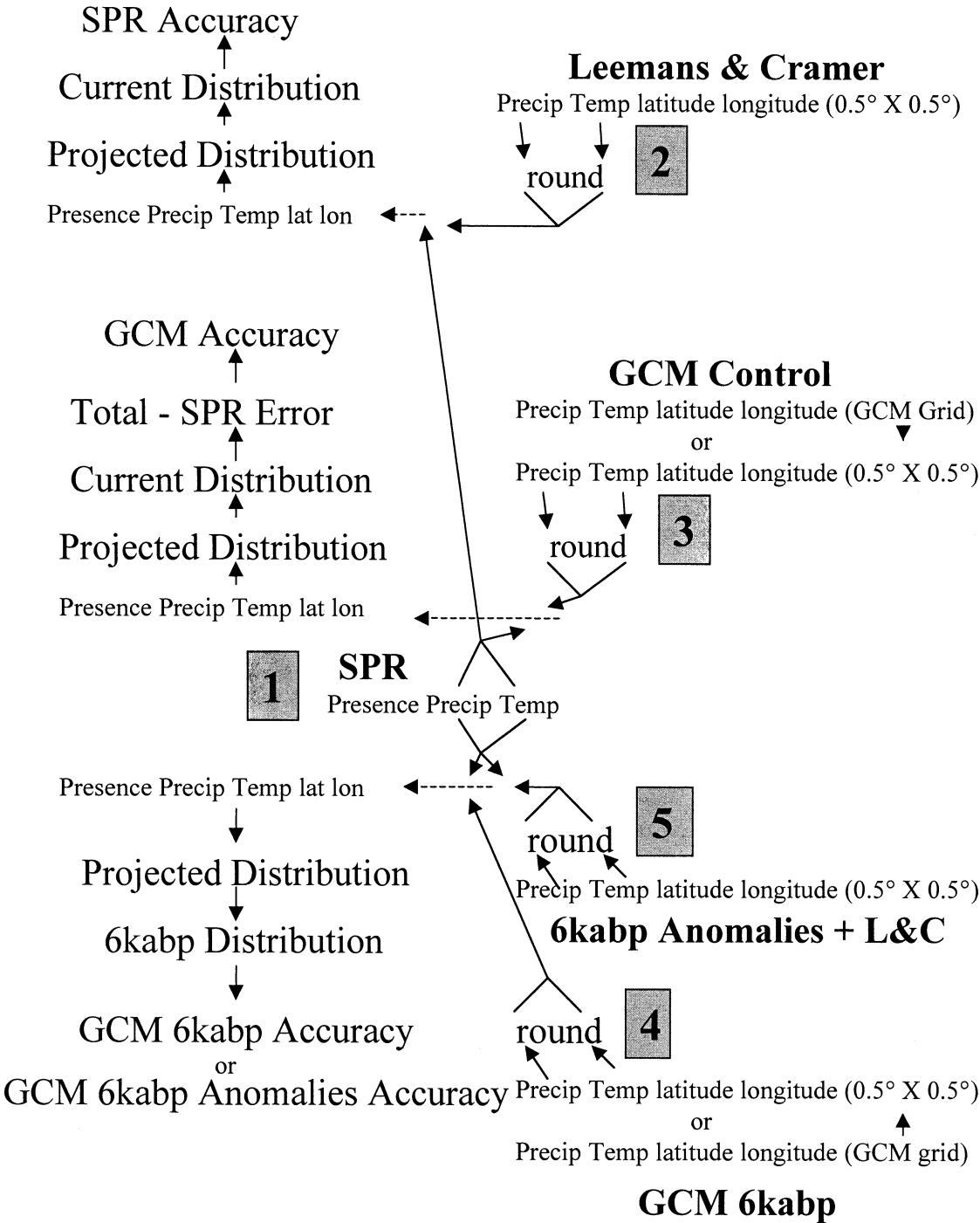


FIGURE 1. Schematic presentation of a method used to validate General Circulation Model (GCM) outputs for present (control) and past climates (6 kyBP) using the response of *Sphagnum*-dominated peatlands (SPR). The method is calibrated using a global terrestrial climate database (Leemans & Cramer 1991). Numbers in shaded boxes indicate the sequence of the steps as outlined in the text.



CO<sub>2</sub> based on bryophyte indicator species. Since the geographic distribution of peatlands closely follows the distribution of the boreal forest and its ecotones, they tentatively projected, by extension, the future range of the boreal forest. This was accomplished by classifying the different types of peatlands in the study area based on the presence, absence, and abundance of several bryophyte indicator species (Nicholson & Gignac 1995; Nicholson et al. 1996). Then, the modern climatic response of each indicator species was quantified along climatic gradients and the distribution of each type of peatland was reconstructed based on the relationship between indicator species and peatland groups (Gignac et al. 1998*b*). The climatic distribution of the peatlands was then calibrated against their present geographic distribution using the same technique as described in Step two of Figure one. The accuracy of the projections was between 70 and 100% depending on the type of peatland.

The future geographic range of the different peatland types was then reconstructed for climate scenarios produced at 2× CO<sub>2</sub> by two GCMs using a method similar to the one described in Step three of Figure one (Gignac et al. 1998*a*). The result of this analysis indicated a northward migration of the southern limits of peatlands and by extension of the boreal forest of approximately 780 km in the study area. The analysis also reconstructed the location of the boreal and subarctic ecotones.

As is the case with all empirical models, this analysis uses space as an analogue of time and assumes that vegetation types and species occurring on present landscapes will occur on future landscapes as the climate changes, but in different locations. There are some problems inherent with these assumptions. Firstly, it assumes that indicator species have the ability to disperse and establish in new areas. This assumption may not be entirely correct for bryophytes and peatland ecosystems since other such factors as surface water chemistry and the nature of the mineral soil also affect their distribution patterns. Secondly, the model does not consider the effects of increased atmospheric CO<sub>2</sub> levels on a species ability to resist climatic change. Furthermore, projections based on empirical models indicate the geographic distribution of ecosystems at equilibrium with the climate. They do not account for the lag that is always present between climate change and vegetation responses. Although peatland bryophyte indicator species are sensitive to changes in the height of the water table brought about by changes in the climate, there is no accurate prediction of the length of time needed for climate to affect water levels. Also, the length of time required for the different types of ecosystems to respond to climate change is not accurately known.

For example, along the present southern limits of peatland distribution, small basin bogs that have relatively shallow accumulations of peat may disappear relatively quickly from the landscape as the climate warms perhaps even within a few years if the dieback process is accelerated by fire. However, large peatlands with deep peat accumulations that are found in large drainage basins may require hundreds or even thousands of years before they disappear from the landscape. It is quite likely that the climate will change again perhaps even cool as a result of changes in the sun-earth orbitals or the collapse of the thermohaline before the process is complete. Thus, predictions of future distributions made by empirical models may never occur.

Another problem with empirical models is that they rely implicitly on the accuracy of GCM projections of climate change. As demonstrated earlier, GCM predictions for the same geographic area can vary significantly. These variations can translate into large differences in the modern geographic distribution of both species and ecosystems ranges and therefore undermine the validity of estimates based on empirical models. Although there are many problems inherent to empirical models, they can serve a useful purpose since they provide a possible end result for the effects climate change on ecosystem migration given the accuracy of GCMs. They also can indicate trends that could be verified using other analytical means.

A second utilization of bryophyte indicator species could be to monitor climate change and its effects on ecosystems. This type of analysis could answer the question as to how rapidly will climate change affect species and ecosystems. Although bryophytes have been successfully used to monitor deposition of heavy metals, acid rain, and radionuclides, to my knowledge, they have never been used to monitor climate change, even though some studies have used the distribution or phenology of vascular plants in that capacity (see Lewis Smith 1994 for an example). Effects of climate change on bryophytes can be monitored in two ways 1) effects on their growth, and 2) effects on the distribution of individual species, community assemblages, and the ecosystems that they represent.

As a result of climate change, the growth of bryophyte species will be affected long before they disappear from the landscape. It could be possible to monitor changes in growth rate for a species within an area or region over a period of several years and from this data, determine the potential effects or lack of effects on the species distribution. Before a species is selected for this type of monitoring, it must be demonstrated that its growth is clearly related to the mesoclimate. This can be accomplished by measuring its growth under different

climatic conditions over a wide geographic area. It would also help if growth can be relatively easily measured. *Hylocomium splendens* (Hedw.) B.S.G. is an excellent example of a species that would fit these criteria since it is widespread in boreal climates, its annual growth is clearly marked, and growth is correlated to the mean annual total precipitation (Vitt 1990).

Monitoring studies involving bryophyte species or bryophyte community assemblages can be divided into two groups 1) individual species whose distribution is clearly restricted by the mesoclimate, and 2) species assemblages that are indicative of climatically sensitive habitats or ecosystems. Studies involving both groups would necessitate permanent quadrats in which the abundance and distribution of the bryophyte vegetation would be quantified and mapped. In subsequent years, those permanent quadrats would be re-analyzed to determine changes in the species composition and distribution. Monitoring studies require several years before bearing fruitful results and perhaps for this reason are not popular. However, they may provide very useful information regarding the effects of climate change particularly at the distribution limits of either species or communities.

The following criteria could be used to select a useful indicator species of climate change 1) the distribution of the species must be clearly limited by the mesoclimate, and 2) the species must be found at several localities within the study area. Identification of a good indicator species could be determined from bryogeographical and physiological data. A classic example of this approach is the work of Foreman (1964) using *Tetraphis pellucida* Hedw. He determined the range of conditions favorable for the growth of the species in culture. From these results and records of such mesoclimatic variables as mean monthly maximum and minimum temperatures from many climatic stations, he was able to predict the distribution of the species. There was good agreement between the predicted and actual distribution. Thus, *Tetraphis pellucida* would be considered a good indicator species. Many other species could be identified for all climate zones using the same method. Also, such species as *Polytrichum alpinum* and *P. norvegicum* that were previously used as indicators of past climate change could also be used as to monitor future changes. However, caution must be exercised when selecting species to include only species that are relatively widely distributed so as to eliminate species that are limited by dispersal rather than climate. For example, neoendemics should be eliminated since they are limited by the amount of time that they have had to disperse rather than by climate.

The second group of monitoring studies involves changes in species assemblages that are indicators of climatically sensitive ecosystems. For example, as a result of the predicted warming and drying in continental areas, the quantity of water found in peatlands should diminish creating a drier environment at the peat surface. Peatland bryophytes are very sensitive to moisture conditions and therefore species found in moist or wet environments should be replaced by species of drier environments. Such species as *Scorpidium scorpioides* (Hedw.) Limpr., *Meesia triquetra* (Richt.) Aongstr., *Calliergon trifarium* (Web. & Mohr) Kindb., and *Drepanocladus revolvens* (Sw.) Warnst. that are found in the wettest conditions in rich fens would be replaced by *Sphagnum warnstorffii* Russ. and *Tomenthypnum nitens* which in turn would be replaced by *S. fuscum*, *Mylia anomala* (Hook.) S. Gray, *Pleurozium schreberi* (Brid.) Mitt., and *Polytrichum strictum* Brid. The same type of species turnover could also be monitored in poor fens and bogs.

The advantage of using bryophytes as indicators of changes in water levels rather than vascular plants is that the latter are not as sensitive to drying since their rooting system enables them to obtain water from lower in the peat column. Bryophytes do not have this advantage and are thus more sensitive to changes in water level. Therefore, changes in bryophyte species composition and distribution can be used to warn us of impending changes to the ecosystem. It would appear that this process has already begun since there is no free water to be found at the surface in some small peatlands in hydrological isolated basins in northern Alberta (pers. obs.). It is highly likely that a bryophyte monitoring study of such peatlands would produce results relatively quickly and be invaluable in determining the potential effects of warming on the vascular flora.

A second possible example of a monitoring study involves epixylic and epiphytic species found in forests. Many of those species are sensitive to exposure to direct sunlight and subsequent drying. This can be readily observed in woodlots where exposed trees at the edge have fewer bryophytes covering the trunk than those found in the shaded interior. Also, downed woody debris in shaded areas supports a variety of species, particularly hepatics that are not found on material that is exposed to direct sunlight. The absence of species on exposed wood may be due to the intolerance of those species to drying conditions or to changes in the rotting wood. The moisture content of exposed rotting wood is much less than that found in more shaded and humid conditions. This produces downed woody debris that is very hard on the outer surface that may be unsuitable as a habitat for most

bryophytes of rotting wood. In either case, epixylic species are indicative of shading and moisture conditions in the forest.

One of the expected effects of global warming is a migration of the different types of forest towards the poles. This change will probably become visible in forest patches that occupy higher and drier areas along the limits of its distribution before it occurs elsewhere. Forest dieback occurs when older trees die and are not replaced. As the bigger trees die they create gaps where sunlight can penetrate thus creating warmer and drier conditions that are not suitable for bryophyte indicator species. Thus, the number and abundance of species within those areas should diminish proportionally to the number of gaps. Therefore the disappearance of epixylic and epiphytic species could be used as an indicator of the number of gaps in the forest that are indicative of the disappearance of the forest as a whole.

Monitoring studies do not categorically prove that climate change has caused shifts in the distribution and abundance of indicator species. There are many other factors that could be responsible for those shifts particularly if only one or two events are observed. However, if such shifts occur throughout a region, they would offer strong indications that climatic changes are responsible. The interesting aspect of this type of research is that it may offer early warning of other more largescale changes to the ecosystem within the region.

In conclusion, bryophytes have been successfully used in several studies to identify or to corroborate results from other types of climate change analyses. They are presently being used to validate GCM outputs and as the base component of empirical models to project effects of future climate change on the distribution of ecosystems. Also, because of their close affinity to climatically sensitive habitats and ecosystems, they offer several possibilities as monitors of climate change before the habitat or ecosystem itself is affected. The suggestions I present here are not intended to be exhaustive and I am sure that they're many others that I have not thought of. However, I would hope that some of the ideas that I have presented would spark some interest in the utilization of bryophytes as indicators of the impending climate change.

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