

Concepts of fen and bog re-examined in relation to bryophyte cover and the acidity of surface waters

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Abstract

Studies of surface-water pH and bryophyte assemblages in 440 plots from five peatland regions across northern North America reveal a very distinct, two-fold division into fens with a pH mode at 6.76-7.00, in which *Amblystegiaceae* are prominent, and bogs with a pH mode at 4.01-4.25, in which *Sphagnaceae* are dominant. The relevance of the data to past and current views on peatland classification is explored.

Key words: peatland, classification, fen, bog, water acidity, bryophyte

INTRODUCTION

EARLY STUDIES

Studies of peatlands began a long time ago, and they were classified in a great many ways (G o r h a m 1953). The concepts of fen and bog date back at least to the early nineteenth century, when investigators both Scottish (N a i s m i t h 1807, A i t o n 1811) and German (D a u 1823) recognized that peatlands receiving their mineral supply solely from atmospheric precipitation, which we now call ombrotrophic bogs, bore plant communities different from those of peatlands that receive in addition waters that have been enriched by percolation through the mineral soils of surrounding uplands. These we now call minerotrophic fens. At that same time it was recognized (H o m e 1757, R e n n i e 1810, T h a e r 1810) that peat deposits are often acid. Several organic acids, as well as sulfuric acid, were suggested as the cause by these and other investigators. The

clear dependence of free hydrogen-ion concentration (usually expressed as pH) upon complex, colored organic acids was recognized much later (Thompson et al. 1927, Gorham et al. 1985).

MODERN CLASSIFICATIONS OF PEATLANDS

During the twentieth century there have been many attempts to classify peatlands in terms of plant communities, the chemistry of surface waters and peats, and hydrology. The earlier divisions were often bipartite — into (1) acid *Sphagnum*-dominated bogs with surface waters poor in mineral matter, notably calcium and (2) circumneutral and floristically much more diverse fens, characterized by a less conspicuous moss flora dominated by species other than *Sphagnum*, and by surface waters distinctly richer in mineral matter, especially calcium (e.g., Warming 1909, Tansley 1911, Kurz 1928, see also Sjörs 1983 concerning early Swedish practice). However, tripartite divisions interpolating a transitional stage were also common, for example the Übergangsmoor of many Central Europeans is transitional between Hochmoor (bog) and Flachmoor or Niedermoor (fen); the transition bog of the Polesie (Kulczyński 1949) is interpolated between raised bog (bog) and valley bog (fen); and the *Molinietum* — characterized by *Molinia caerulea*, *Myrica gale*, and several species of *Sphagnum* — is transitional between moor (bog) and fen (Tansley 1911, see also the lacustrine bog of Pearsall 1938). Still other classifications (e.g. Kivinen 1935) used more categories, usually based on diverse plant communities.

Nowadays the division of peatlands into minerotrophic fens and ombrotrophic bogs, on the hydrological basis of whether or not the peat surface receives water that has percolated through adjoining mineral soil, is widely accepted (Gore 1983), with the fens often subdivided further into rich and poor fens, and sometimes additional categories (e.g., Du Rietz 1949, Sjörs 1950). It should be pointed out, however, that the boundary between fen and bog is seldom recognized on a hydrological basis, but rather by the use of “fen indicator plants” that are not observed in truly ombrotrophic conditions. The possibilities for circular argument are obvious.

PROBLEMS IN CLASSIFYING PEATLANDS

There are of course difficulties with any classification, whether based on vegetation, chemistry or hydrology. Conway (1949) found it impossible to separate acid from circumneutral bogs in Minnesota, seeing a continuous gradient from one to the other. She therefore devised a classification into four major communities, based partly on vegetation (moss heath, bog forest) and partly on topographic position (pioneer mat, marginal fen — comparable to the Swedish lagg). Sjörs (1950), dividing plant communities along the fen/bog

gradient into seven categories: extreme rich fen, transitional rich fen, intermediate fen, transitional poor fen, indeterminate poor fen, extreme poor fen, and moss (= ombrotrophic bog), observed considerable overlap in pH amongst them all. For instance, weakly minerotrophic extreme poor fens ranged as low as pH 3.8, far into the ombrotrophic-bog range of 3.7 to 4.6. Numerous other studies of both pH and calcium concentrations demonstrated similar overlaps (e.g., Glaser et al. 1981). Sometimes this may be owing to the persistence of some species long after conditions suitable for their colonization and establishment have disappeared (e.g., *Phragmites communis*, Auer 1923, Chapman 1964; *Nartheceum ossifragum*, Sumnerfield 1972). For instance, a “poor fen” may be defined by the persistence of a few scattered plants of one or two supposedly minerotrophic-fen species in what would otherwise fit clearly into the category of ombrotrophic bog. This is a phenomenon that I have termed elsewhere (Gorham 1957) “biological inertia”.

Gorham (1950), in a study of surface-water chemistry along the boundaries of *Carex lasiocarpa* in two Swedish peatlands, pointed out several difficulties in defining the “mineral soil water limit” (Thunmark 1942, Du Rietz 1949) between minerotrophic fen and ombrotrophic bog, and in establishing its coincidence with the “fen plant limit” (Sjörs 1948, Du Rietz 1949). Finally, some plant species taken to indicate these limits in one area do not do so in other areas (Du Rietz 1949, Gorham 1956).

AIMS OF THIS STUDY

Our aims in this investigation were threefold: (1) to examine the frequency distribution of pH in the surface waters of peatlands; (2) to elucidate the relationships of bryophyte cover — by *Sphagnaceae*, *Amblystegiaceae*, and other species — to pH; and (3) to examine further questions of peatland classification and “fen-indicator” species. In pursuit of these aims we examined primarily data from bryophyte plots in five widely separated regions across boreal North America (Fig. 1). We also considered the relevance of transect data and of stratigraphic data illustrating the transition from fen to bog.

METHODS

Five major North American regions are represented in the database for peatland surface-water pH and associated bryophytes (Fig. 1). (1) The southeastern Alaskan sites are near Glacier Bay National Park and in the Juneau area. (2) The Minnesota sites are scattered throughout the state and represent both large and small peatlands. (3) The New York sites are from the Adirondack Mountains. (4) Most Maine sites are from the northern part of the state, except for one coastal site. (5) The sites in the Atlantic Provinces of Canada are from Fourchu, Nova Scotia, and Carmanville, Newfoundland. The total number of

plots collected in each region is indicated on Fig. 1. These plots were 50 x 50 cm square and were selected in homogeneous peatland communities to represent the major peat-forming bryophytes present. Bryophyte cover for each species was estimated on a 5-point scale (1 = only a single or a few gametophores present, 2 = up to approximately 5% of total cover, 3 = more than 5% to 25% of the plot, 4 = more than 25% to 75% cover, and 5 = more than 75% cover). The species importance values along the pH gradient were calculated by summation of cover values within each pH class and division by the total number of sites.

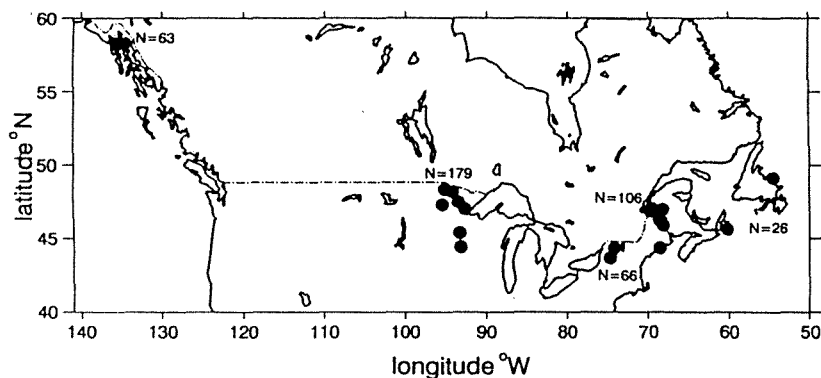


Fig. 1. Locations and numbers of bryophyte plots studied (west to east) in Alaska, Minnesota, New York, Maine, and the Atlantic Province of Canada

Samples of peatland surface water were collected as near to the plots as possible, mostly within one meter. Most samples were stagnant surface water or were collected in peatland hollows by depressing the moss surface slightly. A few samples ($N = 33$) were obtained from shallow pits that were dug and allowed to fill. The pH was measured soon afterward, usually on the same day, with a Radiometer pH meter and combination electrode (Janssens 1987, 1988).

RESULTS

When pH data for all 440 plots from five regions of North America are plotted as a frequency histogram (Fig. 2A) it is apparent that the distribution is distinctly bimodal. There is a strongly acid group of plots exhibiting a mode at pH 4.01-4.25 and a circumneutral group of plots with a mode at pH 6.76-7.00. Most of the more acid plots have a moss flora in which species of the *Sphagnaceae* (all of the genus *Sphagnum*) are an important element (Fig. 2B), whereas in the circumneutral plots members of the *Amblystegiaceae* are prominent (Fig. 2C). Substitution in Fig. 2B and 2C of plots with more than 75% instead of more than 25% cover for a single species yields a similar picture, though with lower frequencies.

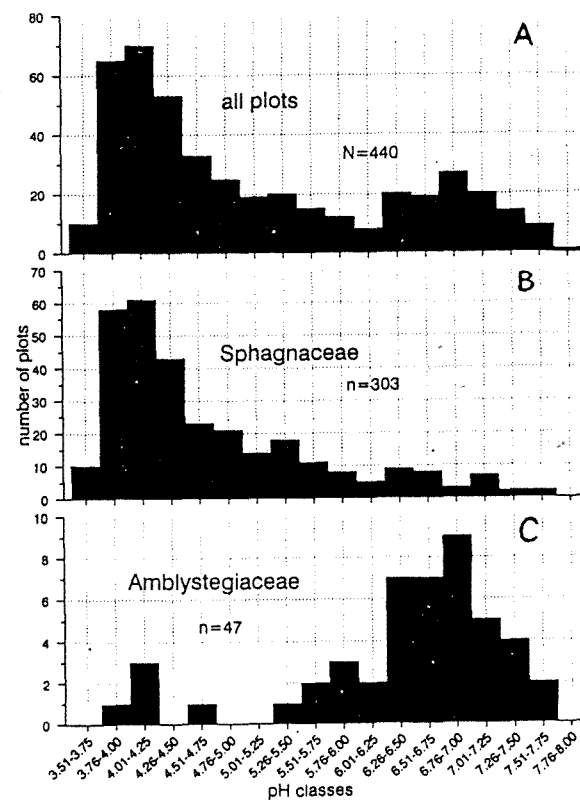


Fig. 2. Frequency distributions of pH for (A) all plots, (B) plots with at least one species of the genus *Sphagnum* covering more than 25% of total area, and (C) plots with at least one species of the family *Amblystegiaceae* covering more than 25% of total area

In order to compare on a more equal basis the pH preferences of the *Sphagnaceae* and of the much less abundant *Amblystegiaceae*, Fig. 3 (top) shows separately the percentage of plots in each pH class for the 303 plots with at least one species of the *Sphagnaceae* at > 25% cover and for the 47 plots with at least one species of *Amblystegiaceae* at > 25% cover. It is again very clear that the *Sphagnaceae* are usually associated with acid conditions and the *Amblystegiaceae* with circumneutral conditions.

The individual species distributions (Fig. 3, bottom) show that there are exceptions to the general rule noted above. For instance, among the *Sphagnaceae* *S. subsecundum* tends to occupy the middle ground in the overall pH range, and *S. warnstorffii* is distributed at the circumneutral end of the range. In contrast, among the *Amblystegiaceae* two species, *Drepanocladus fluitans* and *Calliergon stramineum*, are found under acid to moderately acid conditions.

percent number of plots in family per pH class
plots with at least one species >25% cover

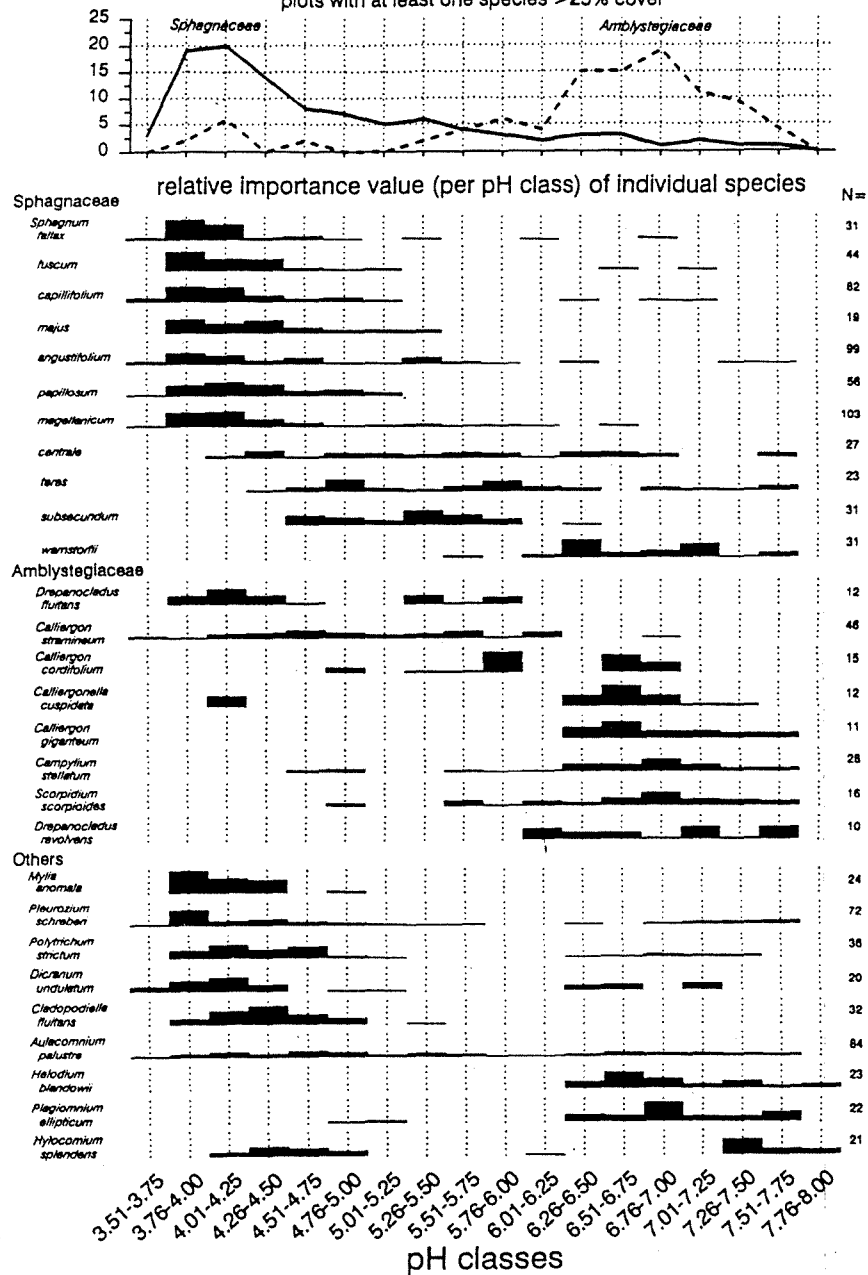


Fig. 3. A comparison of the percentage distributions, along a pH gradient, of plots with > 25% cover by at least one species of *Sphagnaceae* and of plots with > 25% cover by at least one species of *Amblystegiaceae*. Shown below are individual bryophyte-species distributions, weighted by importance values, along the pH gradient

Bryophytes other than *Sphagnaceae* and *Amblystegiaceae* are about equally prone to be most prominent at the acid end of the pH spectrum (e.g., *Mylia anomala*) and at the circumneutral end (*Helodium blandowii*), but *Aulacomnium palustre* appears to be indifferent to pH.

Similar patterns are to be found in the peatlands studied by Sjörs (1948) in Bergslagen, north Sweden (Fig. 4).

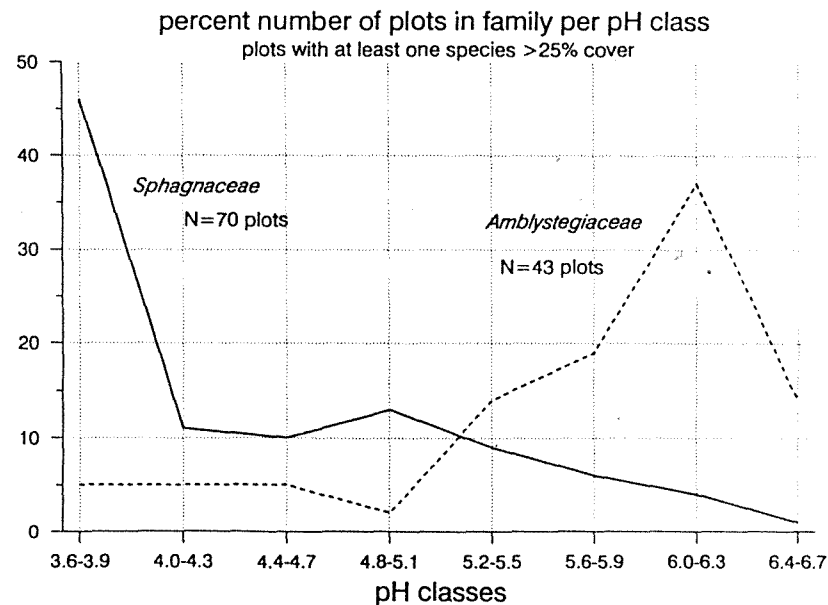


Fig. 4. The relationship between pH and the abundance of *Sphagnaceae* and *Amblystegiaceae* in the peatlands of Bergslagen, Sweden (data of Sjörs 1948). Construction as in Fig. 3 (top)

DISCUSSION

The results described above require consideration in three different ways, concerning: (1) the reality and cause of the bimodal pH-frequency distribution, (2) its relationship to horizontal and vertical pH gradients in peatlands, and (3) its usefulness in the differentiation and classification of peatlands and their plant communities.

REALITY AND CAUSE OF THE BIMODAL pH DISTRIBUTION

The reality of the bimodal frequency distribution of peatland pH is borne out by the fact that our data show it within 4 of the 6 regions of this study, and also within a single very large peatland, the Red Lake Peatland of Minnesota described by Glaser et al. (1981) and Wheeler et al. (1983). In the

Adirondacks — where acid deposition is severe — there is only an acid mode, and in the Atlantic Provinces only ombrotrophic bogs were examined. Data of Sjörs (1950) from North Swedish peatlands also exhibit a distinctly bimodal pH distribution (Fig. 5). Such bimodal pH frequencies are also exhibited by lakes in Nova Scotia (Underwood et al. 1982), Sudbury (unpublished diagram of E. Gorham and A.G. Gordon), and Norway (Wright and Henriksen 1977). It may be objected that our data were not collected at random, but the Norwegian lake data were collected by stratified random sampling. Moreover, our collections — designed to obtain adequate representation of all available types of bryophyte assemblage — probably over-sampled transitional ecotones (in the intermediate pH range) that account for only a very small part of the peatland area. This was certainly true in the Red Lake Peatland, as will be shown.

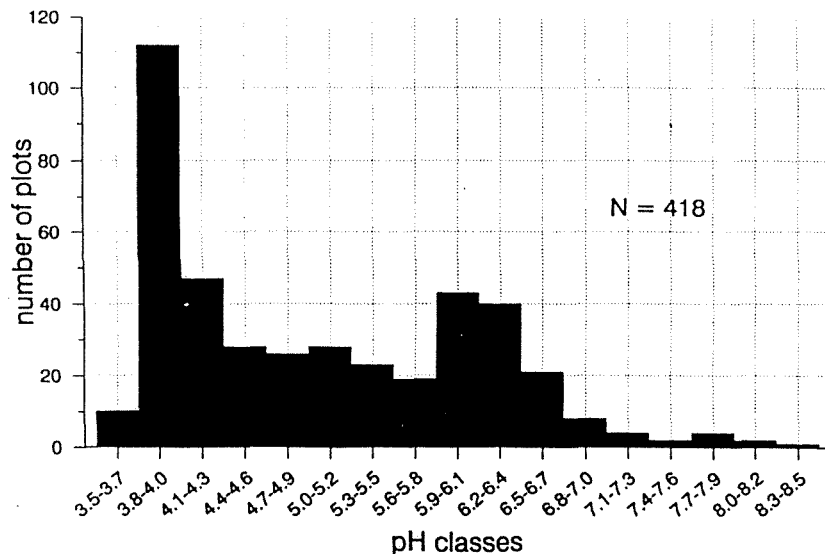


Fig. 5. Frequency distribution of pH in northern Swedish peatlands (data of Sjörs 1950)

It should be emphasized that these peatland pH-frequency distributions do not necessarily reflect the relative abundance of bog and fen, although we are convinced of the reality of the bimodal distribution. No attempt was made to weight the number of collections of any one type of moss assemblage by the area it covered in the region. In our studies, but not in those of Sjörs (1948, 1950), communities with few or no bryophytes were excluded.

The reality of the bimodal pH distribution is further supported by evidence as to cause. As shown by Gorham et al. (1984), once peat accumulates

sufficiently to isolate a fen surface from most minerotrophic inputs of bases (notably calcium bicarbonate) its surface water is liable to exhibit a sharp drop in pH, from above 6 in fens to around 4 in bogs. This happens as peat accumulation (normally derived largely from *Sphagnum* remains) domes the peatland surface well above ground-water level, so that the site becomes a hydrologic recharge area instead of a discharge area (cf. Kulczyński 1949). As minerotrophic inputs cease, base supply is no longer sufficient to neutralize the acids produced by the decomposition of plant detritus, alkalinity declines to zero, and the surface water becomes strongly acid. The triple point at which this shift tends to take place is defined, in one example studied, by a pH close to 6, calcium concentrations of about 150-250 $\mu\text{equiv L}^{-1}$, and an alkalinity (titrated to pH 4.5) of about 40 $\mu\text{equiv L}^{-1}$ (Gorham et al. 1987). That this pH shift is likely to be rapid can be explained as a consequence of the interaction of two different buffer systems (Urban et al. 1989).

Minerotrophic fens are buffered by bicarbonate from groundwater sources. As base supply is reduced by the vertical and horizontal accumulation of peat the concentration of bicarbonate declines, whereas that of organic acids — derived from the decomposition of plant detritus — increases because they are no longer diluted by ground water. The pK_a values of such organic acids are less than 4.5 (Urban et al. 1989), whereas calcium and bicarbonate alkalinity become abundant only above about pH 6.0 (Gorham et al. 1984, 1987). Because peatland waters are, therefore, poorly buffered between pH 4.5 and 6.0, slight shifts in the balance of bicarbonate and organic acids will result in large, sudden alterations in pH. Consequently, relatively few peatland sites will be found within the transitional range of unstable buffering. Figs. 2 and 3 suggest that the transitional range for North American sites may actually lie between about pH 4.8 and 6.2, whereas Fig. 5 suggests for north Sweden a transitional range between about pH 4.4 and 5.8. Perhaps base supply is lower on average in the north Swedish sites.

SPATIAL AND TEMPORAL GRADIENTS OF pH IN PEATLANDS

Transects across peatlands, particularly the larger ones, also reveal sudden transitions in pH, as in the Red Lake Peatland of Minnesota (Hofstetter 1969). Where the long western water-track fen (23 km from west to east) meets the bog-island complex of the west-central watershed (Fig. 6), pH changes sharply — within 200 m — from above 7 (after bubbling with CO_2 — free air) in the sedge fen to below 4 (with negligible effect of bubbling, see Gorham 1960) in the *Sphagnum* bog. Ecotone communities with transitional pH values are generally very narrow in this peatland (see also Glaser et al. 1981, Janssens et al. in press), and have therefore been over-sampled on an area basis.

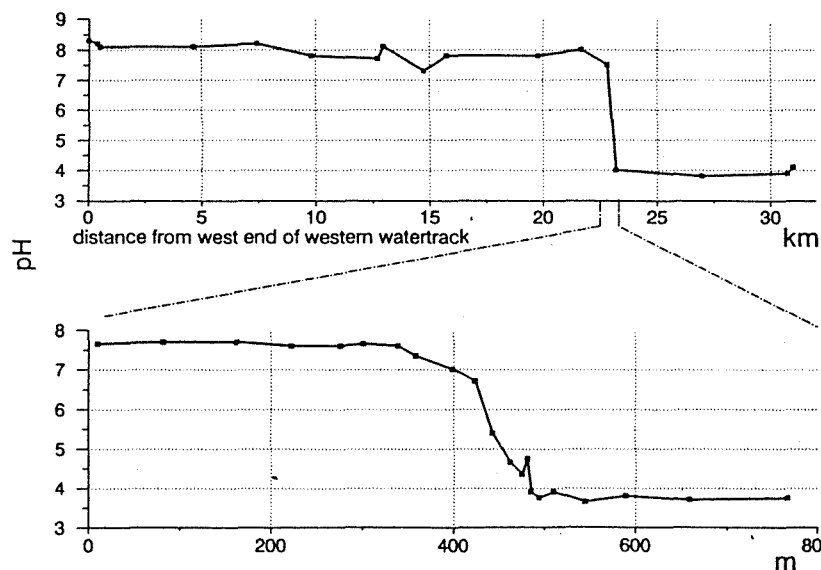


Fig. 6. Changes in pH along a 30-km west-to-east transect in the Red Lake Peatland, northern Minnesota (modified from Hofstetter 1969)

Stratigraphic studies of bryophyte-fossil assemblages in peat cores, coupled with data on pH tolerances in bryophytes currently occupying fen and bog surfaces, allow the reconstruction of pH profiles in fens and bogs (Gorham et al. 1987, Janssens 1987, 1988). These reveal (Fig. 7A) sudden transitions from a stable, circumneutral-fen environment to a stable, acid-bog condition, or sometimes (Fig. 7B) fluctuations in pH at a site where — owing to alterations in local hydrology — a narrow fen water-track between ovoid islands of bog expands and contracts. Kulczyński (1949) reported local shifts from fen to bog and back to fen again in karst-limestone sinkholes of the Polesie region.

DIFFERENTIATION AND CLASSIFICATION OF PEATLANDS AND THEIR PLANT COMMUNITIES

The data presented above can be used to support both bipartite and tripartite classifications of peatlands and their plant communities.

A bipartite separation into fen and bog is preferable in paleoecological studies (Fig. 7), because intermediate stages are transient and difficult to find and identify in the stratigraphic record. It is also useful where topographic gradients are steep and ecotones are therefore narrow. In such cases, and particularly in paleoecological research, it might be best to employ the old classification into acid bogs dominated by *Sphagnaceae* and circumneutral fens in which *Amblystegiaceae* are often prominent. The dividing line should probably be set in the

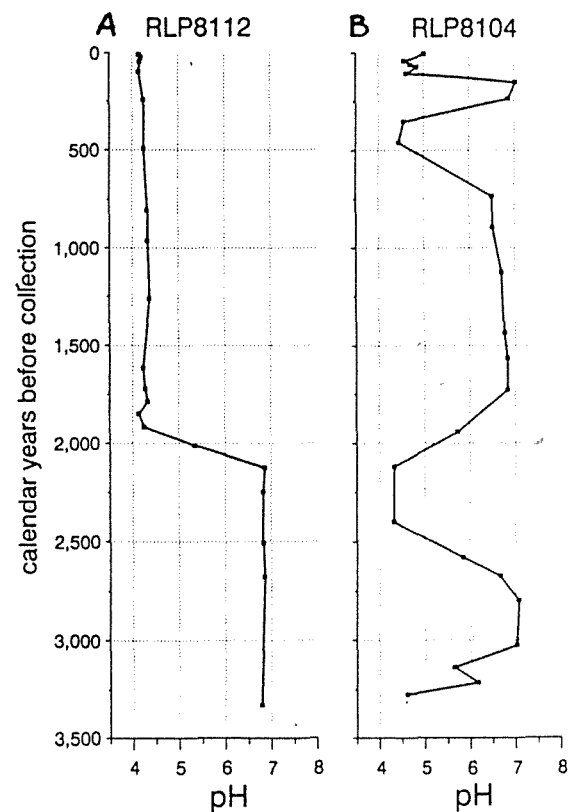


Fig. 7. Changes in pH during the development of fens and bogs in the Red Lake Peatland, Minnesota: (A) a sudden shift from stable fen to stable bog conditions, and (B) shifting back and forth owing to local alterations in hydrology along a narrow fen water-track dividing two bog "islands" (Janssens et al. in press)

vicinity of pH 5.7, where the two moss families overlap in Fig. 3 (top). That is the pH of distilled water in contact with atmospheric CO_2 , and sites with higher pH reflect the over-riding influence of base-rich water from the mineral soil, whereas sites with lower pH reflect the greater influence of acids generated by plant decomposition. Most species of mosses (and higher plants too) are abundant only on one side or the other of that boundary. Because water chemistry can fluctuate considerably in response to patterns of precipitation and evaporation, particularly when poorly buffered, a vegetational definition of fen and bog is to be preferred over one based solely on pH.

Such a bipartite division is quite different from the widely accepted division into minerotrophic fen and ombrotrophic bog. In both northern Sweden

(Sjörs 1950) and central to eastern North America (Gorham et al. 1985), ombrotrophic bogs do not occur above pH 4.6. Poor fens in the sense of Durietz (1949), which are often dominated by *Sphagnum* but include at least some "fen-indicator" plants, occur over a wide range of pH, 3.8-6.5 (Sjörs 1950), and many of them would be included as *Sphagnum* bogs if pH 5.7 were to be used as the fen/bog boundary. In this connection, rich fens are not found in northern Sweden below pH 5.8 (Sjörs 1950).

For a slightly more precise classification, or on very flat topography where ecotones are broad, a tripartite classification may be useful, and the present data-sets suggest possible boundaries. Figs. 2 and 3 indicate a rather steep rise in the cover of *Sphagnaceae* below pH 4.8, which is close to the boundary at pH 4.6 between minerotrophic and ombrotrophic conditions of mineral supply. A similar rise in the frequency of *Amblystegiaceae* occurs above pH 6.2, at which level calcium and bicarbonate alkalinity begin to rise sharply in fen waters (Gorham et al. 1984, 1987). Sites within the pH range 4.8-6.2 might therefore be regarded as a transitional group. Alternatively, the data of Sjörs (1950) for northern Sweden suggest a transitional pH range of 4.4-5.8. They also indicate that ombrotrophic bogs do not occur below pH 4.6 and minerotrophic rich fens do not occur below pH 5.8. The Intervening pH range, 4.6-5.8, might therefore be taken as an alternative in representing transitional sites. However, as noted above, the vegetation data of Sjörs show considerable overlap of his poor-fen community to both lower and higher pH values, with an overall range of 3.8-6.5. Given such a diversity of pH ranges, transitional types of peatland should probably be defined on a specific regional basis.

Few bryophyte species have their pH distributions centered in any of the transitional pH ranges described above. *Sphagnum subsecundum* is one of them (Fig. 3); in Minnesota it is often the first *Sphagnum* species to form true carpets in sedge meadows, preceding the invasion of more acidophilic carpet-forming *Sphagna* such as *S. recurvum* agg. and the development of strongly acid bog hummocks with species such as *S. magellanicum*, *S. capillifolium*, and *S. fuscum*. In the Red Lake Peatland of Minnesota the vascular plants *Potentilla palustris* and *Eriophorum tenellum* often accompany *Sphagnum subsecundum* in transitional ecotones between circumneutral sedge fens and strongly acid *Sphagnum* bogs (Gorham et al. 1987). Three peatland species rare in Minnesota — *Juncus stygius* var. *americanus*, *Xyris montana*, and *Rhynchospora fusca* — are also found in these ecotones.

These data indicate that pH frequency distributions, considered in conjunction with the abundance of *Sphagnaceae* and *Amblystegiaceae*, can provide information helpful in devising classifications of peatlands into fen and bog, with or without an intermediate transitional phase.

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Nowa interpretacja troficznego podziału torfowisk na podstawie udziału mszaków i odczynu wód powierzchniowych

Streszczenie

Badaniami objęto pięć dużych obszarów torfowiskowych w Północnej Ameryce, gdzie na 440 powierzchniach analizowano szatę roślinną i mierzono odczyn wód powierzchniowych. Otrzymano dwie wyraźne grupy ekologiczne torfowisk. Na jednej z nich dominują mszaki należące do *Amblystegiaceae* (z pH w zakresie 6,76-7,00), na innych torfowiskach wyraźną przewagę mają *Sphagnaceae* (wówczas pH wód powierzchniowych wynosi 4,01-4,25). Grupy te odpowiadają torfowiskom o typie "fens" i "bogs".

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