THE RESPONSE OF VEGETATION TO CHEMICAL AND HYDROLOGICAL GRADIENTS IN THE LOST RIVER PEATLAND, NORTHERN MINNESOTA

PAUL H. GLASER, JAN A. JANSSENS* AND DONALD I. SIEGEL†

Limnological Research Center, 220 Pillsbury Hall and *Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, MN 55455 and Department of Geology, Syracuse University, Syracuse, NY 13244, U.S.A.

SUMMARY

(1) Two peat mounds have developed in the Lost River peatland of northern Minnesota. One has the chemical and physical properties of an extremely rich fen and the other has the properties of a raised bog. The two mounds are separated by a water track with poor-fen vegetation and chemistry.

(2) The vegetation at Lost River can be divided into five types that correspond to landform units: spring-fen channel, spring-fen forest, marginal swamp forest, water track, and raised bog. These vegetation types have well-defined ranges for pH and calcium concentration.

(3) Ordinations of the vascular plant and bryophyte data indicate a close relationship between the vegetation and both moisture and chemical gradients. The link between vegetation and chemistry is also supported by plots of species richness vs. pH and calcium concentration in which the peak in species numbers occurs within the rich-fen range.

(4) The chemistry of the surface waters at Lost River is largely determined by the mixing of alkaline groundwater with precipitation, because the entire peatland is located at least seasonally within a discharge zone for groundwater. Mixing models indicate that the amount of groundwater within the surface waters ranges from 50% in the spring-fen channel to 1% on the raised bog.

(5) The development of the two peat mounds was reconstructed from peat cores collected near the crests of the spring-fen mound and raised bog. The raised bog developed over a depression, which was first filled in with fen peat before minerotrophic sphenog invaded the site around 2625 B.P. By 2200 B.P. all fen indicator species had disappeared and the site was dominated by assemblages similar to those in the present raised bog.

(6) The spring-fen mound, however, developed over a rise in the mineral substrate, which was not covered by peat until 3000 B.P. The mound was quickly colonized by Sphagnum and no fen indicators appeared until 1160 B.P. At this time the bog vegetation was replaced by a sedge fen containing assemblages similar to the present spring-fen channel.

(7) This sharp reversal from bog to fen under the spring-fen mound can best be explained by the discharge of alkaline groundwater at the peat surface in sufficient quantities to convert the bog vegetation to a spring-fen channel.

INTRODUCTION

The path of plant succession in boreal peatlands is closely linked to the rate and pattern of peat accumulation. Peatlands that develop a concave morphometry are exposed to runoff from mineral uplands, which provides a continual supply of alkaline, cation-rich water (Von Post & Granlund 1926; Sjörs 1948; Kulczyński 1949). The development of a convex peat mound, however, apparently isolates the peatland from this source because (i) the peat surface is raised above the flood level of soligenous runoff, and (ii) groundwater cannot penetrate through the dense layers of impermeable peat (Weber 1902; Von Post & Granlund 1926; Sjörs 1948). The mound is then nourished solely by atmospheric

1021
precipitation (ombrotrophic), which is not sufficiently alkaline to prevent *Sphagnum* establishment, and subsequent acidification of the site (Skene 1915; Clymo 1963). A convex peat mound should therefore develop into a raised bog, which has been considered a stable end-state of plant succession (Weber 1902; Walker 1970).

An important exception to this successional pathway occurs in the Lost River peatland of northern Minnesota, where two peat mounds have developed with contrasting vegetation and water chemistry. One of these mounds is a spring fen with the vegetation and chemical properties of an extremely rich fen. The other mound is indistinguishable from the other raised bogs of the region, which are presumed to be ombrotrophic. The unexpected anomaly between morphometry and peatland type at Lost River indicates that the relationship between hydrology and peat accumulation is not as straightforward as implied by the traditional pathway outlined above.

Only a few studies have sought to determine the development of raised peat mounds by both hydrogeological and ecological techniques (Wilcox, Shedlock & Henderson 1986; Siegel & Glaser 1987). The major advantage of such a study in the Lost River peatland is the close proximity of two different types of peat mounds. Previous papers on the Lost River area have described the topography and hydrogeology of this peatland (Almendinger, Almendinger & Glaser 1986; Boldt 1986; Chasson & Siegel 1986; Siegel & Glaser 1987). The present paper describes the vegetation and surface-water chemistry and reconstructs the development of these peat mounds by the stratigraphical analysis of peat cores.

**METHODS**

The Lost River peatland (48°12′N, 94°19′W) is located within the Glacial Lake Agassiz peatlands of northern Minnesota, which cover over one million hectares (University of Minnesota Agriculture Experiment Station 1980, 1981). The study area of 780 ha includes three different landforms: a spring-fen mound, a raised bog and a narrow water track that separates these two peat mounds (Fig. 1). The crest of the spring-fen mound and raised bog are nearly at the same altitude although the spring-fen mound is located over a rise in the mineral substratum, and the bog occupies a depression (Almendinger, Almendinger & Glaser 1986; Fig. 2). The slopes are gentle except for a slightly steeper drop on the western end of the spring fen. Peat depths range from about 2 m under the spring-fen mound to 3.3 m under the bog.

Both the spring-fen mound and the raised bog are located in discharge areas for groundwater, despite their raised topography and significant accumulation of peat (Siegel & Glaser 1987). The hydraulic-head gradients at the crest and margin of the raised bog reversed seasonally in 1983, when the vertical direction of water movement changed from a downward to an upward direction in the peat column. When upward gradients prevailed, the entire peat mass swelled, raising the elevation of the benchmarks, apparently as a response to a rise in pore pressure (Almendinger, Almendinger & Glaser 1986). The discharge of groundwater within an apparently ombrotrophic bog is quite unexpected. This finding was nevertheless supported by the chemistry of the pore water under the bog, in which the pH and calcium concentration at a depth of 1 m were similar to the values found in the underlying calcareous till. The past and present response of the peatland vegetation to this hydrological regime are described below.

The vegetation and water chemistry in the study area were sampled during July of 1982 and 1983. The stratigraphic cores were collected in November 1982 and July 1983. A
FIG. 1. Aerial photograph of the Lost River peatland, northern Minnesota. The features marked are: (1) spring-fen mound, (2) spring-fen channel, (3) marginal swamp forest, (4) water track, and (5) raised bog. The peat cores were collected from (A) the head of a spring-fen channel and (B) near crest of the raised bog.

FIG. 2. Topography and peat stratigraphy of the Lost River peatland, northern Minnesota. The site of the peat cores are marked by L8101 and L8204. Surface altitudes and depth to mineral soil were determined by Almendinger, Almendinger & Glaser (1986).
The helicopter provided access into this remote peatland, and sampling was conducted from a small base camp. The vegetation was described by relevés according to methods described by Glaser et al. (1981). A 10-m x 10-m plot was used for non-forested stands, whereas a larger 20-m x 20-m plot was laid out in forested stands (Westhoff & van der Maarel 1973). The relevés were arranged in vegetation tables partly by methods described by Shimwell (1971). However, the arrangement of the relevés in Tables 1 and 2 also follows their position along the topographic transect, which coincides with the chemical gradient. Separate tables were made for the bryophytes and vascular plants to compare their relative response to the important environmental gradients.

Nomenclature follows Fernald (1970) for vascular plants, Ireland et al. (1980) for mosses, Crum (1984) for Sphagnum spp., and Stotler & Crandell-Stotler (1977) for liverworts. Voucher specimens for all taxa are deposited either in the authors’ herbaria or the herbarium of the University of Minnesota.

The relevés were ordinated by two multivariate methods: detrended correspondence analysis for indirect gradient analysis (Hill 1979; Gauch 1982); and canonical correspondence analysis for direct gradient analysis (ter Braak 1986, 1987; Jongman, ter Braak & van Tongeren 1987). Three DCA ordinations were made for (i) the vascular-plant data, (ii) the bryophyte data, (iii) both the vascular plants and bryophytes. All samples were included in the ordination, and the individual species were weighted according to their cover value. The combined data set was also ordinated with CCA. The measured environmental variables were pH, conductivity, tree cover, herb/shrub cover, area of standing water, and the concentrations of Ca, Mg, Fe and SiO2. The number of species of vascular plants and bryophytes per relevé was plotted against calcium concentration and pH to evaluate the response of the vegetation to the water chemistry.

A water sample was collected in each plot in a 250-ml acid-washed plastic bottle. In each case it was possible to sample standing water, to avoid the problems associated with pits (Glaser et al. 1981). The samples were analysed for pH with a field pH meter and for conductivity with a field conductivity meter. The conductivity owing to hydrogen ions was subtracted (Sjörs 1950) to eliminate the effect of varying acidity. All pH and K corr readings were made at the end of each day in the field. The samples were then filtered and acidified for later analysis of the major cations, which were determined by direct-current plasma-emission spectrometry.

Peat cores were collected with a 10-cm-diameter piston-corer equipped with a serrated cutting edge (Wright, Mann & Glaser 1984). The core sections were cut longitudinally with a serrated knife to expose fresh, flat surfaces. The cores were then described according to the methods of Troels-Smith (1955) and the major types of macrofossils were identified from the important stratigraphic zones. Dating of peat samples by 14C was conducted by R. Stuckenrath of the Smithsonian Institution and by Beta-Analytic Inc. The samples contained at least 5 gm of peat (dry weight).

RESULTS

Landforms

The peat landforms in the Lost River peatland can be readily identified by their spatial pattern on aerial photographs (Fig. 1). The spring-fen mound is distinguished by an anastomosing network of non-forested channels that drain through the swamp forest covering the mound. The channels originate near the crest of the mound and drain downslope in a centrifugal pattern. The channels contain tree islands or linear fingers of
forest but are dominated by sedges. At the downslope edge of the mound some of the channels contain linear peat ridges (strings) running perpendicular to the slope.

The raised bog, in contrast, is distinguished by lines of spruce trees radiating from the bog crest. The spruce forms a closed canopy near the crest but downslope the flanks of the bog are covered by stunted trees forming a more open canopy. The outer margin of the bog is marked by the abrupt transition to a non-forested water track. The water track that separates the bog from the spring fen is essentially non-forested and contains a subtle linear pattern of shrubs or stunted trees parallel to the slope. Along the western edge of the spring fen, however, the water track grades into a tamarack swamp, which also has a subtle linear banding parallel to the presumed direction of flow.

Vegetation

The vegetation at Lost River can be divided into five noda, which closely correspond to different peat landforms and ranges in water chemistry (Tables 1 and 2). The most distinctive vegetation noda occur in the spring-fen channels, which contain a large assemblage of vascular plants and bryophytes restricted to these stands. The water track and other forested stands, in contrast, are best distinguished by changes in the relative abundance and the number of species plot−1 (Figs 3 and 4). The relevés in Tables 1 and 2 are generally arranged according to their position along the topographic transect, which corresponds to a pronounced chemical gradient extending from the crest of the spring-fen mound to the crest of the raised bog. The vegetation noda defined in Tables 1 and 2 are also distinguished by separate DCA ordinations of the vascular plant and bryophyte data (Fig. 5) as well DCA and CCA ordinations of the combined data set (Figs 5–7).

Spring-fen channels (Scirpus hudsonianus–Cladium mariscoides nodum)

The spring-fen channels are sharply delimited from the surrounding swamp forests by (i) their lower altitude, (ii) the soft substrate of sedge peat, (iii) large area of standing water, and (iv) their lack of forest cover. The vegetation in these channels contains the most sharply defined nodum at Lost River. This nodum is distinguished by a large number of extremely rich fen indicators (sensu Sjörs 1961, 1963) including Scirpus hudsonianus, Cladium mariscoides, Parnassia palustris and Muhlenbergia glomerata. The most important dominants are Scirpus cespitosus, Carex limosa, Cladium mariscoides and Carex lasiocarpa. Scirpus acutus generally forms large clones at the heads of the channels and at certain locations farther downslope. Carex exilis is also locally abundant. Also consistently present are Drosera anglica, D. intermedia, D. rotundifolia, Utricularia intermedia, U. cornuta, Rhynchospora alba, Eleocharis compressa, Carex livida, Sarracenia purpurea, Menyanthes trifoliata and Vaccinium oxyccocos. This nodum also contain several species that are rare plants in Minnesota: Triglochin palustris and Eleocharis rostellata are occasionally found near the channel margins, whereas Carex exilis, Cladium mariscoides, Drosera anglica and Drosera linearis are common in the wet depressions (Glaser 1983a, b). The dominant bryophytes in the channels are Scorpidium scorpioides and Campylium stellatum. Also present are Calliergon trifarium, Drepanoclados revolvens, Fissidens adianthoides, Moerkia hibernica and Cinclidium stygium.

Spring-fen forest (Picea mariana–Carex gynocrates nodum)

The spring-fen forest is more variable in composition, partly because of its more heterogeneous microtopography and the large gaps in the forest canopy created by treefalls. The substrate ranges from fallen logs, hummocks around the base of trees, wet
TABLE 1. Phytosociological table of the vascular plant species at the Lost River peatland, northern Minnesota. Each species is assigned a number, which corresponds to the species numbers in Fig. 7. The indicator species marked are (a) fen indicators, (a1) extremely rich fen indicators, (a2) rich-fen indicators, and (a3) poor-fen indicators (sensu Sjörs 1961, 1963; Wheeler et al. 1983). For any one relevé the species records are of two symbols, separated by a point. The symbols indicate cover and sociability.

<table>
<thead>
<tr>
<th>Relevé No</th>
<th>Spring-fen channel</th>
<th>Spring-fen forest</th>
<th>Swamp forest</th>
<th>Water track</th>
<th>Raised bog</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>107  111  112  113  114  115  109  110</td>
<td>108  116  117  118  119</td>
<td>122  120</td>
<td>121  123</td>
<td>190  191  124  125</td>
</tr>
<tr>
<td>pH</td>
<td>7.1  7.3  7.1  7.1  7  7  7</td>
<td>7.5  7  6.6  6.6  6.8  6.3</td>
<td>4.6  5.3</td>
<td>4  4  3  9  4</td>
<td>0.1</td>
</tr>
<tr>
<td>K_2SO_4</td>
<td>318  305  192  229  227  192  178  222</td>
<td>196  240  150  136</td>
<td>111  68  24  19</td>
<td>62  55  11  14</td>
<td></td>
</tr>
<tr>
<td>Ca</td>
<td>36  45  28  37  35  26  25  20</td>
<td>30  30  19  16</td>
<td>10  8  3  3</td>
<td>0.8  1.1  0.8  1.1</td>
<td></td>
</tr>
</tbody>
</table>

1. *Muhlenbergia glomerata* (a)
   +2  +2  +2  +2  +2
2. *Typha latifolia*
   +1  -  +2  +2  +1  +1
3. *Carex exida*
   3 2  -  1  +2  1  2  2
4. *Drosera anglica*
   +2  +2  +2  +1  +2
5. *Scirpus cespitosus*
   4 4  4  2  4  3  3  3  4  4  3  3
6. *Scirpus hudsonianus* (a2,a3)
   1 2  +2  1  2  1  2  +2  1  2
7. *Habenaria clavellata*
   +1  -  +2  -  +1  +2  +2
8. *Utricularia intermedia* (a3)
   +2  -  1  2  1  2  +2  +2
9. *Carex limosa*
   3 2  2  3  3  3  4  3  2  2  1  2  3  3
10. *Rhyhchospora alba*
    +2  +2  1  2  1  2  2
11. *Cladium mariscusces* (a1)
    +2  1  2  2  2  -  2  3  2
12. *Parnassia palustris* (a1)
    +2  +1  +2  +2  +2  +2  +2  +2
13. *Eleocharis compressa* (a)
    +2  +2  1  2  +2  1  2
14. *Carex liisida* (a2)
    +1  +2  1  2  +2  +1  +1
15. *Utricularia cornuta*
    +2  +2  +2  +2  +2  +2
16. *Carex aquatilis* (a)
    -  -  +1  -  1  2  2
17. *Phegmites communis* (a)
    -  -  +2  -  +1
18. *Thajj occidentalis* (a1)
    +1  +1  +2  -  +2  +1  3  2  1  2  +2  2  2 +2
19. *Carex lastocarpa* (a2)
    2 2  3  2  2  2  2  2  2  2  2  2  2  2
20. *Larix laricina*
    +1  -  +2  +1  +1  -  +2  +2  +1  +2  1  1  2  1  2  2
21. *Menyanthes trifoliata* (a3)
    +2  +2  1  2  1  2  +2  +2  +2  +2  +2  +2  +2  +2
22. *Sarracena purpurea*
    1 2  1  2  1  2  +1  -  1  2  1  2  +2  +2  +2  +2  +2  +2  +2  +2  +2  +2  +2
23. *Betula pumila var. glandulifera* (a3)
    +2  +2  +2  +2  1  2  1  2
24. *Carex interior* (a)
    -  +2  -  -  +2
25. *Rhamnus alnifolia* (a1)
    -  +2  -  -  +2
26. *Carex lepotelea* (a2)
    -  -  +2  -  -  -  2  2  2  2  -  -  +2
27. *Coptis groenlandica*
    -  -  -  -  +1  -  +2  1  2  -  +2
28. *Andromeda glauca)*
    -  +2  2  2  1  2  1  2  +2  +2  +2  +2  +2  +2  3  2  2  1  2  2  1  2
29. *Drosera rotundifolia*
    +1  +2  +2  +1  +2  +2  +2  +2  +2  +2  +2  +2
30. *Ledum groenlandicum*
    +1  -  -  -  -  +2  2  2  3  3  3  2  4  3  2  2  -  -  3  3  4  4  2  2  2
| 31. Vaccinium oxyccoccus | +2 +2 +2 +2 +2 +2 +2 +2 +12 +12 +12 +2 +2 22 22 12 12 |
| 32. Picea mariana | +1 +2 +2 +2 +2 +2 45 42 52 51 +2 22 22 +2 52 52 52 52 |
| 33. Lonicera silvosa var. solon | -2 +2 -2 -2 -2 -2 -2 -2 -2 -2 -2 -12 12 12 +1 +2 +2 |
| 34. Ephedra distilatata (a3) | -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 |
| 35. Eriophorum viridi-carnatum (a2) | -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 |
| 36. Galium labradoricum | +1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 |
| 37. Carex paucipetiola | +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 |
| 38. Carex tenunifolia (a2) | +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 |
| 39. Carex gunctoria (a1) | 33 32 42 22 22 12 12 12 12 12 12 12 12 12 12 12 12 |
| 40. Trientalis borealis | +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 |
| 41. Potentilla palustris (a) | -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 -1 |
| 42. Maianthemum canadense | +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 |
| 43. Rubus pubescens | +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 |
| 44. Carex chordorrhiza (a3) | +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 |
| 45. Lystimachia thyrsiflora (a) | +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 |
| 47. Vaccinium vitis-idaea | +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 |
| 48. Carex trisperma | 22 22 22 22 22 22 22 22 22 22 22 22 22 22 22 22 22 |
| 49. Chamadphne calycata | +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 |
| 50. Gaultheria hispidula | +1 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 |
| 51. Vaccinium myrtilliods | +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 |
| 52. Kalmia polifolia | +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 |
| 53. Eriophorum spumum | +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 +2 |

Additional Species (relêve no., cover, and soccheity): Drosera linearis (107, 1-2); Viola sp. (107, 1-2; 114, +1); Salix pedicellaris var. hypoglauca (107, +1); (122, 2, 121, +2); Triglochin maritima (107, +1; 111, +2; 112, +2; 115, +1; 110, +1; 122, 1-2); Carex praetex (111, +2; 108, +2; 122, +2); Carex interior (111, +2; 115, +2; 116, +2; 122, +2; 120, +2); Salix discolor (111, +1); Salix serratula (111, +2; 122, +2; 108, +1); Salix candida (111, +1; 122, +1; 120, +1; 117, +1); Rubus albus (111, +1; 116, +1; 119, +1; 122, +2); Habanaria hyperborea (111, +2; 109, +1; 115, +2); Carex capillaris (112, +2; 116, +2); Carex diandra (113, +2); Myrica gale (113, +1); Amelanchier humilis (113, +1); Carex distiplo (114, +2); unkn. (114, +1); Potentilla fruticosa (109, 3-2; 110, 2-2); Thelypteris palustris var. pubescens (110, +1; 122, 1-2); Pyrola sp. (109, +1); Lunea borealis (108, 1-2; 116, +2); Cypripedium acule (108, r.1.); Mitella nuda (108, +1; 116, +1); Orchis rotundifolia (108, 2; 116, +2; 117, +2); Habenaria obtusa (108, +1); Rubus hudsonianum (108, +1); Pyrola secunda (108, +1; 119, +2; 120, +1); Epipolium leptophyllum (108, +1); Campanula aparinoides (108, +1; 120, +2); Calitha palustris (108, +2; 117, +2, 118, +2); Malus sibirica (116, +2); Botrychium virgatum (116, +2); Pyrola assarifolia (116, +2; 120, +1); Lonicera oblongata (116, +2; 117, +2); Cornus canadensis (117, +2; 118, +2); Listera cordata (117, +1); cf Calamagrostis (117, +1); Chamaelipa umbellata (118, +1); Calamagrostis inexpansa (119, +2); Salix manchiana (119, +2; 120, +2); Alnus rugosa (122, 1-2); Salix graniis (122, +2); Osmunda cinnamomea (120, +2); Glycyrrhiza striata (120, +2); Calopogon pulchellus (120, +2); Calamagrostis canadensis (120, +2); Eriophorum gracile (190, 2-2); Carex oligosperma (125, 2-2); Carex pseudoflora (125, 2-2).

Cover symbols: +, sparsely present; 1, plentiful but small cover value; 2, very numerous, or covering 1/20 of area; 3, any number of individuals covering 1/20 area, any number of individuals covering 1/2 area, 5, covering more than 2 area. Socchiety symbols: 1, growing singly, isolated individuals, 2, grouped or tufted; 3, in small patches, 4, in small colonies, in extensive patches, or forming carpets; 5, in pure populations.
Table 2. Phytosociological table for the bryophyte species in the Lost River peatland, northern Minnesota. Values are for cover and sociability (for key, see Table 1).

<table>
<thead>
<tr>
<th>Relevé No.</th>
<th>Spring-fen channel</th>
<th>Spring-fen forest</th>
<th>Swamp forest</th>
<th>Water track</th>
<th>Raised bog</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>107</td>
<td>111</td>
<td>112</td>
<td>113</td>
<td>114</td>
</tr>
<tr>
<td>54. Calliergon trifurcatum (a1,a2)</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>55. Campylium stellatum (a1,a2)</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>56. Cinclidium stygium (a1,a2)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>57. Drepanocladius revolutus (a2)</td>
<td>+</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>58. Fissidens adiantoides</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>59. Hypnum lindbergii</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>60. Moerckia hibernica</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>61. Scorpidium scorpioides (a1,a2)</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>62. Aulacomnium palustre</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>63. Bryum pseudotriquetrum</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>64. Riccardia latifrons</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>65. Tomentypnum nitens (a1,a2)</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>66. Lophocolea heterophylla</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>67. Fissidens comandoides</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>68. Campylium hispidulum</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>69. Campylium polygamum</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>70. Dicranum undulatum</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>71. Calliergon giganteum (a1,a2)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>72. Calliergon richardsonii (a2)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>73. Calypogeia integristipula</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>74. Dicranum flagellare</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>75. Dicranum montanum</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>76. Dicranum polysetum</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>77. Hylocomium splendens</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>78. Hypnum pratense</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
moss carpets, and water-filled depressions. The vegetation nodum in this landform is primarily defined by the dominance of *Picea mariana* with *Larix laricina* and *Thuja occidentalis* and by Carex gynocrates with *C. leptalea*, *Ledum groenlandicum*, *Smilacina trifolia* and *Vaccinium vitis-idaea* in the field layer. Also consistently present are *Chamaedaphne calyculata*, Carex trisperma, *C. paupercula*, *Vaccinium oxyccocos* and *Rhamnus alnifolia*. The bryophyte cover on the forest floor is variable and contains between fifteen and fifty-five species per 20-m × 20-m stand. The moss cover is nearly continuous and consists of wet carpets and hummocks that have grown over the trunks of fallen trees. Dominant species include *Pleurozium schreberi*, *Sphagnum angustifolium*, *Hylocomnium splendens*, *Sphagnum capillifolium* and *Dieranum polysetum*. This nodum contains several moses that are rare in Minnesota including *Cinclidium stygium*, *Rhizomnium gracile* and *Calliergon afontianum*, which was previously known only as a fossil (Janssens & Glaser 1983a, b, 1986; Janssens 1989).

**Marginal swamp forest** (*Carex chordorrhiza*–*Lysimachia thrysiflora nodum*)

The ecotonal swamp forest at the eastern edge of the spring fen mound is distinguished by its more open canopy and by its heterogeneous peat surface of moss-covered hummocks and water-filled depressions. The vegetation nodum of this zone is floristically distinguished by *Lysimachia thrysiflora*, *Potentilla palustris*, *Carex chordorrhiza* and *Rubus pubescens*. The canopy is dominated by *Picea mariana* with *Larix laricina*. Most of the important species of the spring-fen forest extend into this nodum, such as *Betula pumila* var. *glandulifera*, *Equisetum fluviatile*, *Eriophorum viride-carinatum*, *Potentilla palustris*, *Kalmia polifolia* and *Lonicera villosa* var. *solonis*. The diversity of bryophytes is high (thirty-two to fifty-one species per 20-m × 20-m plot) but only *Campylium polygamun*, *Brachythecium campestre* and *Calypogeia muelleriana* are restricted to these stands.

**Water track** (*Carex lasiocarpa*–*Utricularia intermedia nodum*)

The water track that separates the bog and spring fen contains well-developed hummocks of *Sphagnum* and scattered pools of standing water. The vegetation nodum in this landform is similar to the *Tryglochin maritima*–*Drosera intermedia* nodum (sensu Glaser et al. 1981) of the Red Lake peatland but it lacks many of the important fen indicator species including the two type species. The fen indicators present in this nodum include *Carex lasiocarpa*, which is the dominant species with *Utricularia intermedia*, *Equisetum fluviatile*, *Potentilla palustris* and *Carex chordorrhiza*. Also present are *Menyanthes trifoliata*, *Sarracenia purpurea*, *Drosera rotundifolia* and the ericaceous shrubs. Small stunted individuals of *Larix laricina* are present on top of the hummocks. The bryophyte cover in the water track is very high and includes *Sphagnum angustifolium*, *S. magellanicum*, *S. warnstorffii*, *S. fuscum*, *Polytrichum strictum* and *Aulacomnium palustre* as the most important dominants.

**Raised bog** (*Carex trisperma*–*Vaccinium vitis-idaea nodum*)

The raised bog at Lost River is characterized by open stands of *Picea mariana* and a continuous cover of *Sphagnum*, which forms an amorphous microtopography of hummocks and hollows. At the crest of the bog the spruce forms a closed canopy forest but on the lower bog flanks the forest is more open. The vegetation is very similar to the *Carex trisperma*–*Vaccinium vitis-idaea* nodum (sensu Glaser et al. 1981) of the Red Lake peatland. The understorey is dominated by the ericaceous shrubs, particularly *Ledum groenlandicum*, *Andromeda glaucophylla*, *Chamaedaphne calyculata* and *Kalmia polifolia*.
Also common throughout the bog are *Smilacina trifolia* and *Carex trisperma*. The vascular flora of the bog is otherwise very small, and no minerotrophic indicator species (*sensu* Sjörs 1963, 1983; Wheeler et al. 1983) are present. The field layer is dominated by *Sphagnum angustifolium*, *S. fuscum*, *S. magellanicum*, *S. capillifolium*, Polytrichum strictum and Pleurozium schreberi.

**Water chemistry**

The chemical gradient at Lost River covers the entire range reported for boreal peatlands (Sjörs 1950, 1983; Heinselman 1970). At one end of the gradient are the spring-fen samples, which are characteristic of other extremely rich fens in Minnesota (Heinselman 1970; Glaser 1983a, 1987a). The pH in these samples is generally above 7, and the Ca concentration ranges from 20 to 45 mg l$^{-1}$ (Tables 1 and 3). The other end of the gradient is represented by the samples from the raised bog that have a pH below 4 and a Ca concentration below 1·1 mg l$^{-1}$. These samples are indistinguishable from those of typical ombrotrophic bogs in Minnesota (Heinselman 1970; Glaser et al. 1981; Glaser 1983c, 1987a). Water chemistry typical of rich fens (pH 6·8–6·3; Ca 18·8–8·1 mg l$^{-1}$) occurs on the east side of the spring-fen mound and marginal forest, whereas poor-fen waters (pH 5·3–4·6; Ca 2·6–3·0 mg l$^{-1}$) characterize the water track.

The chemical gradient at Lost River is closely related to topographic position along the transect line. The pH, specific conductance ($K_{corr}$) and calcium concentration are highest on the west slope of the spring-fen mound near the crest. Downslope from the crest these values decline but the gradient is steeper on the east side of the mound. On the raised bog, however, there is no noticeable change in the water chemistry from the crest to the lower bog flanks.
**Species richness**

The response of the vegetation to the chemical gradient at Lost River was also analysed by plotting the number of species found in each relevé vs. the pH and calcium concentration of the surface water (Fig. 3). The species richness data fit a relatively smooth curve except within the rich-fen range, where a peak in species abundance occurs. The number of vascular plant and bryophyte species is very low within the ombrotrophic bog, but the number of bryophyte species is even lower within all but one stand of extremely rich fen. The number of vascular plant species, in contrast, generally rises with increasing pH and Ca, although the peak in abundance occurs within the chemical range associated with rich-fens in Minnesota (*sensu* Heinselman 1970; Glaser 1987a). The effect of substrate variability is indicated by the shaded data points for forested stands, where the peat substrate is generally more variable. The outlier point in the bryophyte species-richness curve is from a forested stand within the extremely rich fen range.

In each vegetation type a close relationship exists between the number of vascular plant species and the number of bryophyte species found within a relevé (Fig. 4). All the relevés may be sorted into their different vegetation types on the basis of this relationship, which is particularly close in the raised bog and spring-fen channel relevés. Only one relevé from a large gap in the spring-fen forest falls within the range of another vegetation type. The forested stands generally have higher species number and more variability between samples. However, no noticeable difference was recorded between forested and non-forested stands on the raised bog.

**Detrended correspondence analysis**

The major environmental gradients controlling the vegetation patterns at Lost River were also inferred by detrended correspondence analysis, in which the major patterns of variation in species composition may be compared to environmental gradients. The relative role of the more deeply rooted vascular plants was compared to that of the more shallow absorbing organs of the bryophytes by running three separate ordinations: the vascular plant scores (Fig. 5a), the bryophyte scores (Fig. 5b), and the combined data set (Fig. 5c).

These three ordinations produce very similar results, indicating a similar response of the major plant types to water level and water chemistry. Most of the variation in the data sets is expressed along axis 1, which corresponds to a moisture gradient. The spring-fen relevés, which have the wettest surface, are grouped on the right side of this axis, whereas the drier forested stands are positioned to the left. The chemical gradient does not directly correspond to any of the DCA axes, but each of the vegetation types delineated by the ordination represents a distinct range in pH and calcium concentration. Thus, the ordinations strongly support the vegetation types identified in the vegetation tables.

**Canonical correspondence analysis**

The quantitative relationship of the species and relevés to the environmental variables at Lost River was approximated by canonical correspondence analysis (ter Braak 1986, 1987; Jongman, ter Braak & van Tongeren 1987). The species and relevés are indicated by points on the joint plot, whereas the environmental variables are plotted as arrows, which determine the axes of the diagram (Figs 6 and 7). The weighted averages of the species with respect to the environmental variables are approximated by projecting a perpendicular line from each species point on to the axis of each environmental variable. The end-
Fig. 3. Species richness along chemical gradients in the Lost River peatland. The number of bryophyte species found in the relevés is indicated by triangles, whereas the vascular plants are indicated by circles. The dashed lines indicate ranges in water chemistry corresponding to the bog-poor-fen-rich-fen-extremely rich fen series identified by Heinselman (1970) and Glaser (1987a) for northern Minnesota. Shaded symbols indicate larger relevés (20 m x 20 m) from forested stands. The curves show the major trends in the data set.
points of these perpendiculars indicate the centre of a species distribution (weighted average) along a particular environmental axis. Environmental variables with long arrows are more strongly related to the pattern of variation in the species composition than those with short arrows.

The CCA diagram for the relevés (Fig. 6) indicates that axis 1 most closely corresponds to the area of standing water (STAGW), which has the highest canonical coefficient (113) and inter-set correlation (961) for axis 1 (Table 4). Tree cover has the strongest negative correlation to axis 1, and the direction of its arrow is nearly the opposite of that for standing water. Chemical variables, such as Ca concentration, conductivity, SiO₂ concentration and pH, have progressively lower inter-set correlations for axis 1. Ca concentration, however, has a very high variance inflation factor (VIF > 21) indicating that it is almost perfectly correlated with another factor, such as conductivity (VIF > 9.5), and therefore has no unique contribution to the regression coefficient. These chemical variables are also related to pH (VIF > 14).

Axis 2 most closely corresponds to Fe concentration, which has an inter-set correlation of 692 (Table 4). The pH of the surface waters has the strongest negative correlation for axis 2 and the direction of its arrow on the ordination diagram is nearly the opposite of that for Fe.

The CCA ordination diagram for the relevés indicates that the spring-fen relevés have the highest weighted averages for standing water, whereas the spring-fen forest and raised bog relevés have the lowest (Fig. 6). The swamp forest and water track relevés are centred at an intermediate position along this gradient but are located closer to the drier end. With respect to pH, the spring-fen relevés have the highest inferred weighted averages and the raised bog relevés the lowest, whereas the relevés from the spring-fen forest, swamp forest, and water tracks have intermediate averages.
The CCA ordination for the species (Fig. 7) shows the approximate centre for the distribution (inferred weighted averages) of each species along the various environmental gradients at Lost River. *Muhlenbergia glomerata, Carex exilis, Drosera anglica, Typha latifolia* and *Rhynchospora alba*, for example have the centre of their distributions at the wettest end of the gradient for standing water (STAGW), whereas *Dicranum flagellare, Carex trisperma, Dicranum polysetum, Hylocomnium splendens* and *Kalmia polifolia* are located at the driest end. For pH, *Kalmia polifolia, Carex trisperma, Vaccinium oxyccocos, Dicranum flagellare, Sphagnum russowii and Mylia anomala* are respectively centred near the lowest values, whereas *Carex aquatills, Moerckia hibernica, Calliergon trifarium*, etc.
Chemical and hydrological gradients

**Fig. 6.** Canonical correspondence analysis ordination diagram of the Lost River peatland vegetation relevés with the environmental variables represented by arrows. The environmental variables are: standing water (STAGW), conductivity (cond.), pH, Ca concentration (Ca), Fe concentration (Fe), SiO₂ concentration (SiO₂), tree cover (TCV), and forb/shrub cover (FSCV). The relevés are: (▲) spring-fen channel, (◇) spring-fen forest, (◇) swamp forest, (□) water track and (■) raised bog. The eigenvalues are 0.67291 for axis 1 and 0.22853 for axis 2. The diagram accounts for 65% of the variation of the weighted averages.

**Table 4.** Canonical coefficients and inter-set correlations of environmental variables with the first two axes of CCA for Lost River data.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficients</th>
<th>Correlations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Axis 1</td>
<td>Axis 2</td>
</tr>
<tr>
<td>STAGW</td>
<td>113</td>
<td>37</td>
</tr>
<tr>
<td>Ca</td>
<td>-4</td>
<td>-2</td>
</tr>
<tr>
<td>Cond.</td>
<td>17</td>
<td>19</td>
</tr>
<tr>
<td>SiO₂</td>
<td>-23</td>
<td>19</td>
</tr>
<tr>
<td>pH</td>
<td>28</td>
<td>-78</td>
</tr>
<tr>
<td>FSCV</td>
<td>-3</td>
<td>5</td>
</tr>
<tr>
<td>Fe</td>
<td>28</td>
<td>3</td>
</tr>
<tr>
<td>TCV</td>
<td>-40</td>
<td>19</td>
</tr>
</tbody>
</table>

*Thuja occidentalis, Lonicera villosa* and *Galium labradoricum*, respectively, are centred at the highest values.

**Stratigraphy**

The development of the two peat mounds at Lost river was determined from two cores taken near the piezometer nests described in Siegel & Glaser (1987). The first core (8201) was collected near the head of a spring-fen channel (Fig. 2) and contains five biostratigraphic units (Tables 5 and 6; Fig. 8). The upper part of this core (0–70 cm)
consists of sedge peat with the minerotrophic bryophytes *Bryum pseudotriquetrum*, *Calliergon trifarium* and *Drepanocladus revolutens*. At 70 cm there is a sharp contact with the lower zone (70–195 cm) of *Sphagnum*/wood peat. The *Sphagnum* zone is composed of *S. fuscum* and *S. magellanicum* and abundant remains of *Picea*. The lower part of this *Sphagnum* zone (195–214 cm) contains deeply humified peat, which may be of detrital origin. Below 214 cm there is a thin layer of deeply humidified peat that grades into the basal layer of sandy clay and gravel at 220 cm.

The longer core (8204) from the raised bog has a different stratigraphy. *Sphagnum* peat interspersed with layers of wood extends from the surface to a depth of 250 cm. The upper portion of this *Sphagnum* zone (0–205 cm) is characterized by *S. magellanicum* and *S.
angustifolium, with needles of Picea. Below 205 cm Larix needles replace Picea, but there are no minerotrophic indicators until a depth of 232 cm. From 232 to 250 cm the woody peat contains remains of Sphagnum subsecundum, S. sect. Squarrosa, Drepanocladus sp. and leaves of Ericaceae. Very large pieces of wood occur between 260 and 279 cm and the peat contains the remains of Calliergon trifarium. The wood layer is replaced below by sedge peat (298–314 cm), which contains Calliergon trifarium, C. giganteum, cf. Tomentypnum nitens, Bryum pseudotriquetrum, Carex, Scirpus, Menyanthes, Potamogeton, Tomentypnum nitens. Below 314 cm the deeply humified peat grades into the basal layer of silty clay.

The chronology of peat development at Lost River was determined from seven radiocarbon dates (Tables 7 and 8; Fig. 8). The relative elevation of these dated levels within the peat column can be determined because the surface of the coring sites was established from the nearest benchmark of the topographic survey (Almendinger, Almendinger & Glaser 1986; Siegel & Glaser 1987). Organic matter first began to accumulate in the depression under the raised bog at 8295 ± 105 B.P. (SI-5997), whereas accumulation did not begin on the mineral rise under the spring fen until 2925 ± 55 B.P. (SI-5993). Minerotrophic Sphagnum appeared at the raised bog site by 2625 ± 70 B.P. (SI-5996), and by 2240 ± B.P. (SI-5995) the minerotrophic species had all been replaced by assemblages similar to the present bog vegetation. At the spring fen, however, the reversal from bog to fen assemblages at 70 cm is dated at 1160 ± 80 B.P. (Beta-20660).
TABLE 5. Stratigraphy of spring-fen channel.

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Sediment type</th>
<th>Reconstruction</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–9</td>
<td>3Dh^1Dg^3</td>
<td>Spring-fen channel</td>
</tr>
<tr>
<td>9–13</td>
<td>2Db^1Dh^1Dg^3</td>
<td>Spring-fen channel</td>
</tr>
<tr>
<td>13–19</td>
<td>1Dh^3Dg^3</td>
<td>Spring-fen channel</td>
</tr>
<tr>
<td>19–38</td>
<td>2Dh^2Dg^3</td>
<td>Spring-fen channel</td>
</tr>
<tr>
<td>38–45</td>
<td>1Dh^1Dg^2Tb^2</td>
<td>Spring-fen channel</td>
</tr>
<tr>
<td>45–68</td>
<td>1Dh^1Tb^2Dg^3</td>
<td>Spring-fen channel</td>
</tr>
<tr>
<td>68–70</td>
<td>2Dh^2Dg^2+Tb^2</td>
<td>Spring-fen channel</td>
</tr>
<tr>
<td>70–89</td>
<td>2Db^1Dh^3Dg^3</td>
<td>Bog forest (Larix)</td>
</tr>
<tr>
<td>98–119</td>
<td>3Db^1Dg^3+Dh^2,Db^2</td>
<td>Bog forest (Picea)</td>
</tr>
<tr>
<td>119–122</td>
<td>2Dl^2Dg^3+Dh^2</td>
<td>Bog forest (Picea)</td>
</tr>
<tr>
<td>122–147</td>
<td>2Tb^2Db^2+Dg^3,Dh^2</td>
<td>Bog forest (Picea)</td>
</tr>
<tr>
<td>147–195</td>
<td>2Db^1Dg^3+Dh^3,Db^2</td>
<td>Bog forest (Picea)</td>
</tr>
<tr>
<td>195–214</td>
<td>2Dl^1Db^1Dg^3+Dh^3</td>
<td>Bog forest (Picea)</td>
</tr>
<tr>
<td>214–218</td>
<td>4Dg^4</td>
<td>Fen?</td>
</tr>
<tr>
<td>218–222</td>
<td>1Dg^3As (very firm)</td>
<td>Till</td>
</tr>
<tr>
<td>222–238</td>
<td>4As+Ga (maj.)</td>
<td>Till</td>
</tr>
</tbody>
</table>

The symbols for the sediment and peat types follow Troels-Smith (1955): Tb (Turfa bryophytica), bryophyte remains with the leaves still attached to the stems; Db (Detritus bryophyticus), fragments of bryophytes < 2 mm; Di (Detritus lignosus), fragments of ligneous plants < 2 mm; Dh (Detritus herbosus), fragments of herbaceous plants < 2 mm; Dg (Detritus granosus), unidentifiable fragments < 2 mm; Ld (Limus detritosus), plant and animal remains < 0.1 mm; As (Argilla steatodes), particles of clay < 0.002 mm; Ga (Grana arenosa), mineral particles 0.6–0.2 mm. The superscripts are classes of humification on a scale from 0 (unhumified) to 4 (highest humification).

TABLE 6. Stratigraphy of raised bog core.

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Sediment type</th>
<th>Reconstruction</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–205</td>
<td>2Db^2Db^1Dl^2</td>
<td>Bog forest (Picea)</td>
</tr>
<tr>
<td>205–232</td>
<td>2Db^2Db^1+Di^2</td>
<td>Bog forest (Larix)</td>
</tr>
<tr>
<td>232–250</td>
<td>2Db^2Db^3+Di^2</td>
<td>Swamp forest (Sphagnum)</td>
</tr>
<tr>
<td>250–279</td>
<td>1Db^2Dh^2Dg^3+Di^2</td>
<td>Swamp forest (Larix, Calliergon)</td>
</tr>
<tr>
<td>279–298</td>
<td>2Db^2Db^1Dg^3+Di^3</td>
<td>Swamp forest</td>
</tr>
<tr>
<td>298–314</td>
<td>3Dbh^1Dg^3</td>
<td>Sedge fen</td>
</tr>
<tr>
<td>314–320</td>
<td>3Dg^3Si (very firm)</td>
<td>Fen</td>
</tr>
<tr>
<td>320–327</td>
<td>3SiAs (very firm)</td>
<td>Lake Sediment</td>
</tr>
</tbody>
</table>

For explanation of symbols see Table 5.

TABLE 7. Radiocarbon dates from the spring-fen channel.

<table>
<thead>
<tr>
<th>Core No.</th>
<th>Lab. No.</th>
<th>Sample depth (cm)</th>
<th>^14C age (years B.P.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LR-8203</td>
<td>Beta-20660</td>
<td>65–70</td>
<td>1165 ± 85</td>
</tr>
<tr>
<td>LR-8203</td>
<td>SI-5994</td>
<td>90–95</td>
<td>1545 ± 95</td>
</tr>
<tr>
<td>LR-8203</td>
<td>SI-5993</td>
<td>225–230</td>
<td>2925 ± 55</td>
</tr>
</tbody>
</table>


**Table 8. Radiocarbon dates from the raised bog core.**

<table>
<thead>
<tr>
<th>Core No.</th>
<th>Lab. No.</th>
<th>Sample depth (cm)</th>
<th>$^{14}$C age (years B.P.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LR-8204</td>
<td>SI-5994</td>
<td>90-95</td>
<td>1165 ± 85</td>
</tr>
<tr>
<td>LR-8204</td>
<td>SI-5995</td>
<td>185-190</td>
<td>2240 ± 100</td>
</tr>
<tr>
<td>LR-8204</td>
<td>SI-5996</td>
<td>232-237</td>
<td>2625 ± 70</td>
</tr>
<tr>
<td>LR-8204</td>
<td>SI-5997</td>
<td>320-325</td>
<td>8295 ± 105</td>
</tr>
</tbody>
</table>

**DISCUSSION**

**Vegetation patterns**

The vegetation in boreal peatlands is very sensitive to water chemistry, and different vegetation types correspond to different ranges in pH and Ca concentration (Sjörs 1950, 1983; Heinselman 1970). According to northern European concepts these types are related to different hydrogeochemical regimes, and the vegetation and chemistry in peatlands can be used as a surrogate for hydrological data. At Lost River these assumptions can be directly tested because the hydrology of the site was previously determined by measuring head gradients in piezometers and analysing the chemistry of interstitial pore waters (Siegel & Glaser 1987).

At Lost River the presence of indicator species provides a consistent means of separating relevés with the chemical properties of fens (pH > 4.2 and Ca > 2 mg l$^{-1}$) from those of bogs (pH < 4.2 and Ca concentration < 2 mg l$^{-1}$). Finer ranges of chemistry, however, can only be predicted by the vegetation in the non-forested fens. The distinctive species assemblage in the spring-fen channels contains a large group of extremely rich fen indicators, whereas the lower number of fen indicators in the water track correlates with its poor-fen waters.

Within the forested fens, however, the more variable species assemblages provide much less evidence for changes in water chemistry. Despite the steep chemical gradient from the crest of the spring-fen mound (pH 7.5; Ca 29-6 mg l$^{-1}$) to the margin of the water track (pH 6.3; Ca 8-1 mg l$^{-1}$) there is no consistent change of fen indicator species. The species richness curves, however, seem to exhibit a clearer response to the chemical gradient.

The number of species generally reaches a peak in the rich-fen range of the gradient, although stands with the highest number are also forested (Figs 3 and 4). Above a calcium concentration of 20 mg l$^{-1}$ there is no further rise in the number of vascular plant species and the number of bryophytes actually declines with increasing calcium. The peak in species richness within the rich-fen range at Lost River contrasts with other ecosystems reviewed by Tilman (1982, 1986), in which maximum species diversity occurs in moderately resource-poor habitats.

The degree of heterogeneity of the substrate clearly plays a significant role in controlling the composition of the vegetation. The marginal swamp forest has the most variable surface in the Lost River peatland with a continuous microtopographic gradient from high hummocks at the base of the trees to water-filled depressions. The bryophytes seem to be particularly sensitive to this substrate factor, because the number of species plot$^{-1}$ is lowest in the vegetation types with the most uniform microtopography. Species diversity is lowest in the spring-fen channels, apparently because of the high water table and lack of structural support, whereas the relatively uniform carpets of *Sphagnum* in the raised bog provide little differentiation to the surface.

The conspicuous difference in structural characteristics between vascular plants and
bryophytes may account in part for the different shapes of their species curves across the chemical gradient at Lost River. The importance of the substrate in determining the composition of the vegetation is supported by the DCA and CCA ordinations in which the first and most important axis most closely corresponds to a wetness gradient, with the wettest spring-fen channels on the right and the drier forested relevés on the left (Figs 5 and 6).

The vegetation and water-chemistry data from Lost River, however, should still provide unambiguous indicators for the hydrology of the three landforms: the spring-fen channels, the water track and the raised bog. The extremely high pH and Ca concentration in the spring-fen channels can only be maintained by a continuous discharge of groundwater from the underlying calcareous till. This assumption is verified by the upward gradients in hydraulic head that were measured in the piezometer nest near the head of a channel and by the chemistry of the interstitial pore waters (Siegel & Glaser 1987). The marked chemical gradient in the surface waters downslope from the head of a channel further indicates that the source of these drains is a focus for the upwelling of groundwater.

The poor-fen chemistry and vegetation of the water track would be expected if this site received all its water and salts from surface runoff. The nearest mineral outcrops are located 16 km to the north, and the alkalinity in these waters should decline with increasing distance from this source because of (i) dilution with rainwater, (ii) the active assimilation of cations by living plants, and (iii) the sequestering of cations by cation exchange. The piezometric measurements, however, indicate that the edge of the water track is seasonally in a discharge area for groundwater. The higher pH and Ca concentration of the interstitial pore waters at depth may account for the dominance of the deeper-rooted Carex lasiocarpa, which otherwise does not attain such high cover values in poor fens (Glaser 1987a). Apparently the volume of groundwater discharging at the peat surface provides insufficient alkalinity to buffer the fen waters at a higher pH.

The most unexpected finding is the occurrence of apparently ombrotrophic bog vegetation on a landform that is periodically in a discharge area for groundwater. Despite the very low pH (4·1 or lower), and low Ca concentration (1·1 mg l$^{-1}$) at the surface of the bog, the chemistry of the interstitial pore waters rises to that found in the underlying calcareous till at only 1 m in depth (Siegel & Glaser 1987). The upwelling groundwater is apparently diluted in the uppermost 1 m of peat by infiltrating surface water to the point where it is indistinguishable from that of typical ombrotrophic water. The vegetation is apparently too shallow-rooted to be affected by the highly minerotrophic waters at less than 50 cm depth. This lower zone of minerotrophic pore-water is not a relict of previous fen vegetation, because the bog is underlain by several metres of Sphagnum peat that lacks fen indicators.

**Surface-water chemistry**

The surface-water chemistry at Lost River is primarily controlled by the degree of mixing between groundwater upwelling from the calcareous mineral substrate and atmospheric precipitation. The linear relationships between specific conductance ($K_{corr}$) and the concentration of dissolved cations, such as calcium and magnesium, indicates that the concentrations of these dissolved solids varies mostly in response to mixing (Fig. 9). The approximate proportion of groundwater in the surface water can therefore be calculated from the mixing eqns 1 and 2:

$$C_s = f_p C_p + f_g C_g$$  \hspace{1cm} (1)
and because \( f_p + f_g = 1 \)

\[
  f_g = (C_s - C_p)/(C_g - C_p),
\]

(2)

where \( C_s \) = concentration of solute in surface water, \( C_p \) = concentration of solute in precipitation, \( C_g \) = concentration of solute in groundwater, \( f_g \) = the fraction of groundwater, \( f_p \) = the fraction of precipitation.

The concentrations of calcium and magnesium in the groundwater at Lost River are 2.15 and 1.43 mmol l\(^{-1}\), respectively (Siegel & Glaser 1987), whereas the concentrations of these two cations in the regional precipitation are 20 and 4 \( \mu \)mol l\(^{-1}\), respectively (Munger & Eisenreich 1983). Substitution of these values in eqns 1 and 2 yields 1\% as the approximate amount of groundwater in the surface water of the raised bog in 1982, whereas in the spring-fen channel it ranged as high as 50\%.

The isotopic content of surface waters from the Lost River area indicates that evaporation does not significantly alter the calculated proportions of discharge in forested stands by concentrating solutes (Fig. 10). The ratio of stable isotopes of oxygen (\( \delta^{18}O \)) and hydrogen (deuterium) in surface water from forested stands in the Lost River peatland are identical to that of precipitation in northern Minnesota (U.S. Geological Survey, unpublished). The isotopic content of surface water from non-forested fens, in contrast, was enriched with respect to the \( ^{18}O \) content of precipitation. This trend of isotopic enrichment is typically produced by evaporation. The amount of groundwater discharge to the spring-fen channels may therefore be overestimated by the mixing model, but it is probably of the same order of magnitude because calculations of discharge volumes using hydrogeological analysis (Siegel & Glaser 1987) produce similar results.

Although mixing of groundwater and precipitation is the major process that controls the surface-water chemistry, decreasing calcium–magnesium quotients against specific conductance (\( K_{corr} \)) from about 1.6 in groundwater to as low as 0.9 in bog surface water (Fig. 11) indicates that calcium is preferentially assimilated by mire plants and removed.
The isotopic content of mire waters from the Lost River area, northern Minnesota. The samples were collected from forested bogs (□) and non-forested fens (■) during the summer of 1981. Samples enriched with respect to $^{18}$O are indicative of evaporative concentration. All values are relative to standard mean oceanic water (SMOW).

The Ca–Mg quotient in surface water decreased from about 1·5 at the head of a spring-fen channel to about 1·3 approximately 1 km downslope further indicating the preferential assimilation of calcium by mire plants, or adsorption to peat. Calcium was not being removed in the channels by inorganic precipitation, because no marl was observed either in the channel pools or within the peat profile. The surface water in the channels is probably undersaturated with respect to calcite, assuming the partial pressures from solution. The decreasing ratio is not related to mixing with greater proportions of atmospheric precipitation, because the Ca–Mg quotient in precipitation at Lost River is about 5, or 3·3 times greater than that found in groundwater.

The Ca–Mg quotient in surface water decreased from about 1·5 at the head of a spring-fen channel to about 1·3 approximately 1 km downslope further indicating the preferential assimilation of calcium by mire plants, or adsorption to peat. Calcium was not being removed in the channels by inorganic precipitation, because no marl was observed either in the channel pools or within the peat profile. The surface water in the channels is probably undersaturated with respect to calcite, assuming the partial pressures

---

**Fig. 10.** The isotopic content of mire waters from the Lost River area, northern Minnesota. The samples were collected from forested bogs (□) and non-forested fens (■) during the summer of 1981. Samples enriched with respect to $^{18}$O are indicative of evaporative concentration. All values are relative to standard mean oceanic water (SMOW).

**Fig. 11.** Relationship of the calcium–magnesium quotient to specific conductance. The line shows the major trend in the data set. The water samples were collected at Lost River peatland, northern Minnesota from (■) the raised bog, (□) the mineral soil under the peat, (●) the spring-fen channel, (○) the swamp forest, and (●) the water track.
of carbon dioxide in the acrotelm is $10^{-2}$ atmosphere, a value commonly found in soil profiles containing oxidizing organic material (Freeze & Cherry 1979; Fig. 12).

The behaviour of silica in the spring-fen channels differs from that of calcium and magnesium, indicating that the concentration of silica is not controlled by simple mixing of precipitation and groundwater (Fig. 13). Silica appears to be oversaturated with respect to quartz in surface water at a pH greater than 6.5. The concentration of silica in the spring-fen channel is sometimes higher than that found in groundwater from the underlying mineral soil, suggesting that there must be an internal source of silica within the peat column.

Bennett & Siegel (1987) report the dissolution of quartz by organic acids that form complexes with silica in solution and maintain supersaturation with respect to quartz at neutral pH. It is possible that diatom frustules are dissolved in the peat column, releasing silica, which is then maintained in solution by silica–organic complexes. This hypothesis is supported by findings that although diatoms are common in surface samples of peat, they are absent in peat cores (Kingstone 1982a, b).

Further evidence for organic-acid–metal complexes is the elevated concentration of iron in dilute bog waters, compared to generally negligible iron in the surface waters of the spring fen and swamp forest and in the groundwater of the underlying mineral soil (Table 3). Iron is commonly maintained in solution in surface waters having large amounts of dissolved humic material (Thurman 1985).

**Stratigraphy**

The stratigraphy from the peat cores (Fig. 8) indicates that the development of the peat mounds at Lost River was controlled by three important variables: climate, topography and hydrology. The initial accumulation of telmatic peat at Lost River occurred around

---

**Fig. 12.** The relationship of calcium concentration to pH in surface water at Lost River peatland, northern Minnesota. The solid line shows the theoretical saturation of water with calcite in a system open to a partial carbon dioxide pressure of 0.01 atmospheres (Drever 1982). Symbols as in Fig. 11.
3000 B.P., when the climate of north-western Minnesota became cooler and moister following the warm mid-Holocene (Janssen 1968; Griffin 1977). Limnic sediment under the bog, however, apparently started to accumulate much earlier, although the older date may also be the result of contamination with lignite from the basal mineral sediment.

The topographic relief of the mineral substrate played an important role in determining the initial development of the Lost River peatland. Organic matter first started to accumulate in the depression under the raised bog and then spread to the more elevated portions of the spring-fen mound and water track. The rapid shift to woody Sphagnum peat under the spring-fen mound probably indicates the development of a raised bog that existed at the site until about 1100 B.P. Apparently groundwater was not discharging at the site at this time, and the rise of the mineral substratum provided the initial relief necessary to prevent the developing mound from being flooded by runoff from the adjacent peatland.

Runoff would readily drain into the depression that underlies the raised bog, and Sphagnum could not become established at this site until the basin was filled in with organic matter. A sedge fen first became established in this depression, but it was soon replaced by a Larix swamp forest with minerotrophic Sphagnum and Amblystegiaceae mosses. This forest was invaded by Sphagnum, and the peat above 200 cm contains assemblages typical of the present bog forest. Nevertheless, the elevation of the basal boundary of this Sphagnum-bog-forest assemblage is very close to the basal Sphagnum boundary under the spring fen, indicating that the initial succession from fen to bog at Lost River was controlled by the elevation of the peat surface. Despite the difference in the topography of the mineral substrate under these two peat mounds, the ages of the Sphagnum rise under the bog and spring-fen mound are similar, implying a close linkage between peat accumulation and hydrology.
Once *Sphagnum* invaded the raised bog site there was no significant change in the peat except for several deeply humified bands containing wood. At the spring fen, by contrast, there is a pronounced change at a depth of 70 cm, where the underlying woody *Sphagnum* peat is replaced by sedge peat rich in mosses of the Amblystegiaceae characteristic of the present spring-fen channel.

The most likely explanation for this sudden change is the discharge of groundwater at the peat surface in quantities sufficient to raise the pH into the range of an extremely rich fen. Discharge may not have occurred on the adjacent raised bog because the greater depth of peat at this site may have permitted the peatland to adjust to the increased pore pressure by swelling (Almendinger, Almendinger & Glaser 1986). During the study period in 1982 and 1983 all the topographic benchmarks along the survey line rose in elevation, but the rise was much greater on the bog than on the spring-fen mound. The sudden discharge of groundwater at the spring-fen mound could have been indirectly caused by climatic changes. A rise in the water table at the recharge areas for this peatland could have provided the hydraulic head necessary to drive flow cells that initiated the discharge of groundwater at the spring-fen mound.

*General implications*

A raised bog is usually considered a potential end state of peat accumulation, which will continue to grow until it is in equilibrium with the prevailing climate (Granlund 1932; Kulczyński 1949). The conversion of a bog to a fen, however, has seldom been reported in the literature. Tolpa (1932) described the development of raised bogs in karst sink-holes from Poland in which the bogs were periodically submerged under alkaline waters when the bottom of the sink-hole collapsed. Aside from this special case, Lewis & Dowding (1926) described the formation of a peat lake with alkaline waters that apparently developed because of groundwater discharge.

Groundwater may, however, play a much more pervasive role in the development of boreal peatlands. In areas of exceptionally low relief such as the Glacial Lake Agassiz region only slight changes in hydraulic head may cause groundwater to discharge at the surface and dramatically alter expected pathways of plant succession (Siegel 1983; Siegel & Glaser 1987). The mixing of as little as 10% groundwater from the calcareous parent material that underlies the major peatland regions in the interior of North America with acid bog waters is sufficient to raise the pH from 3.6 to 6.8 (Siegel 1983). The hydrological and ecological data collected at Lost River therefore suggest that the upwelling of groundwater from the calcareous till to the peat surface may represent the major source of alkalinity controlling the development of peatlands in these large peat basins. The development of these peatlands may be much more sensitively adjusted to groundwater flow patterns than previously expected (Glaser & Janssens 1986; Glaser 1987b).

**ACKNOWLEDGMENTS**

This project was supported by contracts from the Peat Program of the Minnesota Department of Natural Resources, National Aeronautics and Space Administration and grants from National Science Foundation and Graduate School of Syracuse University. We thank H. E. Wright Jr and several referees for carefully reading the manuscript, L. Andrew for piloting the helicopter, and N. Aaseng, J. C. Almendinger, J. E. Almendinger, D. Foster, E. Gorham, D. Janecky, G. King, A. Loiselle, G. Seltzer, D. Wedin, and H. E. Wright Jr for field assistance or valuable discussion.
REFERENCES


This content downloaded from 144.92.119.96 on Wed, 16 Dec 2015 17:06:11 UTC
All use subject to JSTOR Terms and Conditions
Chemical and hydrological gradients


(Received 7 April 1988; revision received 27 August 1990)