Vegetatio **120:** 147–159, 1995.
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Relationships of bryophytes and lichens to environmental gradients in Maine peatlands

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Accepted 10 May 1995

Key words: Bryophytes, lichens, Maine, Multivariate analysis, Peatlands, *Sphagnum*

Abstract

The most important environmental gradients of Maine peatlands are geologic substrate and alkalinity. Other gradients are coastal-inland climate, moisture content of the peat, P and K concentrations, and shade. Abundance weighted means of pH, Ca, and moisture content of peat are given for the 48 most frequently occurring bryophyte and lichen species. A TWINSPAN differentiated twenty associations. Environments of the first four TWINSPAN dichotomies differed largely by pH and related variables, though Fe, $\%H_2O$, shade, microtopography, and degree of humification were also significant. A CCA with forward selection entered pH, P, Fe, Na, $\%H_2O$, shade, and a climate factor as the minimum number of variables which best account for the species variation. Bryophyte and lichen distributions are determined primarily by edaphic and hydrologic factors, which determine the kinds and amounts of mineral solutes in peat interstitial water. Two independent chemical gradients were identified: (1) the acidity-alkalinity gradient related to base cation concentrations, and (2) a gradient of Fe, Al, Mn, and Si related to shallowness of peat and inputs from granitic lithologies.

Introduction

Bryophytes play a primary role in peatland initiation and development and, together with lichens are important components of the peatland flora. Despite this, only a little work has been done in Maine to quantify relationships of bryophyte and lichen species to environmental factors in peatlands (Davis & Anderson 1991). Such quantitative relationships recently have been published for Minnesota (Vitt & Slack 1984; Janssens & Glaser 1986; Glaser *et al.* 1990; Gorham & Janssens 1992a,b; Janssens 1992) and western Canada (Horton *et al.* 1979; Gignac & Vitt 1990; Vitt & Chee 1990; Gignac *et al.* 1991).

The primary objective of this paper is to describe the quantitative relationships of bryophyte and lichen taxa to environmental gradients in Maine peatlands. These relationships will be useful for future paleoecological studies to interpret peatland development and to infer past environmental conditions. Our second objective is to delineate and describe the bryophyte/lichen associations of Maine peatlands and to characterize their physical and chemical environments.

Davis (1989) has postulated that the great diversity of fen and bog types in the small geographic area of Maine is a function of the state's steep climatic gradients. Our third objective is to test the hypothesis that climatic factors are important for determining the distributions of peatland bryophytes and lichens in the state.

Methods

Study sites

The 96 studied peatlands are distributed across the state (Fig. 1) and include the nine Maine peatland types

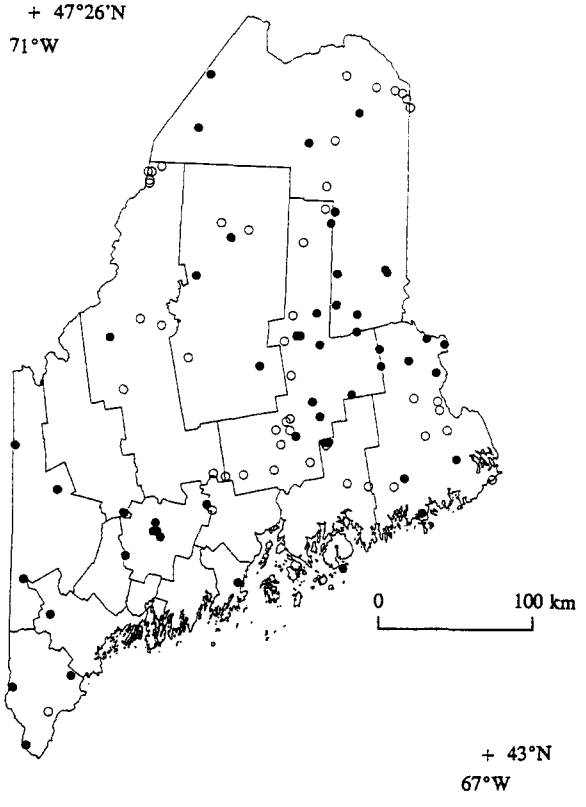

Fig. 1. Locations of the 96 Maine peatlands. Darkened circles indicate the 51 peatlands with interstitial water chemistry data which are the main focus of this paper. Names and additional information for individual peatlands are available from the authors.

identified by Davis and Anderson (1991). A subset of 51 of these peatlands which have data on interstitial water chemistry to relate to the vegetation data is the main focus of this paper. These 51 peatlands include 20 open-basin and valley (unpatterned) fens, 6 closed-basin (kettle) fens, 1 ribbed fen, 3 bogs without pattern, 4 bogs with concentric pattern, 15 eccentric bogs, and 2 coastal bogs. All of the bogs are complexes surrounded by fen areas which were also sampled.

Field studies

One summer field day was spent at each peatland, with the exception of four of the larger (> 350 ha) peatlands with 2 to 4 days each. Relevés measuring 5 × 5 m were used to sample as many association types as possible. There were 1 to 15 (mean = 5.6) relevés per peatland, 289 relevés in all. Cover estimates (Braun-Blanquet 1932) for every species were recorded for each of four strata. Bryophyte and lichen results come only from the ground stratum. Additional species which occurred within 15 m of each relevé were tallied to ensure as complete a species list as possible for each association. Maximum microrelief was estimated for each relevé.

At 263 relevés a 150 ml sample of peat interstitial water was collected from the top of the water table using a pointed and perforated 60-cm-long by 3-cm-diameter cellulose carbonate collection tube. The water was drawn from the tube by a hand vacuum pump. The polyethylene collection bottles had been pretreated by an overnight soak in 10% HCl followed by glass-distilled water rinses. Water samples were kept at *ca.*5 °C until treatment in the laboratory (generally within 24 h).

A cubic 250 cm^3 sample of peat was cut from just below the living green surface layer and put in a plastic bag to prevent water loss. Depth of peat to mineral substrate was determined with a Davis peat sampler at 259 relevés.

Laboratory analyses

Water samples were filtered through Nucleopore 0.65 μm cellulose membrane filters. The filtrate was split for analyses of (1) pH and total alkalinity, (2) dissolved organic carbon (DOC), and (3) conductance (k_{corr}) and selected chemical elements. The DOC subsample was preserved with strong acid, and all subsamples were refrigerated until analysis.

The first two splits were analyzed, respectively, with (1) a Radiometer Acid Rain Analysis System (ARAS) automated Gran-plot titrator, and (2) an OI-700 Total Carbon Analyser (TCA). The pH sample was aerated with standard air just prior to pH determination and titration with 0.02N H_2SO_4. Precision for pH was 0.01 unit. The TCA was calibrated with standard $KHC_8H_4O_4$. Detection limit for DOC was 0.01 ppm.

The third split was analyzed for Ca, Mg, P, Al, Fe, Mn, Zn, and Si by plasma spectrometry (Jarrel-Ash ICP); K and Na by flame spectrometry (Instrumentations Mod. Video 12); anions by ion chromatography (DIONEX Mod. 2000 I/SP with conductance detector); and specific conductance. Conductance at 25 °C was corrected for hydrogen ions (Sjörs 1950) (corrected conductance = k_{corr}). The detection limit for Cl was 0.001 ppm; for Mg, Mn, Zn, and SO_4 0.005 ppm; Ca, P, and Si 0.01 ppm; Fe 0.02 ppm; Al and Na 0.05 ppm; and K 0.1 ppm. There was a total of 16 chemical variables.

Degree of humification of peat follows the 10-class scale of von Post (1924). Percent water content (%H_2O), determined by drying peat at 90 °C, is used as an indicator of site wetness, since depth to water table was not measured. Mineral residue (minres) after ignition (550 °C) of the peat and acid digestion of the ash was filtered on 1.5 μ glass fiber filters and weighed after drying.

Taxonomic references used were Hale (1979) for lichens, Schuster (1966–1992) for liverworts, Anderson *et al.* (1990) for mosses other than Sphagnopsida, and Crum (1984) for Sphagnopsida.

Database and statistical analyses

Braun-Blanquet cover class estimates were converted to percentages by taking the geometric mean of the range for each class. Shade was calculated by summing the total % species cover of the tree stratum, high shrub stratum, and dwarf shrub stratum.

Two synthetic climatic variables were calculated for each peatland based on the method of Briggs and Lemin (1992). Using 38 climate variables from 63 meteorological stations in Maine from 1954 to 1983, they computed the principal components. The first principal component, accounting for 66% of the variance, reflected south to north and coastal to inland gradients. Temperature variables for all seasons but summer, heat accumulation, spring and fall PET, and number of frost-free days had high positive correlations, and snow accumulation and summer precipitation had high negative correlations. The second principal component, accounting for 10% of the variance, reflected high continentality and seasonality. Spring and summer extreme maximum and summer average maximum temperatures were correlated (+) with this component. To extrapolate the results from the principal components analysis across the state, Briggs and Lemin (1992) developed stepwise multiple linear regression equations relating each principal component to latitude, longitude, and altitude. Using these equations, we calculated principal component scores for each of our peatlands and use them as climatic factors (CF1 and CF2) for multivariate statistical analyses (described below).

To define the most important environmental gradients in the data set, we carried out a principal components analysis of the correlation matrix (with varimax rotation) of 16 chemical variables, %H_2O, minres, shade, CF1, and CF2. All variables except pH, shade, CF1, and CF2 were first log transformed due to their skewed distributions. Negative alkalinities (min. −370.0) were eliminated by adding 370.0 to all alkalinity values before transformation. Degree of humification and depth to substrate were not included in the multivariate analyses due to numerous missing values, but they were later correlated with the PCA and CCA axes.

The 48 bryophyte and lichen species which occurred in at least four relevés were considered for statistical analyses. Taxon abundance-weighted-means (AWM) and standard deviations (AWSD) of pH, Ca, and %H_2O were calculated to estimate optima and tolerances for each species. TWINSPAN (Hill 1979) was used to define the bryophyte/lichen associations. Dichotomies (splits) were maintained if the eigenvalue was >0.25 and the residual was less than the tolerance. Mean values for selected environmental variables were calculated for the first several dichotomies. Significantly different means were determined by *t*-tests (Zar 1984).

Canonical correspondence analysis (CCA) was performed on the combined biological and environmental data sets using CANOCO version 3.1 (ter Braak 1988, 1990). An exploratory CCA was performed using all environmental (explanatory) variables, followed by a CCA with forward selection, which progressively enters the variables which best account for the biological variation, until further addition of variables provides no additional statistical significance (as assessed by Monte Carlo permutation tests; p = 0.05). The CCA with forward selection was evaluated by examining the canonical coefficients (significance assessed by approximate *t*-tests) and the intraset correlations (ter Braak 1986). The exploratory CCA was evaluated using only the intraset correlations, since the canonical coefficients were unstable due to inclusion of highly correlated variables.

Results

Descriptive statistics for all environmental variables are given in Table 1.

Environmental gradients

The first six PCA axes account for 71.2% of the variance (var) in the environmental data (Table 2). The first component (PC1), accounting for 19.8% var, has high positive loadings for pH, alkalinity, Ca, Mg, k_{corr}, and Si and high negative loadings for DOC and Zn. This

Table 1. Summary of chemical and physical characteristics of the relevés. Variables lacking units are in $mg \cdot l^{-1}$, except pH (air-equilibrated), $\%H_2O$ (% moisture content of the fresh peat), and degree of humification which is based on a 10 point scale. BDL = below detection limit.

Variable	N	Mean	SD	Minimum	Maximum
Ca	259	1.97	3.60	0.01	27.20
K	259	0.36	0.63	BDL	7.28
Mg	259	0.47	0.57	0.02	3.11
P	259	0.05	0.05	BDL	0.42
Al	259	0.14	0.15	BDL	0.94
Fe	259	0.28	0.46	BDL	3.64
Mn	259	0.02	0.03	BDL	0.20
Na	259	1.57	1.94	0.20	14.00
Si	259	1.31	1.47	BDL	9.47
Zn	259	0.02	0.02	BDL	0.16
Cl	259	1.86	3.10	0.08	26.10
SO_4	259	0.38	0.69	0.02	7.50
$k_{corr}\mu S \cdot cm^{-1}$ at 25 °C	258	24.5	23.4	1.4	142.1
pH	258	4.74	1.22	3.60	8.35
DOC	257	38.4	14.2	1.8	87.9
Alkalinity	255	−11.3	226.4	−364.7	1397.0
$\%H_2O$	289	89.5	6.4	55.3	98.6
Minres ($mg \cdot g^{-1}$ dry wt)	289	0.031	0.076	0.001	0.626
Microrelief (cm)	225	27	16	0	99
Shade (Σ % cover)	289	89.8	39.3	0.4	240.6
Substrate depth (m)	259	3.6	2.1	0.3	9.1
Humification degree	230	3.3	2.4	1.0	9.0

component largely reflects the supply of base cations from mineral sources and represents an alkalinity gradient. Depth to substrate is negatively correlated with this axis. Component 2 (PC2; 16.7% var) has high positive loadings for the lithophilic elements Fe, Al, Mn and Si, and CF2 and minres. This component reflects the influence of granitic substrates on the interstitial water. Depth to substrate is most highly correlated (−) with this axis. Component 3 (PC3; 15.7% var) is related to marine salts and climate. Cl, Na, CF1, and k_{corr} have high positive loadings; CF2 has a high negative loading. Degree of humification is most highly correlated (+) with this axis, reflecting the condition of surface peats in the more southern and coastal sites. Component 4 (PC4; 7.6% var) reflects moisture content, PC 5 (6.0% var) the plant nutrients P and K, and PC 6 (5.4% var) shade.

Bryophyte and lichen autecology

The 96-peatland database of 155 bryophyte and lichen taxa is available from author DSA. One hundred and forty-four taxa, including 24 Sphagnopsida and 14 lichens were recorded for the 51 peatlands which have water chemistry data. Descriptive statistics for the 48 bryophyte and lichen species that occurred in at least four relevés are presented in Table 3. The most frequently encountered species was *Sphagnum magellanicum*, followed by *S. recurvum* agg., *S. capillifolium* var. *tenellum*, *S. capillifolium* var. *capillifolium*, *S. fuscum*, and *Pleurozium schreberi*. *Cladina rangiferina* was the most commonly encountered lichen species. All of the lichen species, along with *Mylia anomala*, *Dicranum undulatum*, *Pohlia nutans*, *Ptilidium ciliare*, and *Bazzania trilobata*, had the lowest AWM pHs. *Sphagnum capillifolium* var. *tenellum*, *S. fuscum*, *S. flavicomans*, and *S. majus* had the lowest AWM pHs among the Sphagnopsida. Highest AWM pHs were recorded for *Sphagnum warnstorfii* and *Campylium stellatum*, which were found in open or semi-open habitats of moderate-rich fens, and for *Plagiomni-*

Table 2. Rotated factor loadings for the six axes extracted by the PCA of 21 environmental variables. Correlations (r) of substrate depth and degree of humification with the six axes are also given (** $p = 0.001$;* $p = 0.05$).

Variable	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
Ca	0.784	0.423	0.082	−0.262	−0.033	−0.067
K	−0.001	0.130	0.269	−0.206	0.641	−0.334
Mg	0.683	0.414	0.407	−0.215	−0.040	−0.069
P	0.086	0.126	−0.027	0.035	0.839	0.136
Al	−0.038	0.814	0.169	−0.154	0.067	0.161
Fe	0.139	0.853	0.148	0.095	0.104	0.133
Mn	0.162	0.652	−0.015	0.134	0.101	−0.095
Na	0.317	0.206	0.856	−0.111	0.049	−0.025
Si	0.513	0.579	0.100	−0.078	0.117	0.064
Zn	−0.473	0.330	0.143	0.008	−0.108	−0.328
Cl	0.155	0.095	0.909	−0.034	0.113	−0.053
SO_4	0.103	0.158	0.176	−0.648	−0.096	−0.254
k_{corr}	0.626	0.228	0.519	−0.158	0.140	−0.098
pH	0.897	0.192	0.144	−0.088	0.032	−0.053
DOC	−0.621	0.236	0.065	−0.279	0.054	0.061
Alkalinity	0.838	0.107	0.012	0.045	0.080	−0.010
$\%H_2O$	0.035	0.231	−0.042	0.789	−0.181	−0.199
Minres	0.268	0.489	0.336	−0.418	0.087	−0.042
Shade	−0.084	0.158	0.066	0.011	−0.028	0.828
CF1	−0.173	0.029	0.824	−0.181	−0.039	0.081
CF2	0.017	0.569	−0.533	−0.118	−0.076	−0.125
Variance (%)	19.8	16.7	15.7	7.6	6.0	5.4
Substrate depth	−0.24**	−0.44**	−0.13	0.05	−0.08	−0.12
Humification	0.19*	0.18*	0.26**	−0.20*	0.19*	0.07

um ellipticum, *Hylocomium splendens*, *Rhytidiadelphus triquetrus*, *Sphagnum wulfianum*, and *Ptilium crista-castrensis*, species typical of wooded fen habitats. Ranking of species by AWM Ca roughly parallels the ranking for AWM pH. Species with the lowest values for AWM H_2O include *Cladina stellaris*, *Dicranum polysetum*, *Ptilidium ciliare*, *Campylium stellatum*, *Cladina mitis*, and *Sphagnum capillifolium* var. *capillifolium*. Species with the highest values for AWM H_2O include *Sphagnum majus*, *Cladopodiella fluitans*, *S. papillosum*, *S. cuspidatum*, and *S. teres*.

Bryophyte and lichen associations

The TWINSPAN analysis differentiated twenty bryophyte and lichen associations (Fig. 2 and Table 4). The first division separated 15 relevés (Group C) representing various types of fens from the other 265 relevés (Group AB). *Sphagnum fimbriatum*, *S. centrale*, and *Aulacomnium palustre* are characteristic of Group C. pH and related factors and degree of humification differ significantly between C and AB (Table 5). The first division of AB separated 147 relevés (Group A) with *Sphagnum capillifolium* var. *tenellum*, *S. fuscum*, *S. capillifolium* var. *capillifolium*, *Cladina rangiferina*, and *Mylia anomala* as indicator and preferential species (Hill 1979), from 118 relevés (Group B) with *S. recurvum* agg. and *S. magellanicum*. The significantly higher means of pH, Ca, and Fe indicate that Group B is more highly minerotrophic, and it has shallower and more humified peat. Group A relevés are mostly from bogs and very poor and poor fens, and Group B relevés are from poor and moderate-rich fens. Group A is subdivided into A1 with *S. cuspidatum* and *Cladopodiella fluitans* as indicator species, and A2 which has the same indicator and preferential species as Group A

Table 3. Descriptive statistics for the 48 bryophyte and lichen taxa that occurred in at least four of the 289 relevés. Mean cover of each species is based only on the number of relevés of occurrence (N). AWM = abundance weighted mean. AWSD = abundance weighted standard deviation.

Species Species code	N	Mean (SD) % Cover	AWM (AWSD) pH	AWM (AWSD) Ca ($mg \cdot L^{-1}$)	AWM (AWSD) $\%H_2O$
Aulacomnium palustre	22	1.0	5.44	3.18	92.1
APA		(2.8)	(1.29)	(3.97)	(3.7)
Bazzania trilobata	35	3.6	4.09	0.64	87.1
BTR		(10.7)	(0.82)	(2.15)	(4.4)
Calliergon stramineum	8	0.4	5.62	3.55	90.1
CST		(0.6)	(1.55)	(2.92)	(1.8)
Campylium stellatum	5	12.8	7.76	14.19	86.2
CMS		(27.3)	(0.11)	(2.40)	(0.2)
Cladina gracilis	4	0.2	4.07	0.68	88.6
CLG		(0.0)	(0.25)	(0.95)	(3.1)
Cladina mitis	23	1.0	3.95	0.42	86.5
CLM		(0.9)	(0.21)	(0.43)	(6.4)
Cladina rangiferina	82	3.2	4.10	0.19	88.3
CLR		(5.9)	(0.23)	(0.27)	(5.1)
Cladina stellaris	14	0.4	3.99	0.49	82.6
CLS		(0.6)	(0.31)	(0.39)	(10.5)
Cladonia cristatella	16	0.5	4.05	0.45	88.5
CLC		(0.7)	(0.64)	(1.28)	(2.9)
Cladonia pyxidata	9	0.2	3.92	0.84	87.4
CLP		(0.0)	(0.29)	(0.61)	(5.3)
Cladonia squamosa	15	4.0	3.94	0.40	88.9
CLQ		(9.5)	(0.12)	(0.19)	(3.6)
Other *Cladonia* spp.	7	2.6	3.86	0.36	89.7
CLO		(4.9)	(0.11)	(0.22)	(2.3)
Cladopodiella fluitans	19	11.4	4.26	0.52	95.3
CDF		(21.0)	(0.34)	(0.46)	(0.9)
Dicranum polysetum	14	0.8	4.84	5.12	85.8
DPO		(0.9)	(1.60)	(8.64)	(5.1)
Dicranum scoparium	7	0.4	5.64	1.98	92.7
DSC		(0.7)	(1.68)	(1.94)	(2.8)
Dicranum undulatum	54	2.1	4.03	0.50	87.2
DNU		(4.0)	(0.39)	(1.79)	(6.8)
Other *Dicranum* spp.	53	0.9	4.21	0.56	87.2
DSP		(1.9)	(0.61)	(1.20)	(3.9)
Hylocomium splendens	11	6.3	7.60	8.22	88.2
HSP		(11.1)	(0.38)	(4.78)	(1.4)
Mylia anomala	40	0.4	4.00	0.32	87.0
MAN		(0.5)	(0.27)	(0.33)	(5.0)
Plagiomnium ellipticum	11	1.4	7.97	5.40	89.8
PGE		(3.9)	(0.81)	(2.63)	(0.9)
Pleurozium schreberi	87	4.5	4.44	1.92	87.1
PLS		(12.0)	(1.00)	(4.25)	(7.1)
Pohlia nutans	5	0.2	4.04	0.26	90.9
PNU		(0.0)	(0.15)	(0.08)	(4.2)
Polytrichum commune	5	2.8	4.24	1.28	93.2
PCO		(5.8)	(0.33)	(0.55)	(0.9)
Polytrichum strictum	62	3.5	4.16	1.37	90.6
PST		(9.1)	(0.60)	(2.21)	(3.2)
Ptilidium ciliare	36	1.7	4.05	0.21	86.0
PTC		(3.6)	(0.21)	(0.45)	(5.9)
Ptilium crista-castrensis	7	2.3	7.09	6.72	87.6
PLC		(4.8)	(0.93)	(2.82)	(1.0)
Rhytidiadelphus triquetrus	6	0.8	7.56	13.58	88.0
RTR		(0.9)	(0.65)	(8.20)	(1.1)
Sphagnum capillifolium var. *capillifolium*	122	9.0	4.62	2.73	87.0
SCA		(14.7)	(1.40)	(5.36)	(5.6)
Sphagnum capillifolium var. *tenellum*	126	31.4	4.10	0.43	92.5
SCT		(33.1)	(0.42)	(1.18)	(4.7)
Sphagnum centrale	17	7.9	5.71	3.16	92.5
SCE		(11.9)	(1.05)	(1.83)	(4.0)
Sphagnum cuspidatum	29	19.1	4.48	0.66	94.9
SCU		(33.0)	(0.91)	(1.02)	(3.7)
Sphagnum fimbriatum	15	3.8	5.07	3.84	90.2
SFI		(9.6)	(0.77)	(1.46)	(4.0)
Sphagnum flavicomans	5	22.2	4.13	0.29	93.4
SFL		(19.3)	(0.03)	(0.05)	(0.3)
Sphagnum fuscum	94	13.8	4.10	0.30	90.3
SFU		(17.2)	(0.31)	(0.95)	(3.8)
Sphagnum girgensohnii	10	10.4	4.81	1.79	91.8
SGI		(14.6)	(0.86)	(0.85)	(1.1)
Sphagnum imbricatum	10	12.1	4.36	0.94	91.1
SIM		(18.4)	(0.74)	(1.71)	(3.2)
Sphagnum magellanicum	166	8.4	4.42	1.04	92.2
SMA		(14.7)	(0.78)	(1.37)	(3.5)
Sphagnum majus	6	15.6	4.17	0.60	96.0
SMJ		(35.1)	(0.10)	(0.18)	(0.5)
Sphagnum palustre	7	0.2	6.08	4.12	88.5
SPL		(0.0)	(1.44)	(2.65)	(5.8)
Sphagnum papillosum	13	33.2	4.39	1.44	94.9
SPA		(38.7)	(0.61)	(1.89)	(2.1)
Sphagnum recurvum s.l.	133	21.8	4.64	1.74	92.2
SRE		(24.4)	(0.81)	(1.66)	(3.0)
Sphagnum russowii	9	2.0	4.32	3.03	88.8
SRU		(4.2)	(1.61)	(1.52)	(1.3)
Sphagnum subsecundum s.l.	6	3.6	6.04	5.77	91.1
SSU		(4.8)	(1.12)	(4.25)	(2.6)
Sphagnum teres	6	0.5	6.01	2.40	94.1
STE		(0.7)	(0.81)	(1.69)	(2.5)
Sphagnum warnstorfii	6	4.5	8.30	20.67	88.5
SWA		(6.7)	(0.13)	(1.70)	(0.8)
Sphagnum wulfianum	6	0.5	7.33	4.41	90.4
SWU		(0.7)	(0.44)	(1.28)	(2.0)
Thuidium delicatulum	10	1.9	5.32	4.31	89.4
TDE		(4.0)	(0.76)	(2.91)	(1.4)
Warnstorfia fluitans	4	0.2	5.68	1.82	93.7
WFL		(0.0)	(1.24)	(1.51)	(3.6)

with the addition of *S. recurvum*, *Dicranum undulatum*, *Pleurozium schreberi*, and *Polytrichum strictum*. A1 and A2 environments differ largely by microrelief and shade. Group A1 relevés are from open lawn and mud bottom communities, and Group A2 are mostly from shrub heath, wooded shrub heath, forested bog, and poor wooded fen communities. Group B is subdivided into B1 which has the same indicator and preferential species as Group B with the addition of *S. capillifolium* var. *tenellum*, and B2 which has *S. girgensohnii*, *Hylocomium splendens*, *Bazzania trilobata*, and *Aulacomnium palustre*. These two groups reflect differing degrees of minerotrophy within the poor fens. Also, the peats of Group B2 are typically less saturated in summer.

Relationships between bryophyte and lichen species and environmental gradients

In the exploratory CCA, the percent of the species-environment variance accounted for by the first three axes (and their eigenvalues) are: (1) 17.4 (0.50), (2) 13.2 (0.38), and (3) 12.0 (0.34). The intra-set correla-

Table 4. Mean species' cover (%) and frequency for each TWINSPAN association. Species included are those with $\geq$ 1.0 % mean cover and/or $\geq$ 25 % frequency. (p = present at < 0.5 % mean cover). N, mean pH, mean Ca ($mg \cdot L^{-1}$), mean $\%H_2O$, and mean shade are listed in order with standard deviations in parentheses.

	Cover (%)	Frequency
1. N = 5; 4.37(0.97); 0.49(0.69); 94.8(4.3); 25(31)		
Sphagnum cuspidatum	87.2	5
Sphagnum magellanicum	0.8	2
Cladopodiella fluitans	p	2
Sphagnum capillifolium var. *tenellum*	p	2
2. N = 3; 4.33(0.34); 0.67(0.43); 95.4(1.1); 39(30)		
Cladopodiella fluitans	53.2	3
Sphagnum capillifolium var. *tenellum*	16.5	2
Sphagnum majus	1.3	2
Sphagnum magellanicum	p	1
3. N = 3; 4.34(0.63); 0.20(0.15); 96.7(1.6); 24(19)		
Cladopodiella fluitans	17.2	3
Sphagnum capillifolium var. *tenellum*	5.1	2
Sphagnum cuspidatum	4.5	3
Sphagnum magellanicum	4.4	1
4. N = 3; 4.16(0.21); 0.83(1.18); 81.8(22.9); 80(9)		
Sphagnum capillifolium var. *tenellum*	45.6	3
Sphagnum cuspidatum	0.8	3
Cladopodiella fluitans	0.7	2
Sphagnum magellanicum	p	1
5. N = 28; 4.11(0.32); 0.36(0.52); 94.2(1.5); 93(42)		
Sphagnum capillifolium var. *tenellum*	78.7	28
Sphagnum magellanicum	1.7	10
Sphagnum fuscum	1.7	8
Sphagnum cuspidatum	1.3	2
6. N = 11; 4.36(1.15); 1.27(3.49); 91.5(3.8); 99(42)		
Sphagnum capillifolium var. *tenellum*	39.7	11
Sphagnum magellanicum	19.6	11
Sphagnum recurvum	4.4	7
Sphagnum capillifolium var. *capillifolium*	2.8	6
Cladina rangiferina	p	6
Dicranum spp.	p	5
Mylia anomala	p	4
Sphagnum fuscum	p	3
7. N = 23; 4.07(0.23); 0.18(0.14); 90.4(2.9); 94(40)		
Sphagnum capillifolium var. *tenellum*	25.0	23
Sphagnum fuscum	15.8	21
Cladina rangiferina	5.6	17
Sphagnum flavicomans	1.6	1
Sphagnum magellanicum	1.1	18
Sphagnum capillifolium var. *capillifolium*	1.0	10
Dicranum spp.	p	13
Mylia anomala	p	11
Polytrichum strictum	p	8
Sphagnum recurvum	p	7
8. N = 43; 4.18(0.45); 0.40(0.59); 87.3(7.1); 83(30)		
Sphagnum fuscum	17.5	40
Sphagnum capillifolium var. *tenellum*	7.2	30
Pleurozium schreberi	5.6	26
Bazzania trilobata	2.5	12
Cladina rangiferina	2.4	29
Sphagnum capillifolium var. *capillifolium*	2.0	27
Sphagnum recurvum	1.8	20
Sphagnum flavicomans	1.7	4
Dicranum undulatum	1.2	18
Ptilidium ciliare	1.1	18
Sphagnum magellanicum	0.6	28
Dicranum spp.	0.6	14
Polytrichum strictum	p	12
Mylia anomala	p	11
9. N = 27; 4.17(1.01); 1.65(4.33); 85.3(6.0); 89(30)		
Sphagnum capillifolium var.*capillifolium*	25.9	27
Polytrichum strictum	6.9	19
Sphagnum magellanicum	4.4	13
Sphagnum capillifolium var. *tenellum*	2.5	6
Cladonia squamosa	1.5	7
Sphagnum fuscum	1.3	8
Dicranum undulatum	1.2	12
Pleurozium schreberi	0.8	9
Cladina mitis	p	11
Cladina rangiferina	p	11
10. N = 79; 4.67(0.87); 1.56(1.60); 92.2(3.3); 99(41)		
Sphagnum recurvum	32.4	75

Table 4. Continued.

	Cover (%)	Frequency
Sphagnum magellanicum	11.7	63
Sphagnum capillifolium var. *tenellum*	2.0	18
Sphagnum capillifolium var. *capillifolium*	1.5	33
Sphagnum fuscum	1.3	13
Sphagnum papillosum	1.0	7
Pleurozium schreberi	0.6	31
11. N = 4; 4.28(0.20); 1.09(1.03); 95.6(1.3); 70(44)		
Sphagnum papillosum	87.2	4
Sphagnum magellanicum	3.8	2
Sphagnum cuspidatum	1.0	2
Sphagnum capillifolium var. *capillifolium*	0.5	1
Sphagnum capillifolium var. *tenellum*	0.5	1
Sphagnum recurvum	0.5	1
Cladopodiella fluitans	p	1
Polytrichum strictum	p	1
Sphagnum majus	p	1
12. N = 3; 5.28(1.32); 2.23(0.92); 92.5(2.0); 117(37)		
Sphagnum girgensohnii	28.6	3
Sphagnum recurvum	4.4	1
Sphagnum magellanicum	2.0	3
Pleurozium schreberi	1.3	2
Bazzania trilobata	p	1
Dicranum undulatum	p	1
Hylocomium splendens	p	1
Sphagnum wulfianum	p	1
13. N = 23; 6.45(1.55); 6.16(5.59); 88.9(4.4); 103(46)		
Sphagnum capillifolium var. *capillifolium*	5.6	11
Sphagnum recurvum	3.5	11
Pleurozium schreberi	3.0	15
Hylocomium splendens	3.0	8
Sphagnum magellanicum	p	11
Bazzania trilobata	p	7
Dicranum spp.	p	7
Polytrichum strictum	p	7
Dicranum undulatum	p	6
Plagiomnium ellipticum	p	6
Sphagnum girgensohnii	p	6
14. N = 2; 6.79(1.40); 7.63(3.30); 85.3(0.5); 84(55)		
Sphagnum imbricatum	6.7	2
Rhytidiadelphus triquetrus	p	1
Sphagnum magellanicum	p	1
Thuidium delicatulum	p	1
15. N = 4; 6.04(1.60); 6.39(5.90); 90.5(3.3); 72(17)		
Sphagnum subsecundum	4.8	4
Sphagnum recurvum	1.0	2
Aulacomnium palustre	p	2
Dicranum undulatum	p	2
Bazzania trilobata	p	1
Calliergon stramineum	p	1
Pleurozium schreberi	p	1
Sphagnum capillifolium var. *capillifolium*	p	1
Sphagnum cuspidatum	p	1
Sphagnum magellanicum	p	1
Sphagnum palustre	p	1
Sphagnum warnstorfii	p	1
16. N = 2; 8.11(1.31); 8.35(3.42); 92.5(2.6); 55(19)		
Calliergon stramineum	p	2
Cladonia cristatella	p	1
Sphagnum palustre	p	1
17. N = 5; 5.13(0.98); 3.94(2.19); 92.6(4.5); 114(55)		
Sphagnum recurvum	12.7	2
Sphagnum centrale	12.6	5
Sphagnum fimbriatum	11.1	5
Sphagnum cuspidatum	2.6	1
Aulacomnium palustre	p	2
Dicranum undulatum	p	1
18. N = 2; 7.06(1.14); 1.61(1.13); 75.5(5.2); 90(21)		
Sphagnum cuspidatum	18.2	2
Sphagnum fimbriatum	p	1
19. N = 4; 6.10(0.88); 5.32(3.38); 89.3(2.3); 88(29)		
Shagnum fimbriatum	p	4
Sphagnum palustre	p	2
Aulacomnium palustre	p	1
Dicranum polysetum	p	1
20. N = 2; 8.04(0.43); 20.5(9.47); 86.0(0.3); 54(11)		
Campylium stellatum	31.8	2
Sphagnum warnstorfii	p	2
Polytrichum strictum	p	1
Sphagnum fuscum	p	1

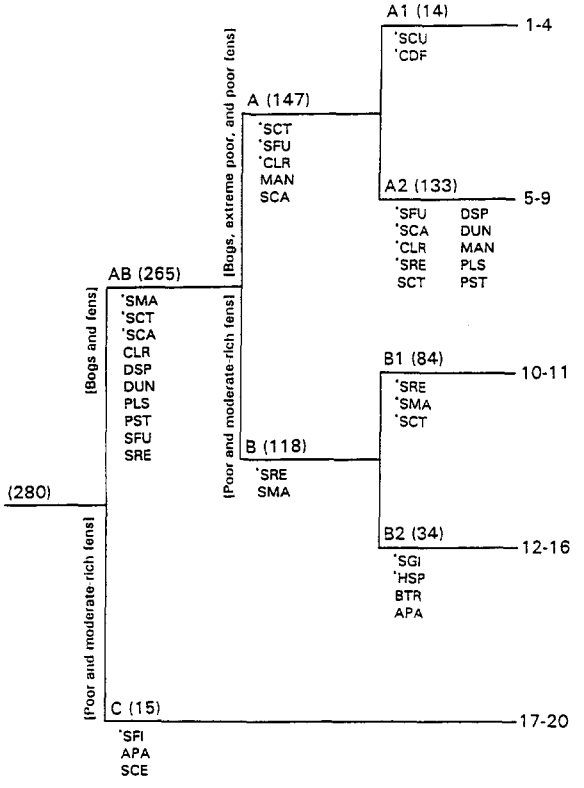

Fig. 2. First four TWINSPAN dichotomies, based on 280 relevés (9 relevés had none of the 48 species used in the multivariate analyses). Numbers of relevés are in parentheses. Indicator species (*) and preferential species are given. Species codes are listed in Table 3. The twenty, numbered "ultimate TWINSPAN communities" (Table 4) are given on the right.

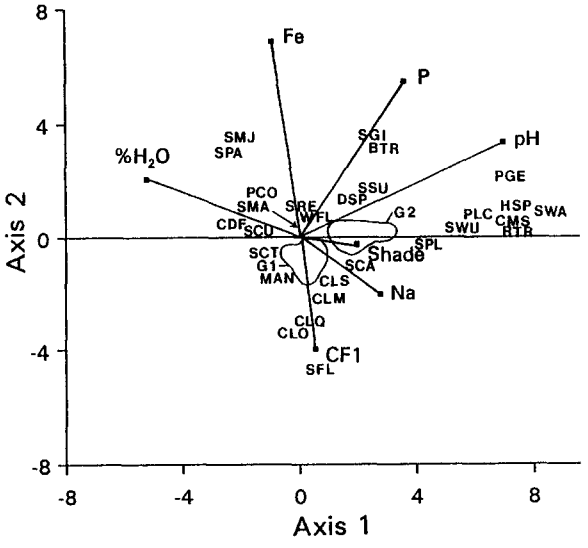

Fig. 3. Biplot of CCA axes 1 and 2 with forward selection showing environmental vectors and species scores. Species codes are given in Table 3. Species in G1 are CLG, CLR, CLC, CLP, DUN, PNU, PST, SFU and SIM. Species in G2 are APA, CST, DPO, DSC, PLS, PTC, SCE, SFI, SRU, STE, and TDE.

tions indicate the relative importance of the environmental variables to the CCA axes (Table 6). Significant ($p = 0.001$) correlations for axis 1 are (+) Ca, pH, alkalinity, k_{corr}, Mg, and SO_4, and (−) $\%H_2O$. Significant correlations for axis 2 are (+) Fe, Si, Al, Mn, P, Mg, CF2, pH, and minres. The relatively low correlation for conductance suggests that electolyte concentration isn't nearly as important as for axis 1. These two CCA axes correspond closely to the first two PCA axes. The third axis is partly redundant with the first two, although it also reflects the climate variables (CF1 and CF2), and distance from the ocean (Na and Cl; Table 6).

In the CCA with forward selection, the variables selected (and % of explained species-environment variation) are pH (10.8), P (9.7), Fe (8.4), Na (8.4), $\%H_2O$ (6.6), shade (5.9), and CF1 (4.5). The percent of the species-environment variance accounted for by the first three axes (and their eigenvalues) are: (1) 24.4 (0.38), (2) 20.7 (0.32), and (3) 15.4 (0.24). As in the exploratory CCA, the first canonical axis primarily reflects an alkalinity-acidity gradient. pH is most strongly correlated with this axis, but P, Na, and shade are also correlated (+), and $\%H_2O$ is inversely related (Table 7; Fig. 3). Degree of humification is also correlated with this axis ($r = 0.35$; $p = 0.001$). The second canonical axis reflects the gradient of Fe and P. CF1 and Na are inversely related to this axis, as is substrate depth ($r = -0.39$; $p = 0.001$). The third axis reflects trophic variation associated with P. pH and $\%H_2O$ are inversely related to this axis.

Species' positions on the biplot (Fig. 3) reflect optima relative to the environmental gradients. Species centered at the alkaline end of the gradient include *Sphagnum warnstorfii*, *Campylium stellatum*, *Rhytidiadelphus triquetrus*, *Hylocomium splendens*, *Plagiomnium ellipticum*, *Ptilium crista-castrensis*, and *Sphagnum wulfianum*. *Bazzania trilobata* and *Sphagnum girgensohnii* are associated with relatively high P and Fe. Species related to high moisture and Fe include *Sphagnum majus* and *S. papillosum*. *Cladopodiella fluitans* and *S. cuspidatum* are also associated with high moisture. Species with high values for CF1 include *Sphagnum flavicomans*, *Cladonia squamosa*, and *Cladina mitis*.

Table 5. Means (and standard deviations) for selected environmental variables (units as in Table 1) for the first four TWINSPAN dichotomies. Significantly different means determined by *t*-tests: ** p = 0.001; * p = 0.05.

Variable	Division 1		Division 2		Division 3		Division 4	
	AB	C	A	B	A1	A2	B1	B2
Ca	1.52	7.57*	0.64	2.76**	0.54	0.65	1.53	6.09**
	(2.98)	(7.91)	(2.05)	(3.58)	(0.67)	(2.15)	(1.58)	(5.12)
Fe	0.26	0.37	0.11	0.48**	0.15	0.11	0.48	0.47
	(0.46)	(0.52)	(0.18)	(0.61)	(0.22)	(0.18)	(0.63)	(0.58)
Cl	1.54	3.29	1.50	1.60	0.75	1.59*	1.65	1.45
	(2.21)	(3.86)	(2.10)	(2.36)	(0.70)	(2.19)	(2.66)	(1.34)
pH	4.58	6.29**	4.17	5.13**	4.31	4.16	4.65	6.41**
	(1.09)	(1.31)	(0.61)	(1.32)	(0.62)	(0.61)	(0.85)	(1.50)
$\%H_2O$	90.5	88.3	89.7	91.5*	92.5	89.4	92.4	89.2**
	(5.7)	(5.7)	(6.7)	(3.8)	(11.0)	(6.0)	(3.3)	(4.2)
Relief	28	22	28	28	9	30**	28	27
	(16)	(13)	(17)	(16)	(6)	(16)	(16)	(16)
Shade	90	89	85	98*	40	90**	97	98
	(40)	(38)	(38)	(42)	(32)	(36)	(41)	(44)
Substrate depth	3.8	3.0	4.7	2.6**	4.9	4.7	2.6	2.5
	(2.1)	(2.0)	(1.9)	(1.7)	(2.1)	(1.9)	(1.8)	(1.6)
Humification	3.0	4.7*	2.4	3.7**	1.4	2.5**	3.5	4.2
	(2.3)	(1.6)	(1.9)	(2.5)	(0.7)	(2.0)	(2.6)	(2.3)

Four of the major TWINSPAN groups are well discriminated by the CCA, and there are relatively few outliers (relevés located outside a group's circumscribed boundary) (Fig. 4). Group A1 occurs as a discrete cluster at low pH and relatively high $\%H_2O$. This is a homogeneous group of relevés as indicated by the small amount of ordination space it occupies. Group A2 also occurs at the low end of the pH gradient, as well as along CF1, indicating proximity to the coast. These relevés are located at the low end of the Fe and P gradients. Group B1 occurs along the same range of pH as Group A2 but is differentiated by higher $\%H_2O$ and Fe. Group B2 occurs at the higher end of the pH, P, and Fe gradients. Group C represents a very heterogeneous group of relevés spread along the length of axis 1, indicating a wide range of pH and $\%H_2O$ conditions.

Discussion

Sjörs (1948) identified three gradients ("directions of variation") that are of primary importance in determining patterns of peatland vegetation. They are degree of "minerotrophy" (which we interpret as alkalinity), height above the water table, and degree of openness from mire margin to mire expanse, which has been interpreted as a shade gradient (Vitt & Slack 1984; Janssens 1992). The direct gradient analyses of this study suggest that alkalinity is the most important gradient affecting the bryophytes and lichens of Maine's peatlands. pH is the best proxy to explain the biological variation along this gradient (covarying factors include Ca, alk, k_{corr}, Mg, and Si). These variables also are related to the major TWINSPAN divisions. A series of CCAs performed on only the relevés with pH $\leq$ 4.75, with and without forward selection, still identifies this gradient as primary (unpublished results). Gorham and Janssens (1992b) show that the pH gradient explains most of the variance in a large bryophyte data base representing five major regions of North America. In a study of vegetation and water chemistry in fens of Alberta, Canada, Vitt and Chee (1990) found bryophyte distributions to be determined primarily by the alkalinity gradient.

Most of the *Sphagnum* species and the lichens occur predominantly at the acidic end of the gradient (Table 3). Exceptions to this distribution include

Table 6. Intra-set correlations of exploratory CCA axes with environmental variables. ** $p = 0.001$; * $p = 0.05$.

Variable	Intra-set correlations Axis 1	Intra-set correlations Axis 2	Intra-set correlations Axis 3
Ca	0.72**	0.14*	−0.25**
K	0.07	0.10	0.21*
Mg	0.50**	0.51**	0.07
P	0.21*	0.51**	0.19*
Al	0.08	0.58**	−0.03
Fe	−0.07	0.62**	−0.31**
Mn	0.00	0.51**	−0.22**
Na	0.16*	0.12	0.37**
Si	0.16*	0.60**	−0.04
Zn	−0.12	0.16*	−0.05
Cl	0.07	0.02	0.34**
SO_4	0.30**	0.07	0.17*
k_{corr}	0.55**	0.17*	0.11
pH	0.64**	0.33**	−0.22**
DOC	−0.04	0.00	0.08
Alk	0.58**	0.20*	−0.21*
$\%H_2O$	−0.41**	0.14*	−0.34**
Minres	0.04	0.29**	−0.02
Shade	0.12	0.11	0.32**
CF1	−0.03	−0.12	0.35**
CF2	−0.04	0.38**	−0.31**

Table 7. Canonical coefficients and intra-set correlations of CCA axes with environmental variables included by forward selection. ** $p = 0.001$; * $p = 0.05$.

Variable	Canonical coefficients Axis 1	Canonical coefficients Axis 2	Canonical coefficients Axis 3	Intra-set correlations Axis 1	Intra-set correlations Axis 2	Intra-set correlations Axis 3
pH	0.78**	0.13	−0.55**	0.70**	0.33**	−0.59**
P	0.31**	0.47**	0.76**	0.36**	0.55**	0.72**
Fe	−0.43**	0.74**	−0.22*	−0.09	0.68**	−0.28**
Na	0.22*	−0.42**	0.05	0.28**	−0.20*	0.01
$\%H_2O$	−0.42**	0.09	−0.16	−0.52**	0.21*	−0.30**
Shade	0.14*	−0.06	−0.06	0.20*	−0.03	−0.08
CF1	0.01	−0.21*	0.11	0.06	−0.40**	0.14*

S. teres, *S. subsecundum*, and *S. palustre*, which have AWM pHs of 6.01, 6.04, and 6.08 respectively, and *S. wulfianum* and *S. warnstorfii*, which have AWM pHs of 7.33 and 8.30. Of the common members of the Amblystegiaceae, *Warnstorfia fluitans* and *Calliergon stramineum* were found under moderately acidic conditions (AWM pHs 5.68 and 5.62 respectively) and *Campylium stellatum* under more alkaline conditions (AWM pH 7.76). Our AWM pH values for Maine bryophyte species correspond well with those published by Gorham and Janssens for five peatland regions across northern North America (1992b). Differences between the two studies can be partly explained by the differing scales of the sampling units.

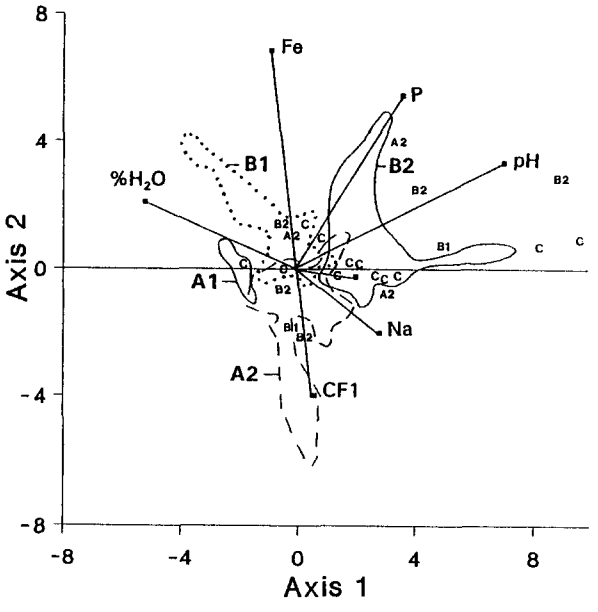

Fig. 4. Biplot of CCA axes 1 and 2 with forward selection showing environmental vectors and outlines of major TWINSPAN groups (letter-number coded). Outlines circumscribe scores of the relevés in each major TWINSPAN group (except C). To preserve clarity, individual relevés are shown for Group C and for outlier relevés in other groups. See Fig. 2 for relationships of major TWINSPAN groups.

Janssens (1987) used 0.50 × 0.50 m quadrats positioned to minimize microtopographic relief, with the dominant bryophyte in the center. Our 5 × 5 m relevés reflect broader, larger scale patterns of variation.

After alkalinity, the next most important gradient determining bryophyte/lichen distributions is related to Fe and P concentrations. Covarying with Fe and P are Al, Mn, and Si, indicating intimate association with granitic mineral soils. Shallowness of peat also appears to heavily influence this axis. This gradient is largely independent of (orthogonal to) the alkalinity gradient, and accounts for some of the differentiation of the poor fen associations. This factor complex has not previously been identified in quantitative investigations of bryophyte/lichen distributions, either because the indicative elements were not measured or because they accounted for little of the variation in data sets from other regions.

The long $\%H_2O$ vector indicates its importance in explaining the biological variation (Fig. 3). A ranking of our taxa from wet to dry based on AWM $\%H_2O$ compares well with data of Gorham and Janssens (1992b), with few exceptions. One of these is *Sphagnum subsecundum*, for which our data indicate drier growing conditions. Crum (1984) and our own field observations support the view of Gorham and Janssens (1992b). Another exception is *Sphagnum palustre*, which grows in similar wet, relatively mineral-rich shrub and/or sedge fens, yet it also has a fairly low AWM $\%H_2O$. Perhaps peats formed in such habitats have less water holding capacity and thus do not reflect well the actual growing conditions. The lichens as a group have among the lowest AWM $\%H_2O$.

Bryophyte/lichen distributions were also related to climate. CF1 was the last factor to be entered in the forward selected CCA. The species related to this vector, such as *Sphagnum flavicomans* and *S. imbricatum*, are primarily coastal (Damman 1977). All of the lichen species are also located high along this vector. The interpretation of CF1 as a measure of coastal influence is supported by the PCA, which groups CF1 with Na and Cl (Table 1). Despite Maine's steep climatic gradients (McMahon 1990), the great variation in bryophytes and lichens to be found within a particular peatland far outweighs differences in geographic distribution (between peatlands) due to macroclimate. However, climate has been found to be of primary significance, along with degree of mineral influence, in determining bryophyte distributions in western Canada (Gignac & Vitt 1990; Gignac *et al.* 1991). Most of that variance, as in this study, is due to the oceanic influence. For example, seven of 18 *Sphagnum* species are limited to oceanic peatlands (Gignac & Vitt 1990). When the oceanic sites are removed from the multivariate analysis, the climate signal is much reduced (Gignac *et al.* 1991).

We have maintained the distinction between *S. capillifolium* var. *capillifolium* (= *S. nemoreum* Scop.) and *S. capillifolium* var. *tenellum* (= *S. rubellum* Wils.) based on the characters given by Crum (1984). As Crum states, the two varieties grade into each other, so occasionally the identification is somewhat arbitrary. Apparently, the distinction between the two is clearer in Maine's cool, humid climate than in more continental regions. Our data suggest that *S. capillifolium* var. *capillifolium* grows under slightly drier and higher pH and Ca conditions. It was usually found higher on the hummocks, just below *S. fuscum*, while *S. capillifolium* var. *tenellum* formed low hummocks or more typically, extensive lawns.

We treated *S. recurvum* as an aggregate rather than distinguishing the three varieties (Crum 1984). This was considered necessary due to the extensive nature of this study, but perhaps more refined estimates of environmental optima could have been calculated and

differences revealed if they had been distiguished. Vitt and Slack (1984) discuss differences in ecological amplitude for two members of this group. They found that *S. fallax* and *S. angustifolium* had the least niche overlap for the gradient relating to height above the water table and the greatest overlap for pH and conductance.

Conclusion

Bryophyte and lichen distributions on Maine's peatlands are determined primarily by mineral influences on peat interstitial water. The primary gradient is related to alkalinity, and a secondary gradient is related to Fe, P, Al, Mn, and Si concentrations. Less important, yet significant factors are moisture content of the peat, shade, and climate. The autecological data presented here will be useful in paleoecological studies of peatland development. Quantitative reconstructions of edaphic conditions should be possible using weighted average calibrations, a logical extension of canonical correspondence analysis (ter Braak & Juggins 1993; Janssens *et al.* 1992).

Acknowledgements

Numerous persons and several agencies helped to make this work possible. For laboratory and field assistance we thank Celeste Doyle, Anne Frazer, Feng Sheng Hu, Timothy Kluge, Lisa Miller, Annie Narahara, and Klara Varga. Chemical analyses were made by Steve Kahl and other personnel of the University of Maine Watershed Manipulation Project and by Bruce Hoskins and other personnel of the Maine Agricultural Experiment Station Analytical Laboratory. The Maine Geological Survey provided access to its air photo collection, and Russ Briggs allowed us to use his climate data set. We thank Dale Vitt and an anonymous reviewer for constructive criticisms of an earlier draft.

We gratefully acknowledge funding from the Maine Agricultural Experiment Station, the Maine Department of Conservation, the Critical Areas Program of the Maine State Planning Office, the U.S. Department of the Interior through the University of Maine Environmental Studies Center, and the A.W. Mellon Foundation (E. Gorham).

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