A SURVEY ON CANTABRIAN MIRES (SPAIN)

by

JUAN JOSÉ ALDASORO*, CARLOS AEDO*, JESÚS MUÑOZ**, CARIDAD DE HOYOS***, JOSÉ CARLOS VEGA****, ANA NEGRO*** & GONZALO MORENO*****

Resumen

ALDASORO, J.J., C. AEDO, J. MUÑOZ, C. DE HOYOS, J.C. VEGA, A. NEGRO & G. MORENO. Un estudio preliminar de las turberas cantábricas. *Anales Jard. Bot. Madrid* 54: 472-489 (en inglés).

Se estudian 39 turberas cantábricas desde el punto de vista de las características químicas del agua y de las especies de carófitas, musgos y plantas vasculares que crecen en ellas. Un análisis de coordenadas principales de los parámetros químicos y climáticos permitió dividir las turberas en cuatro grupos: 1) turberas de tipo "fen", pobres y continentales, 2) turberas tipo "fen", entre pobres e intermedias continentales, 3) turberas tipo "fen", intermedias atlánticas y 4) turberas tipo "fen", ricas en cationes. Los mismos grupos fueron establecidos a partir del análisis de coordenadas principales de la matriz de presencia/ausencia de especies. Los dos ejes principales de ambas ordenaciones fueron la mineralización y la oceaneidad. Del estudio de las preferencias de algunas de las plantas más representativas se concluyó que las especies de los grupos 1 y 4 son muy características, únicamente presentes en estos medios. Por el contrario, las de las turberas intermedias (grupos 2 y 3) pueden aparecer ocasionalmente en turberas pobres o ricas. En consecuencia las últimas parecen inadecuadas para su uso como indicadoras, pues están adaptadas a condiciones fluctuantes. También se discuten otras informaciones acerca de las preferencias ecológicas de las diversas especies.

Palabras clave: Turbera, "fen", mineralización, oceaneidad, vegetación, Cordillera Cantábrica, Sierra Segundera, España.

Abstract

ALDASORO, J.J., C. AEDO, J. MUÑOZ, C. DE HOYOS, J.C. VEGA, A. NEGRO & G. MORENO. A survey on Cantabrian mires (Spain). *Anales Jard. Bot. Madrid* 54: 472-489.

In thirty nine Cantabrian mires, several hydrological parameters were measured and charophytes, bryophytes and vascular plants were identified. Using principal coordinates of the chemical and climatic parameters, the mires were classified into four groups: continental poor fens, continental poor to intermediate fens, Atlantic intermediate fens and rich fens. The same groupings resulted from the analysis of the plants. The two main axis of both ordinations were the mineralization and the oceanity. The preferences of some more representative plants were also studied, with plants of groups 1 and 4 being very characteristic of and restricted to these environments. However, the species of the intermediate groups (2 and 3) appeared occasionally in both rich and poor mires. These species are inadequate for use as indicators because they are adapted to fluctuating conditions. Other details of ecological preferences are discussed.

Key words: Mire, fen, mineralization, oceanity, vegetation, Cantabrian Mountains, Sierra Segundera, Spain.

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INTRODUCTION

Small mire systems are widespread in the N and the NW of the Iberian Peninsula. Although some scattered studies have been carried out, the biological and chemical nature of these ecosystems is still poorly known, in spite of their ecological importance. They represent the last refuge for some Boreo-Alpine species which colonized these areas during the glaciations. Some of these sites are within the limits of the Mediterranean mountain area, but others have a true Atlantic climate. The substrate can be diverse, ranging from acid rock to limestone; thus, extensive ecological variation should be detectable in comparative study of these mires.

The structure and composition of the vegetation is related to the chemical composition of the water and to the climate (HUTCHINSON, 1975; RAVEN, 1988; MARGALEF MIR, 1981). However, the geographic distribution of some taxa could also be related to historical conditions, such as extinction or colonization taking place after the glacial periods.

Although some of these taxa might be more broadly distributed in other smaller peatlands of the N and NW Iberian Peninsula, they have been rarely reported in Spain. Some work had been published concerning the Cantabrian mires, but little information about the ecology of mire plants is included. These studies sometimes followed certain phytosociological procedures which may be open to methodological criticisms.

The early efforts of ALLORGE (1927, 1928) provided an in-depth study of the bryological flora of the Cantabrian Mountains. Thereafter, SIMÓ (1976) reviewed the genus *Sphagnum* and the *Sphagnum* formations in the Atlantic area of Spain. The studies of FERNÁNDEZ ORDÓÑEZ & SIMÓ (1976) and FERNÁNDEZ PRIETO & *al.* (1987) concerning the mires of León and Asturias are of interest but lack chemical data, while the data on *Sphagnum* species were somewhat disconcerting; nothing could be concluded about the trophic conditions in these ecosystems. A substantial work by GACIA & *al.* (1994) on lakes of the eastern Pyrenees included both the vegetation and the main environmental factors (altitude, surface area, pH, conductivity, total phosphorus, nitrates and potassium), although the number of species studied was very limited.

For many years European workers have investigated mire species and classified these environments according to the main chemical and biological data. The most accepted classification divided peatlands into minerotrophic fens and ombrotrophic bogs on a hydrological basis, depending on whether or not the mire surface receives water that has percolated through the mineral soil (GORE, 1983). The fens were subdivided into several categories, mainly: extremely rich fen, rich fen, intermediate fen and poor fen (MOEN, 1985; SJÖRS, 1950a & 1950b; GORHAM & JANSSENS, 1992). Nowadays, multivariate statistical analysis procedures are used extensively to ordinate them. Plant species data are also frequently used, in addition to the main water chemistry and climatic parameters (GIGNAC & VITT, 1990; VITT & CHEE, 1990; GACIA & *al.* 1994).

The first aim of the present work is to present a preliminary but comprehensive classification of Cantabrian mires in consonance with European systems. This classification will be based in physico-chemical, climatic and species data. The second aim will be to delimit the habitat of mire plants (charophytes, vascular plants and mosses) using climate, surface water chemistry and physical parameters.

MATERIAL AND METHODS

In the Sierra Segundera and Cantabrian mountains we were able to distinguish two types of mires: one type lay in effluent basins or hollows on slopes and were usually smaller. A second type was situated in closed basins, which sometimes have little hummocks and hollows, and/or sedge swamps on the shores of a central pool. A total of 39 sites of both types of mires were chosen for study (Fig. 1).

Water samples were collected in July or August from pools and the surface of mires, then filtered. Conductivity, pH and alkalinity were measured immediately in the field. Chlorophyll samples were filtered, extracted with acetone and measured spectrophotometrically. Water samples for all other analyses were first filtered through a 45 Whatman GFC filter, then stored in plastic bottles, except for samples to be analyzed for phosphorus and phosphate which were stored in glass bottles. The phosphomolybdic-acid method was used for phosphate, and total phosphorus was measured after digesting the sample with potassium peroxidisulfate in acid medium at 120 ºC and 1.2 atm. For nitrate analysis, samples were reduced in a cadmium column and the nitrites measured using the sulfanilamide method. Dissolved silica was measured with ammonium molybdate and methol, adding oxalic acid to avoid phosphate interference. Water color was measured spectrophotometrically at

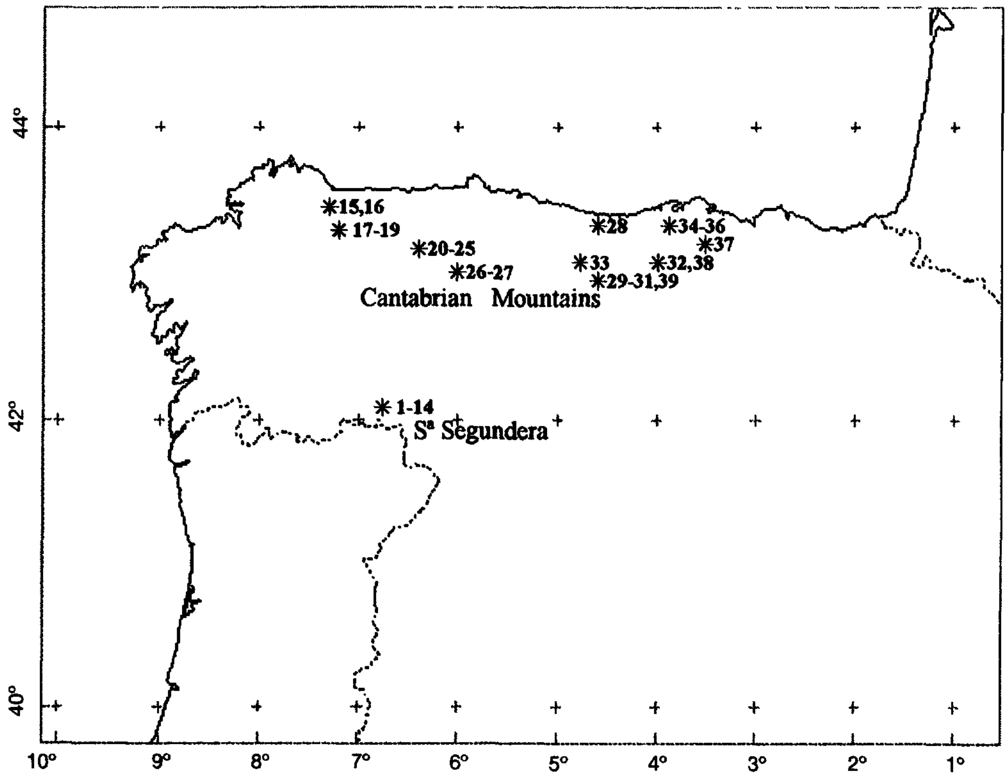

Fig. 1.–Localization of the mires studied in the NW of the Iberian Peninsula. 1: laguna de Aguas Cernidas, 29TPG8172, 1830 m (Za); 2: la Clara, 29TPG8165, 1590 m (Za); 3: la Roya, 29TPG8267, 1610 m (Za); 4: Covadosos, 29TPG8670, 1640 m (Za); 5: laguna de Lacillo, 29TPG8274, 1700 m (Za); 6: Majadavieja, 29TPG8264, 1610 m (Za); 7: Moncalvo-2, 29TPG8073, 1960 m (Za); 8: la Aveseda, 29TPG8765, 1030 m (Za); 9: Truchillas, 29TQG0675, 1850 m (Le); 10: laguna Pedrina, 29TPG8164, 1710 m (Za); 11: Puente Porto, 29TPG7863, 1700 m (Za); 12: Camposagrado, 29TPG7766, 1690 m (Za); 13: laguna de Padornelo, 29TPG7960, 1740 m (Za); 14: Valdecasares, 29TPG7763, 1800 m (Za); 15: Agros, 29TPJ2310, 650 m (Lu); 16: Peña Vieira, 29TPJ2309, 600 m (Lu); 17: Peña Ramiscal, 29TPJ6302, 980 m (Lu); 18: Peña Pumarín, 29TPJ6101, 1000 m (O); 19: La Garganta, 29TPJ6303, 880 m (O); 20: Chouchinas-1, 29TQH9963, 1600 m (O); 21: Chouchinas-2, 29TQH9963, 1650 m (O); 22: Reconcos (1 y 2), 29TQH0364, 1550 m (O); 23: Chagüeño de Abajo, 29TQH0757, 1550 m (O); 24: Chagüeño de Arriba, 29TQH0757, 1630 m (O); 25: Campo de la Braña de Arriba, 29TQH0657, 1600 m (O); 26: laguna de las Verdes-1, 29TQH3366, 1720 m (Le); 27: laguna de las Verdes-2, 29TQH3366, 1720 m (Le); 28: Llano Roñances, 30TUP6403, 200 m (O); 29: Riofrío, 30TUN6166, 1400 m (S); 30: Peña Prieta-1, 30TUN6166, 1770 m (S); 31: Peña Prieta-2, 30TUN6166, 1770 m (S); 32: Abiada, 30TUN9364, 1100 m (S); 33: Cordiñanes, 30TUN4580, 900 m (Le); 34: Pozos de Noja-1, 30TVN3894, 740 m (S); 35: Pozos de Noja-2, 30TVN3894, 740 m (S); 36: puerto del Campillo, 30TVN4086, 820 m (S); 37: Estacas de Trueba, 30TVN4274, 1250 m (Bu); 38: Serna, 30TVN0165, 1000 m (S); 39: las Lomas, 30TUN5763, 2050 m (P).

380 nm following the method of ALEXANDER & BARSDATE (1971), using a 10 cm cell. Cations were measured by atomic absorption spectrophotometry at the Analysis Service of the University of Salamanca.

Box-plots were used to evaluate the distribution of plants in relation to water parameters. These plots contained medians and percentiles, and were calculated using the STATGRAPHICS package. Principal components (PCA) and principal coordinates (PCO) were calculated using the NTSYS-pc package. For chemical and climatic data, a natural logarithms matrix was obtained from the initial matrix (Tab. 1), the correlations were calculated, and principal components were extracted and plotted. For plant species, the indices of Jaccard and Dice were extracted from the presence-absence matrix (Tabs. 2 and 3). The plot of sites was made with the complete matrix and the index of Jaccard. The plot of species was made with a reduced matrix of data and the index of Dice. This method was used to determine what main grouping of mires is supported by both the physico-chemical/climatic data and the plant species.

RESULTS

Mire classification

a) Physical-chemical and climatic data

Four well detached groups could be found in the Principal Coordinate Analysis (PCO) of physico-chemical data (fig. 2). These groups were: 1.- Continental poor mires, situated in the Segundera Mountains; 2.- Oceanic intermediate mires, situated in the Cantabrian coast (except 8, which is in the Segundera Mountains); 3.- Continental poor to intermediate mires, in the Cantabrian Mountains, and 4.- Rich mires, occurring on limestone in the Cantabrian Mountains. In the analysis, the first two components covered 58.38% of the variance and the three first eigenvalues were 1: 9.62, 2: 6.54 and 3: 3.63.

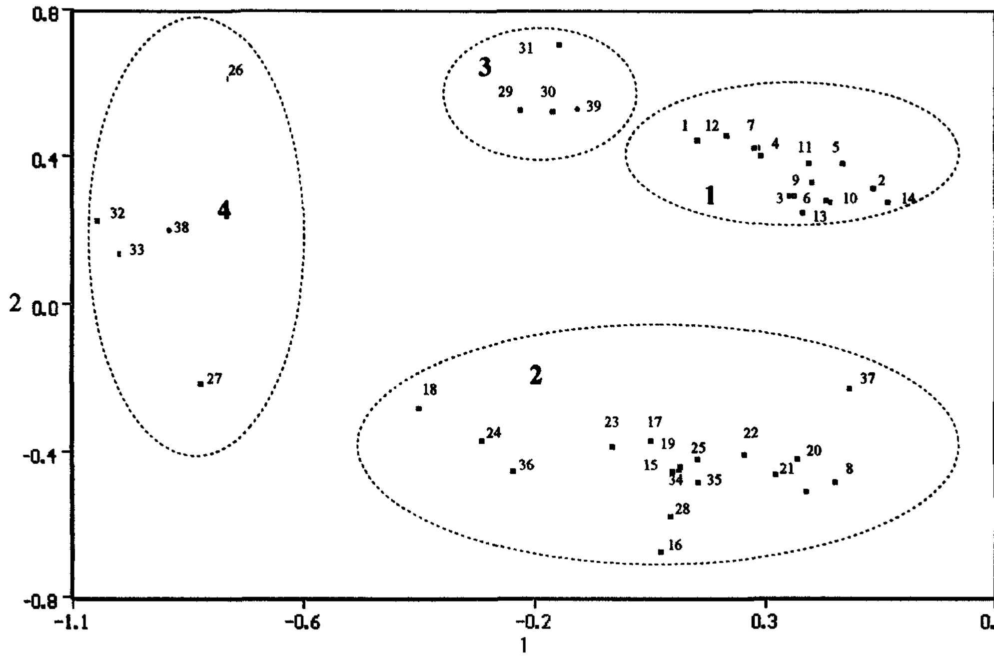

Fig. 2.–Principal Coordinate Analysis of the sites using the chemical and climatic characteristics of the mires. The groups are: 1) continental poor mires in the Segundera Mountains; 2) oceanic intermediate mires, most of them in the Cantabrian area, only the site 8 is in the Segundera Mountains; 3) continental poor to intermediate mires in the Cantabrian Mountains; 4) rich mires in the Cantabrian area. The numbers correspond to the sites, see Figure 1.

Along the first axis, the analysis separated the mires with mineralized waters located on limestones (group 4) from poor fens containing softer waters, which depended more heavily on rainfall (group 1, and to a lesser extent groups 2 and 3). The second axis separated the humid and temperate mires situated at low altitudes in the Cantabrian area (group 2) from those drier and more continentally situated in the Segundera and Cantabrian Mountains (groups 1 and 3).

Figure 3 shows the component loading of each variable. The first axis was related to mineralization (alkalinity, cations and conductivity on the left side and Na^+ on the right), and the second one presumably to climate (oceanity index at the bottom and total phosphorus at the top). Thus, the influence of the bedrock in relation to that of the atmosphere seems to be the main basis of ordination. As a consequence the *Chara*-mires (26, Laguna de los Verdes; 27, Laguna de los Verdes mire; 32, Abiada; 33, Cordiñanes; and 38, Serna) were well-separated from all the others.

The most oceanic mires (group 2) situated near the coast of Lugo and other sites of the Cantabrian provinces were clearly distinguished from those situated toward the interior or at higher altitudes in the Segundera and Cantabrian mountains. Many of the mires situated at lowest altitudes in the N of the Cantabrian Ridge had a very humid and oceanic climate, but those situated on the S face of these mountains or those of the very continental Segundera range were grouped with the continental ones. However, one of the Sierra Segundera mires, the Aveseda site, at 1000 m, and with a climate moderated by the Sanabria Lake, was grouped with the oceanic sites.

Other water characteristics such as colour, nitrate content, and magnesium content, showed a low weight in the multivariate analysis. Other data obtained but not included in this analysis because of their low statistical significance were quantifications of chlorophyll, soluble phosphate, silica, potassium, sulfate and iron.

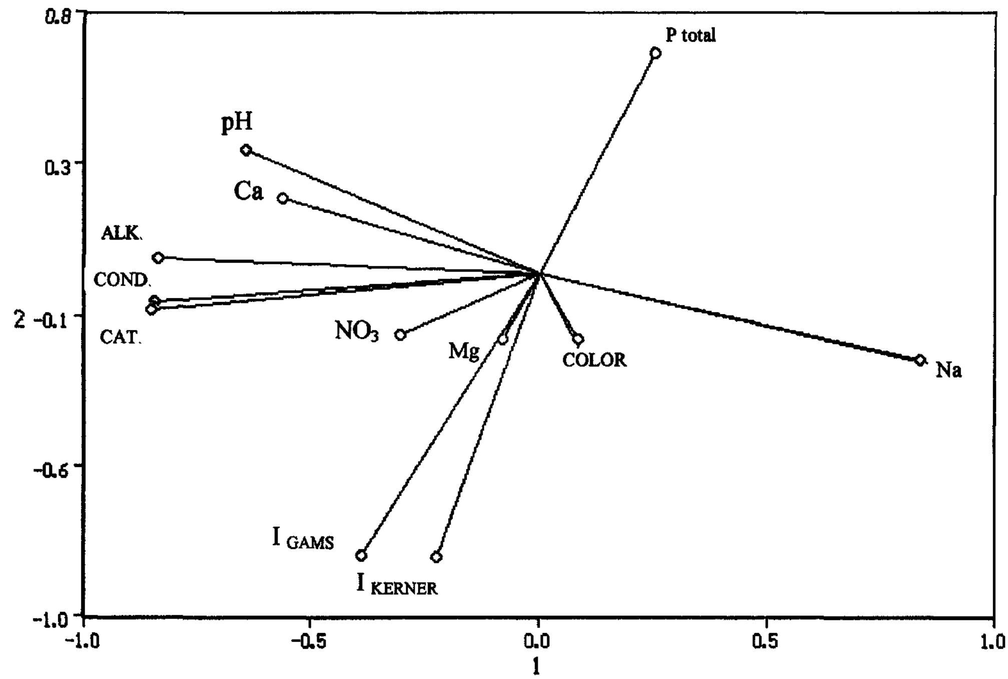

Fig. 3.–Component loading of the variables used in the PCO analysis. Alk: alkalinity; Ca: calcium; Cat: total concentration of cations; Color: absortion at 380 nm; Cond: Conductivity; IGAMS: Index of Gams; IKERNER: index of Kerner; Mg: magnesium; Na: sodium; NO3: nitrate; Ptotal: total phosphorus.

b) Vegetation

The PCO analysis of the vegetation (charophytes, bryophytes and vascular plants) made with the entire matrix of presence-absence (employing the Jaccard index) resulted in four well-separated groups. This classification showed a great concordance with that obtained from surface water chemistry, physical and climatic data (see above); one axis separated the mineralized from the slowly mineralized and the other the continental or high mountain mires from the oceanic ones (Fig. 4). However, in this case the first axis was influenced by climate and the second by water chemistry. The variance covered by the two first axes was only 24.87 % and the three first eigenvalues were: 1: 3.97, 2: 2.03 3: 1.55. Nonetheless, minor differences were found in each case with respect to the PCO ordination based on physico-chemical factors. Some Sierra Segundera sites (7, 11 and 14, the small slope mires) which were classified according to physico-chemical parameters into the group of extremely poor mires were in this ordination in the group of moderately poor ones. The Sierra Segundera slope mires and those of the Cantabrian Mountains basin and slope ones always had an appreciable quantity of minerals depending on bedrock solubility; thus, several species were common in both types of environment but were absent from the poorest Sierra Segundera basin mires. As a consequence, the Sierra Segundera slope mires were differently arranged in the two PCOs. The basin mires have a very poor center where the rich percolating water cannot reach, and richer margins with higher mineralization. These differences are not so evident in the typically smaller Cantabrian mires.

The classification of plants was made with a reduced matrix using only the species which were present at more than two sites. A different index was used (Dice index) and the three first axes were represented (Fig. 5). The following three groups could be recognized: 1- including mainly species of poor mires; 2- including spe-

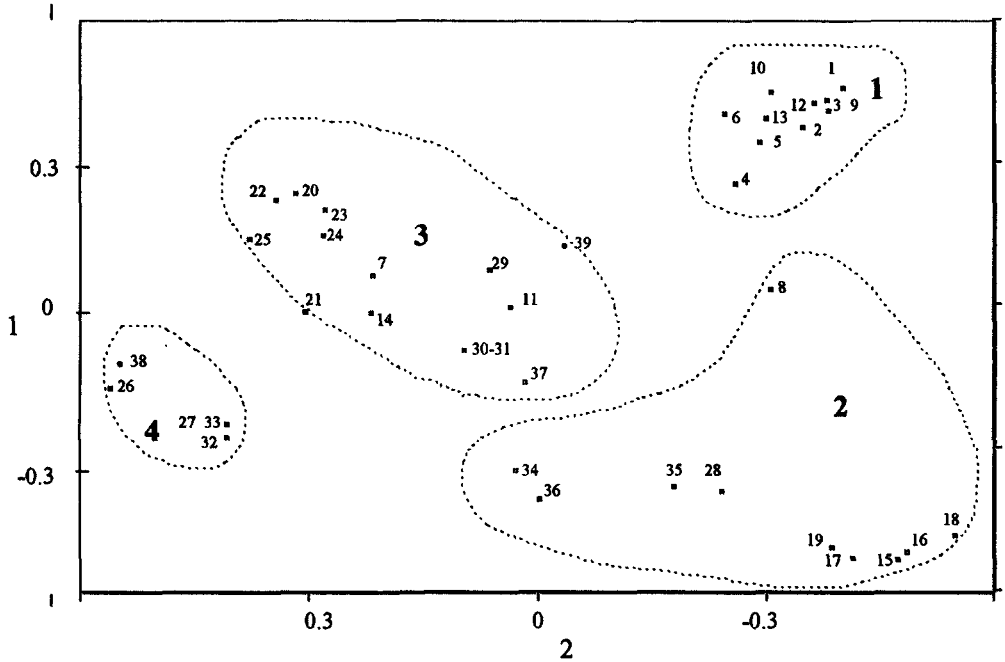

Fig. 4.–Principal Coordinate Analysis of sites using the plant species of the mires. The Jaccard index was used. The groups are: 1) continental poor mires in the Segundera Mountains; 2) oceanic intermediate mires of the Cantabrian area, only 8 is from the Segundera Mountains; 3) continental poor to intermediate mires, most of them in the Cantabrian Mountains, but also some slope mires in the Segundera Mountains (7, 11, 14); 4) rich mires in the Cantabrian area. The numbers correspond to the sites, see Figure 1.

cies of intermediate mires and 3- species of rich mires. These axes summarized only a very low percentage of the variance. Thus, the structure of these groups could not be sufficiently representative of the preferences of species. To determine the true preferences of the more common species, box plots were made. The more important characteristics were used in the PCO ordination: Index of Kerner, Index of Gams, Alkalinity, Conductivity, pH, Nitrate, Calcium and Sodium levels (Fig. 3).

Plant requirements

a) Moss species

The box plots of the calcium levels showed that *Bryum pseudotriquetrum, Philonotis calcarea, Palustriella commutata* and *Calliergonella cuspidata* had preference for highest Ca^{2+} (Fig. 6). They grew under highest pH, alkalinity, conductivity and other cation levels like Na^{+} or Mg^{2+} (Fig. 6 and 7). Water with intermediate levels of Ca^{2+} was favoured by a se-

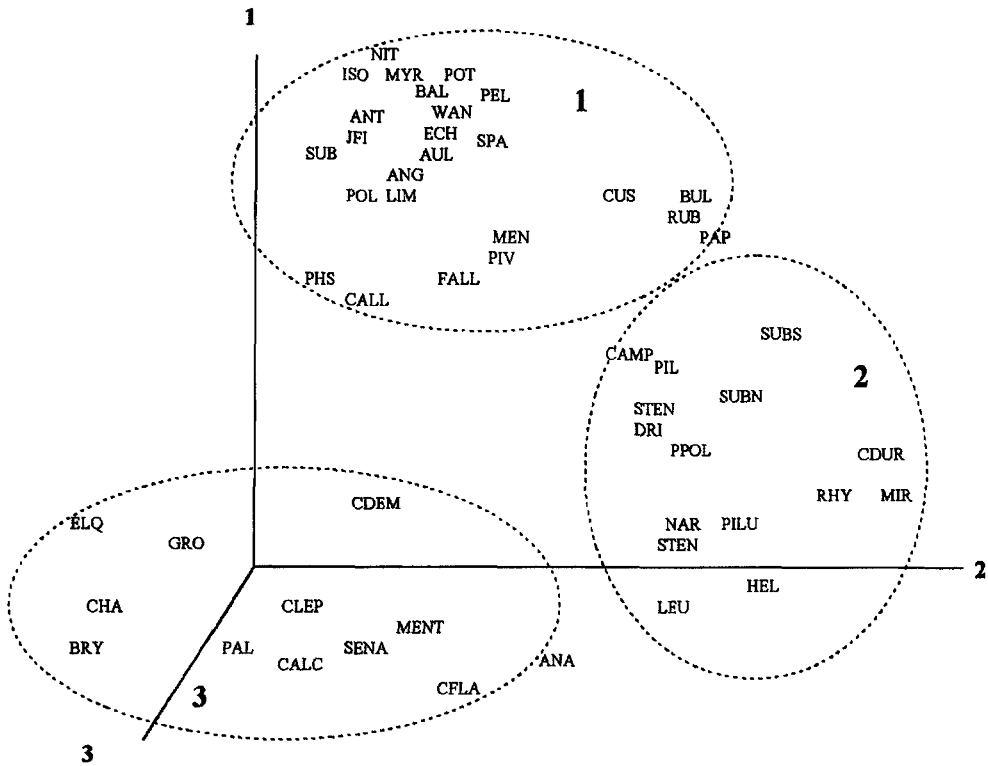

Fig. 5.–Principal Coordinate Analysis of the plant species. The index of Dice and a reduced matrix were used. The groups are: 1- poor mires, 2- intermediate mires and 3- rich mires. Simbols are: ANA: *Anagallis tenella*; ANG: *Sphagnum angustifoliun*; ANT: *Antinoria agrostidea*; AUL: *Aulacomnium palustre*; BAL: *Baldellia alpestris*; BRY: *Bryum pseudotriquetrum*; BUL: *Juncus bulbosus*; CALL: *Calliergon stramineum*; CALC: *Calliergonella cuspidata*; CAMP: *Campylium stellatum*; CDEM: *Carex demissa*; CDUR: *Carex durieui*; CFLA: *Carex flacca*; CLEP: *Carex lepidocarpa*; CHA: *Chara* sp. pl.; CUS: *Sphagnum cuspidatum*; DRI: *Drosera intermedia*; ECH: *Eleocharis acicularis*; ELQ: *Eleocharis quinqueflora*; FALL: *Sphagnum fallax*; GRO: *Groenlandia densa*; HEL: *Hypericum elodes*; ISO: *Isoetes velata*; JFI: *Juncus filiformis*; LEU: *Leucobryum glaucum*; LIM: *Carex limosa*; MEN: *Menyanthes trifoliata*; MENT: *Mentha longifolia*; MYR: *Myriophyllum alterniflorum*; NAR: *Narthecium ossifragum*; NIT: *Nitella flexilis*; PAL: *Palustriella commutata*; PAP: *Sphagnum papillosum*; PEL: *Ranunculus peltatus*; PHS: *Philonotis seriata*; PILU: *Pinguicula lusitanica*; POT: *Potentilla palustris*; PPOL: *Potamogeton polygonifolius*; PIL: *Sphagnum pylaesii*; PIV: *Pinguicula vulgaris*; POL: *Polytrichum sp. pl.*; RHY: *Rhynchospora alba*; RUB: *Sphagnum rubellum*; SPA: *Sparganium angustifolium*; STEN: *Sphagnum tenellum*; SUB: *Subularia aquatica*; SUBN: *Sphagnum subnitens*; SUBS: *Sphagnum subsecundum*; SENA: *Senecio aquaticus*; WAN: *Warnstorfia exannulata*.

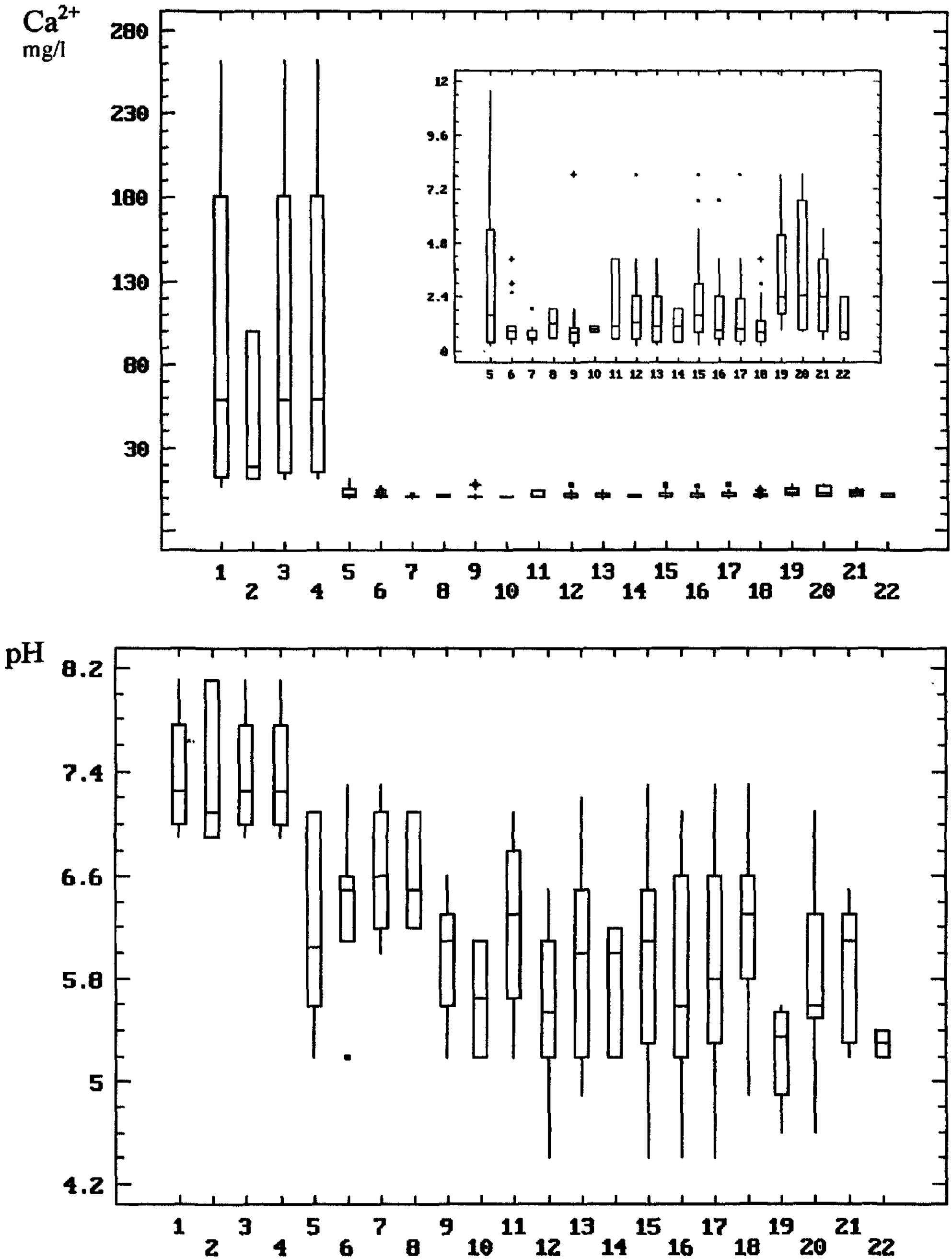

Fig. 6.–Box-plots of the Ca^{2+} levels and pH preferences of the mosses. The bars are the first and third quartiles and the line in the bar is the mediane. Inset is to magnify the scale of Ca^{2+} levels in the less minerotrophic mosses. 1) *Bryum pseudotriquetrum*; 2) *Philonotis calcarea*; 3) *Palustriella commutata*; 4) *Calliergonella cuspidata*; 5) *Calliergon stramineum*; 6) *Warnstorfia exannulata*; 7) *Fontinalis antipyretica*; 8) *Aneura pinguis*; 9) *Aulacomnium palustre*; 10) *Philonotis seriata*; 11) *Sphagnum teres*; 12) *S. subsecundum*; 13) *S. fallax*; 14) *S. magellanicum*; 15) *S. papillosum*; 16) *S. capillifolium*; 17) *S. cuspidatum*; 18) *S. flexuosum*; 19) *Leucobryum glaucum*; 20) *Campylium stellatum*; 21) *Sphagnum subnitens*; 22) *S. tenellum*.

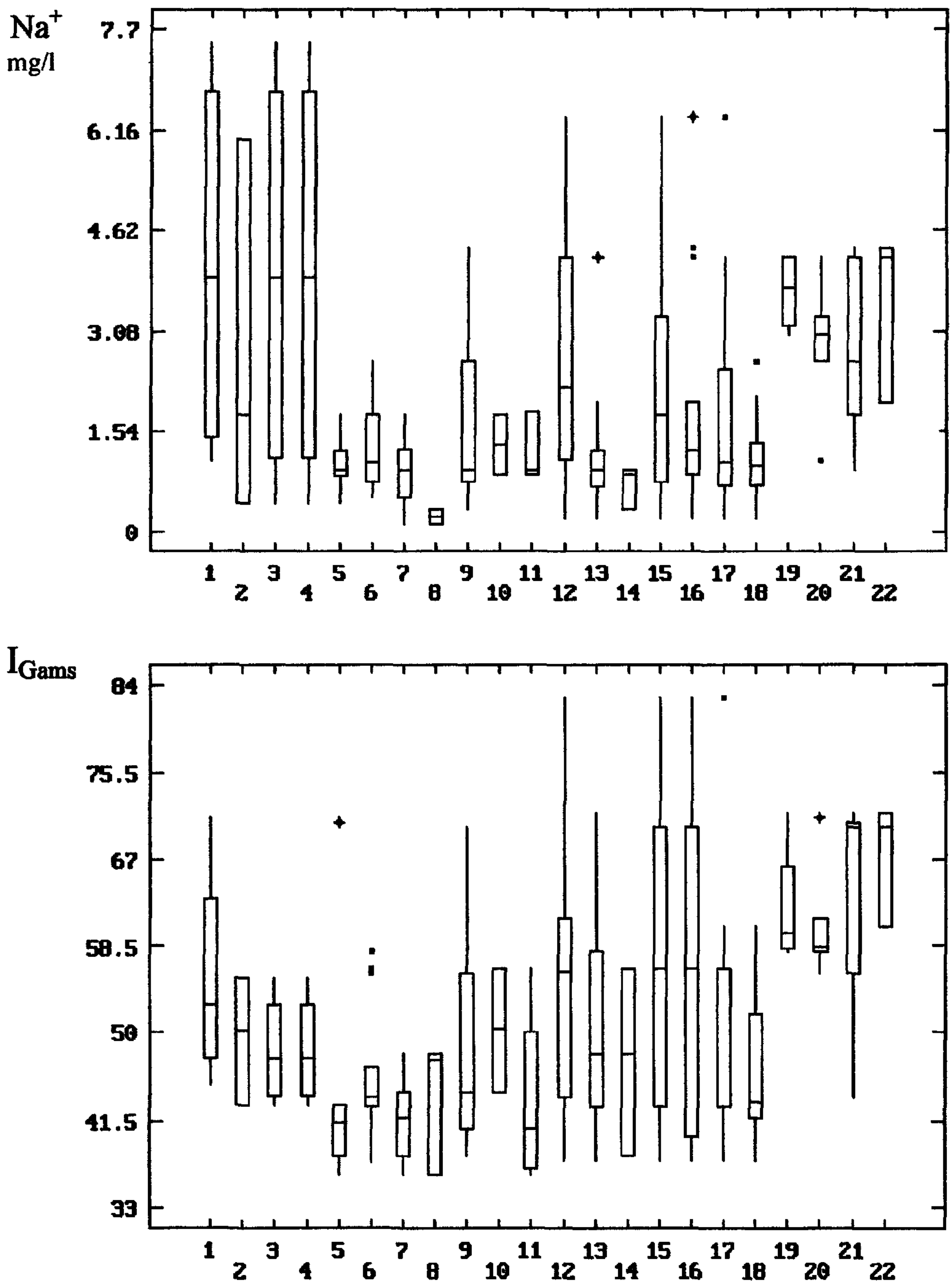

Fig. 7.–Box-plots of the Na^+ levels and Gams index preferences of the mosses. The bars are the first and third quartiles and the line in the bar is the mediane. 1) *Bryum pseudotriquetrum*; 2) *Philonotis calcarea*; 3) *Palustriella commutata*; 4) *Calliergonella cuspidata*; 5) *Calliergon stramineum*; 6) *Warnstorfia exannulata*; 7) *Fontinalis antipyretica*; 8) *Aneura pinguis*; 9) *Aulacomnium palustre*; 10) *Philonotis seriata*; 11) *Sphagnum teres*; 12) *S. subsecundum*; 13) *S. fallax*; 14) *S. magellanicum*; 15) *S. papillosum*; 16) *S. capillifolium*; 17) *S. cuspidatum*; 18) *S. flexuosum*; 19) *Leucobryum glaucum*; 20) *Campylium stellatum*; 21) *Sphagnum subnitens*; 22) *S. tenellum*.

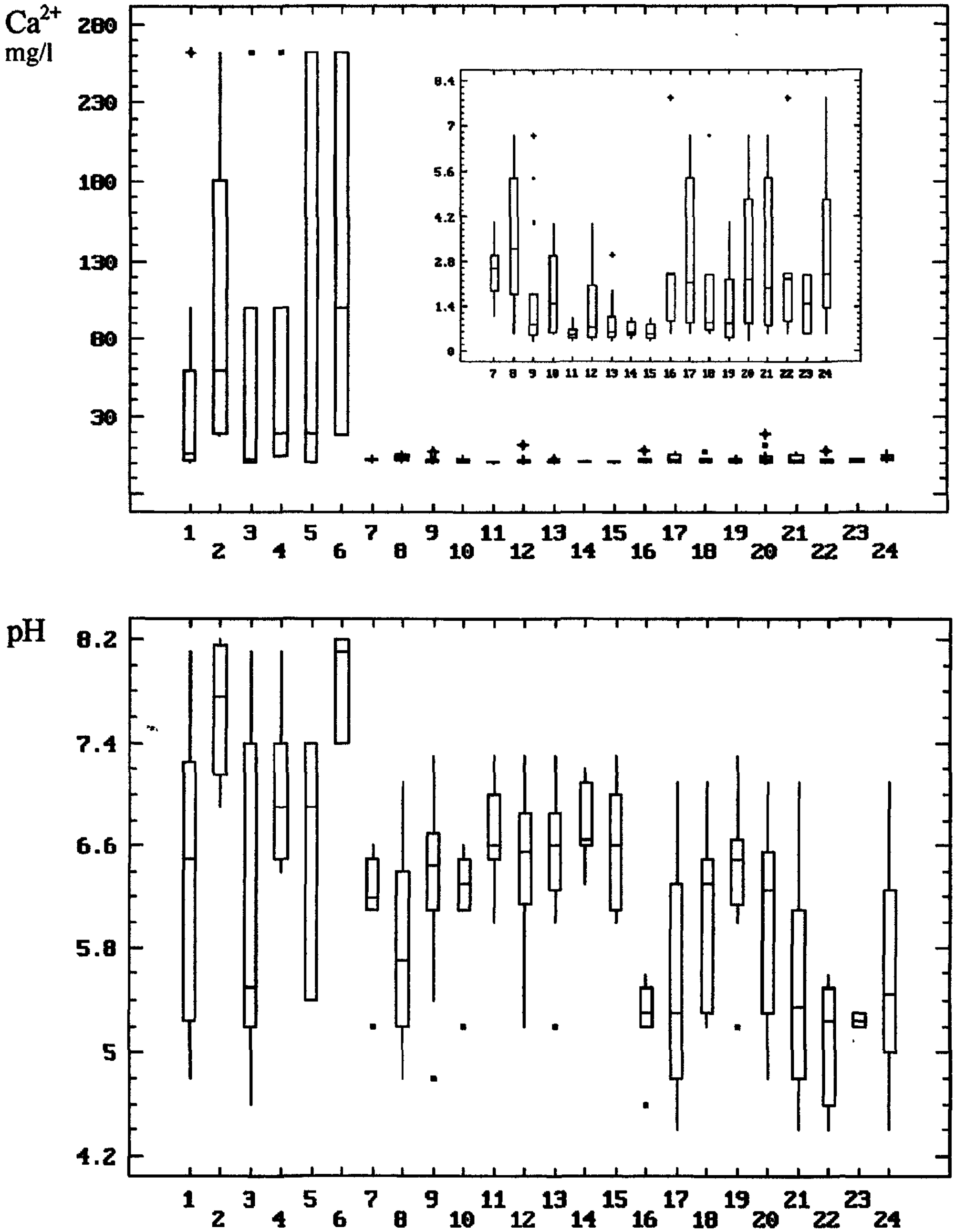

Fig. 8.–Box-plots of the Ca^{2+} levels and pH preferences of the algae and vascular plants. The bars are the first and third quartiles and the line in the bar is the mediane. Inset is to magnify the scale of Ca^{2+} levels in the less minerotrophic algae and vascular plants. 1) *Anagallis tenella*; 2) *Chara* sp. pl.; 3) *Carex flacca*; 4) *C. lepidocarpa*; 5) *Eriophorum latifolium*; 6) *Groenlandia densa*; 7) *Luzula multiflora*; 8) *Hypericum elodes*; 9) *Eriophorum angustifolium*; 10) *Carex canescens*; 11) *Myriophyllum alterniflorum*; 12) *Menyanthes trifoliata*; 13) *Isoetes velata*; 14) *Nitella flexilis*; 15) *Antinoria agrostidea*; 16) *Carex duriaei*; 17) *Rhynchospora alba*; 18) *Potamogeton polygonifolius*; 19) *Potentilla palustris*; 20) *Viola palustris*; 21) *Drosera intermedia*; 22) *Erica mackaiana*; 23) *Myrica gale*; 24) *Narthecium ossifragum*.

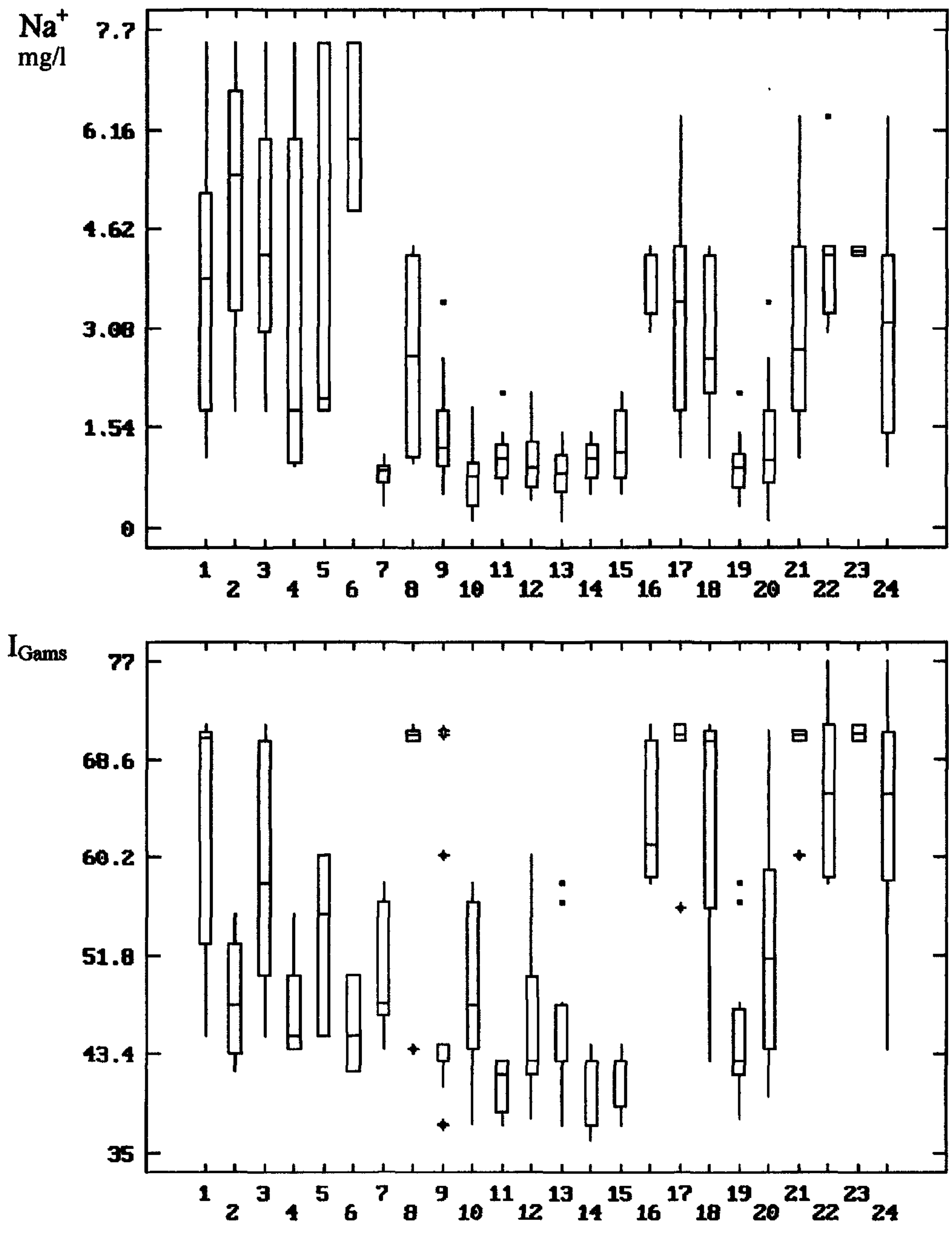

Fig. 9.–Box-plots of the Na^+ levels and Gams index preferences of the algae and vascular plants. The bars are the first and third quartiles and the line in the bar is the mediane. 1) *Anagallis tenella*; 2) *Chara* sp. pl.; 3) *Carex flacca*; 4) *C. lepidocarpa*; 5) *Eriophorum latifolium*; 6) *Groenlandia densa*; 7) *Luzula multiflora*; 8) *Hypericum elodes*; 9) *Eriophorum angustifolium*; 10) *Carex canescens*; 11) *Myriophyllum alterniflorum*; 12) *Menyanthes trifoliata*; 13) *Isoetes velata*; 14) *Nitella flexilis*; 15) *Antinoria agrostidea*; 16) *Carex duriaei*; 17) *Rhynchospora alba*; 18) *Potamogeton polygonifolius*; 19) *Potentilla palustris*; 20) *Viola palustris*; 21) *Drosera intermedia*; 22) *Erica mackaiana*; 23) *Myrica gale*; 24) *Narthecium ossifragum*.

TABLE 1

MAIN CHARACTERISTICS OF THE SITES STUDIED (nd = not determinated)

		Cond. µS/cm	pH	Alkal. mEq/l	Color	Cloroph. µg/l	N03 µg/l	Ptotal µg/l	Silica mg/l	Ca mg/l	Mg mg/l	Na mg/l	K mg/l	Index of Gams	Index of Gorecyn.	Index of Kerner
1	Aguas Cernidas	18	7,10	0,12	0,29	5,8	14,2	16,80	0,04	1,05	0,13	0,54	0,00	40,70	30,09	9,55
2	Clara	8	6,80	0,06	0,17	4,1	31,4	8,20	0,00	1,20	0,42	2,39	0,13	42,80	30,09	9,55
3	Roya	19	7,30	0,13	0,38	22,2	17,2	12,40	0,36	1,02	0,51	1,46	0,22	42,80	30,09	9,55
4	Covadosos	23	6,10	0,03	0,40	3,3	39	18,60	1,66	0,84	0,12	1,81	2,33	44,26	30,09	9,55
5	Lacillo	13	7,10	0,10	0,15	3,9	9,1	24,80	0,44	0,91	0,29	1,27	4,07	41,00	30,09	9,55
6	Majadavieja	11	7,00	0,09	0,20	11,1	39,1	8,20	0,01	0,47	0,14	1,17	0,00	42,80	30,09	9,55
7	Moncalvo-2	20	5,50	0,06	0,03	0,88	57,7	51,70	1,37	0,64	0,30	1,50	0,11	37,60	30,09	9,55
8	La Aveseda	20	6,35	0,06	0,25	1,01	2,96	8,40	0,08	0,88	0,26	2,61	0,00	55,76	19,69	10,80
9	Truchillas	15	4,80	0,00	0,34	3	14,1	19,60	0,23	1,21	0,27	0,61	0,03	37,57	30,09	9,55
10	Pedrina	9	6,70	0,04	0,12	6,3	10,1	6,70	0,43	0,58	0,17	1,45	0,22	39,08	30,09	9,55
11	Puente Porto	12	5,60	0,04	0,08	2,1	9,5	28,00	0,00	1,61	0,17	1,26	0,66	42,78	30,09	9,55
12	Camposagrado	12	6,50	0,03	0,52	4,4	8,9	50,80	0,10	0,30	0,09	0,89	0,00	42,78	30,09	9,55
13	Padornelo	7	6,50	0,04	0,06	2	8,9	10,40	0,08	0,40	0,18	0,96	0,16	39,08	30,09	9,55
14	Valdecasares	12	5,20	0,02	0,20	3,2	10	27,80	0,10	0,24	0,09	0,85	0,00	39,87	30,09	9,55
15	Agros	25	5,30	0,07	0,30	149,5	361	4,48	0,03	0,56	0,26	4,34	0,65	70,14	22,41	17,92
16	Peña Vieira	38	5,20	0,07	0,18	5,67	16	4,17	0,02	0,90	0,30	0,62	0,60	71,56	22,41	17,92
17	Peña Ramiscal	32	4,60	0,00	0,10	7,78	42	2,58	0,01	0,94	0,56	3,03	0,17	58,51	27,92	12,82
18	Peña Pumarín	36	5,50	0,24	0,15	5,67	16	4,17	0,02	2,44	0,47	4,23	0,73	57,99	27,92	12,82
19	La Garganta	63	5,60	0,24	0,08	2,01	152	1,90	0,02	7,86	0,14	3,30	0,14	61,18	28,42	12,69
20	Chouchinas-1	17	5,20	0,02	0,65	1,1	6,34	6,60	0,07	1,08	0,65	0,89	0,34	56,31	35,69	15,56
21	Chouchinas-2	15	4,90	0,00	0,09	5,58	5,28	6,60	0,04	0,21	0,10	0,30	0,00	55,49	35,44	15,18
22	Reconcos-1	37	6,60	0,22	0,17	1,58	21,8	8,35	0,52	3,01	0,16	0,69	0,16	50,79	38,18	14,89
22	Reconcos-2	16	6,20	0,05	0,29	2,76	5,66	10,23	0,11	1,49	0,00	0,67	0,00	50,79	38,18	14,89
23	Chagüeño de Abajo	25	6,20	0,09	0,14	5,98	8,66	10,40	0,14	1,29	0,39	0,35	0,00	47,48	42,10	14,00
24	Chagüeño de Arriba	15	6,50	0,02	0,05	3,64	5,66	6,88	0,00	0,59	0,21	0,13	0,03	47,84	40,85	14,29
25	Campo de la Braña	24	6,10	0,07	0,20	2,67	7,88	6,92	0,25	2,60	0,74	1,11	0,34	46,73	39,85	14,52
26	Verdes-1	77	7,10	0,48	0,10	0,56	73,95	11,60	0,46	11,55	1,46	0,45	0,23	42,93	45,90	9,40
27	Verdes-2	130	7,00	0,92	0,30	11,78	33,07	8,59	0,63	16,52	2,74	0,89	0,31	42,93	46,10	11,28
28	Llano Roñances	77	4,40	0,10	0,38	15,96	15,94	13,22	0,00	2,15	1,05	6,35	0,45	82,87	20,49	20,61
29	Riofrío	33	6,50	0,18	0,36	6,9	5,09	3,68	0,26	4,06	0,13	0,96	0,13	43,8	40,92	9,35
30	Peña Prieta-1	40	6,40	0,14	0,14	26,56	6,34	16,90	0,52	4,04	0,40	0,99	0,40	43,8	40,92	9,35
31	Peña Prieta-2	37	6,30	0,12	0,03	3,57	5,95	5,81	0,61	3,25	0,17	1,17	0,17	43,8	40,92	9,35
32	Abiada	2400	7,40	1,36	0,40	8,61	10,02	11,67	3,95	262	147	7,46	2,41	45	41,67	10,04
33	Cordiñanes	231	6,90	1,64	0,01	1,89	15,36	8,87	1,17	19,03	0,32	1,77	0,32	55,3	39,59	16,60
34	Noja-1	25	6,10	0,26	0,18	102,48	60,1	15,02	0,00	1,82	0,71	5,46	1,09	70,7	27,50	18,65
35	Noja-2	53	4,80	0,10	0,61	5,8	11,14	9,93	0,00	1,85	0,08	3,51	0,08	70,7	27,50	18,65
36	Campillo	94	7,10	0,52	0,14	4,07	19,58	10,12	0,00	6,74	0,00	6,13	0,00	71,13	30,55	15,61
37	Estacas de Trueba	25	5,40	0,01	0,29	2,31	8,54	4,56	0,00	0,82	0,14	1,99	0,14	60,39	31,62	10,53
38	Serna	1600	8,10	2,42	0,03	nd	32,7	11,50	1,82	100	nd	nd	nd	44,50	40,90	9,30
39	Las Lomas	15	7,10	0,01	0,06	nd	44,1	4,26	0,65	1,60	nd	nd	nd	42,00	40,90	9,35

TABLE 2

SPECIES OF ALGAE AND VASCULAR PLANTS USED IN THE MULTIVARIATE ANALYSIS (0: absence; 1: presence)

plant species

site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66
1	1	0	0	1	0	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0
2	1	0	0	1	0	1	1	1	0	1	0	1	0	0	0	1	1	1	1	0	0	1	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	1	1	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0
3	1	0	0	1	0	1	1	1	0	1	0	1	0	0	0	1	1	1	1	0	0	1	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	1	1	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0
4	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
5	1	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	1	1	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0
6	0	0	0	1	0	1	1	1	0	0	0	1	0	0	0	1	1	1	1	0	0	1	1	0	1	0	0	0	0	1	0	0	1	0	1	1	0	1	0	1	1	0	1	0	0	1	0	0	1	1	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0
7	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1
8	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1
9	0	0	0	1	0	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1	1	0	1	0	1	0	0	1	0	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
10	1	0	0	1	0	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	1	1	0
11	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1
12	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0
13	0	0	0	1	0	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1	1	0	1	0	1	0	0	1	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0
14	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
15	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1
16	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	1	1	0	1	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
17	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1
18	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
19	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1
20	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0
21	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
22	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0
23	0	0	0	1	0	0	0	1	1	0	0	1	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1
24	0	0	0	1	0	0	0	1	1	0	0	1	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1
25	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1
26	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
28	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	1	1	0	1	0	1	0	1	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	1	0	0	1	1	0	1	0	0	0	1	1	0	1	0	1	1	0	0	1	0	0	0	0	0	1
30	0	0	0	0	0	0	1	1	1	1	0	1	0	1	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
31	0	0	0	0	0	0	1	1	1	1	0	1	0	1	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
32	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
33	0	1	1	0	1	0	0	1	0	1	0	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
34	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
36	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
37	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
38	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
39	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1

1) *Nitella flexilis*; 2) *Chara* sp. pl.; 3) *Selaginella selaginoides;* 4) *Isoetes velata*; 5) *Anagallis tenella*; 6) *Antinoria agrostidea*; 7) *Baldellia alpestris*; 8) *Caltha palustris*; 9) *Carex canescens*; 10) *C. demissa*; 11) *C. duriaei*; 12) *C. echinata*; 13) *C. flacca*; 14) *C. lepidocarpa*; 15) *C. leporina*; 16) *C. limosa*; 17) *C. nigra*; 18) *C. rostrata*; 19) *Carum verticillatum*; 20) *Dactylorrhiza maculata*; 21) *Drosera intermedia*; 22) *D. rotundifolia*; 23) *Epilobium palustre*; 24) *Equisetum fluviatile*; 25) *Eleocharis acicularis*; 26) *E. multicaulis*; 27) *E. palustris*; 28) *Epipactis palustris*; 29) *Erica mackaiana*; 30) *Eriophorum angustifolium*; 31) *E. latifolium*; 32) *Groenlandia densa*; 33) *Glyceria* sp. pl.; 34) *Hypericum elodes*; 35) *Juncus bulbosus*; 36) *J. filiformis*; 37) *Luzula multiflora*; 38) *Lythrum portula*; 39) *Mentha longifolia*; 40) *Menyanthes trifoliata*; 41) *Molinia caerulea*; 42) *Myrica gale*; 43) *Myriophyllum alterniflorum*; 44) *Narthecium ossifragum*; 45) *Pedicularis mixta*; 46) *Peucedanum lancifolium*; 47) *Pinguicula grandiflora*; 48) *P. lusitanica*; 49) *P. vulgaris*; 50) *Potamogeton natans*; 51) *P. polygonifolius*; 52) *Potentilla palustris*; 53) *Ranunculus ololeucos*; 54) *R. peltatus*; 55) *Rhynchospora alba*; 56) *Sanguisorba officinalis*; 57) *Scirpus caespitosus*; 58) *Senecio aquaticus*; 59) *S. doria*; 60) *Sparganium angustifolium*; 61) *Subularia aquatica*; 62) *Triglochin palustris*; 63) *Typha latifolia*; 64) *Utricularia australis*; 65) *U. minor*; 66) *Viola palustris*. For the sites numbers, see Figure 1; the site number 27 was not used in the species analysis.

cond group which included *Calliergon stramineum, Campylium stellatum, Leucobryum glaucum* and *Sphagnum subnitens*. These environments also showed an ample variation in pH, alkalinity, conductivity and levels of other cations. Finally, some mosses were found in waters with a very low Ca^{2+} concentration (less than 1 mg/l); these species were *Warnstorfia fluitans, Fontinalis antipyretica, Aulacomnium palustre, Sphagnum capillifolium, S. flexuosum, S. magellanicum* and *S. cuspidatum*.

Thus, the main ecological parameter seems

TABLE 3

SPECIES OF MOSSES USED IN THE MULTIVARIATE ANALYSIS (0: absence; 1: presence)

site	plant species																																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	1	1	0	1	0	0	1	0	0	1	0	0	0	0	1
2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	0	0	0	0	1
3	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	0	0	0	0	1
4	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0	1	0	0	1	0	0	0	0	1
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0
8	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	1	0	0	1
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	1	0	0	1	0	0	1	0	0	0	0	1
10	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1	0	1	1	0	1	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1
13	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0
14	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	1	0	1	0	0	0	1	0	1	0	0	0
15	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	1	0	1	1	1	0	0
16	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	1	0	1	1	1	0	0
17	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0
18	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0
19	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0
20	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	1	1	1	1	1	0	0	0	1	1	0	0	0	1	1
21	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1	0	0	1	0	0	0	0	1	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	1	0	0	1	0	1	1	0	0	0	0	1
23	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	1	0	0	0	0	0
24	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1
26	0	1	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	1	0	1	1	1	1	0	1	1
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
32	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
35	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0
36	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	1	0	0	0	0	0	1	0	0
38	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1

1) *Aulacomnium palustre*; 2) *Bryum pseudotriquetrum*; 3) *Campylium calcareum*; 4) *C. stellatum*; 5) *Calliergon stramineum*; 6) *Calliergonella cuspidata*; 7) *Fontinalis antipyretica*; 8) *Hypnum jutlandicum*; 9) *Hylocomium splendens*; 10) *Leucobryum glaucum*; 11) *Palustriella commutata*; 12) *Philonotis calcarea*; 13) *Ph. seriata*; 14) *Polytrichum alpinum*; 15) *P. commune*; 16) *P. formosum*; 17) *Scapania undulata*; 18) *Sphagnum angustifolium*; 19) *S. capillifolium*; 20) *S. compactum*; 21) *S. cuspidatum*; 22) *S. denticulatum*; 23) *S. fallax*; 24) *S. flexuosum*; 25) *S. magellanicum*; 26) *S. majus* subsp. *norvegicum*; 27) *S. papillosum*; 28) *S. pylaesii*; 29) *S. rubellum*; 30) *S. russowii*; 31) *S. subnitens*; 32) *S. subsecundum*; 33) *S. tenellum*; 34) *S. teres*; 35) *Warnstorfia exannulata*. For the sites numbers, see Figure 1; the site number 27 was not used in the species analysis.

to be the level of Ca^{2+}, and other parameters, such as conductivity, alkalinity or pH, were correlated. These data agree with those of other workers who suggested that *Bryum pseudotriquetrum* and *Calliergonella cuspidata* were species useful in distinguishing rich minerotrophic fens from moderately rich and poor ones. These latter mires are characterized by very low Ca^{2+} concentrations, and consequently low pH, alkalinity and conductivity (GORHAM & JANSSENS, 1992; SLACK, 1994). *Campylium stellatum, Calliergon stramineum, Sphagnum teres* and *S. subnitens* were more common in intermediate fens, while *S. flexuosum, S. magellanicum* and *S. cuspidatum* were characteristic of poor fens and bogs (GORHAM & JANSSENS, 1992; HORTON & *al.*, 1979). In the PCO ordination (Fig. 4) these three types of species were discriminated along the first axis.

Another factor in the species ordination was climate (Figs. 3 and 4, second axis). The box plots were elaborated with the Gams Index (depending on the precipitation and inversely related to the altitude) and Na^{+} levels (raised by the sea spray). They show that *Sphagnum tenellum, S. subnitens, Campylium stellatum* and *Leucobryum glaucum* grow preferably in coastal mires (Fig. 7). However, we were not able to find any moss species with distinct continental preferences.

b) Charophyte algae and vascular plant species

The most characteristic plants of the richest fens were *Chara* sp. pl. (mainly *Chara vulgaris), Carex lepidocarpa, Eriophorum latifolium* and *Groenlandia densa,* which grew in Ca^{2+} concentrations between 10 and 250 mg/l and pH from 5 to 8. Other somewhat minerotrophic plants were *Anagallis tenella* and *Carex flacca,* which grew in a slightly lower range of Ca^{2+} values. Some other minerotrophic species such as *Carex mairei, Triglochin palustris, Tetragonolobus siliquosus, Centaurium somedanum* were very scarce in these mires.

Plants of intermediate fens included *Rhynchospora alba, Drosera intermedia, Narthecium ossifragum, Hypericum elodes* and *Viola palustris* (Fig. 4, groups 2 and 3). They can withstand an ample variation in cation levels and grow in a great variety of wet environments from mires (rich or intermediate fens) to springs and small creeks.

By contrast, poor fen plants such as *Myriophyllum alterniflorum, Antinoria agrostidea, Isoetes velata* and *Nitella flexilis* were highly restricted to waters with less than 2 mg/l of Ca^{2+}, growing in lakes, pools and mires. Other more distinctive plants were *Eriophorum angustifolium, Potentilla palustris* and *Carex limosa,* which grew only in the mires (Fig. 8).

The climatic conditions strongly influenced the composition of the vascular flora (Fig. 3). Some Atlantic species such as *Myrica gale, Erica mackaiana,* and *Carex duriei* were restricted to low altitude mires in the western coastal zone of the Iberian Peninsula. Several other Atlantic species were less exigent with respect to climate: *Pinguicula lusitanica, Pilularia globulifera, Rhynchospora alba* and *Drosera intermedia* were spread in lowest altitude mires of the entire Cantabrian area. These mires showed a high Gams index and high Na^{+} concentrations (Fig. 9).

Continental plants such as *Antinoria agrostidea, Potentilla palustris, Carex canescens* and *Isoetes velata* preferred high mountain mires. In contrast to Atlantic species, continental ones should be resistant to more extreme moisture fluctuations (LAITINEN, 1990). Severe summer drought could cause the extinction of the more demanding species, v.gr. *Carex limosa,* which seems to be extinct in most of our small or medium-sized basin mires. Drought could be the cause of a decrease in the diversity of vascular plants already occurring in most of our small mires. Other high mountain species which exhibited a relict area of distribution are *Nuphar pumilum, Drosera longifolia* and *Subularia aquatica.* Low altitude mires with less fluctuations in moisture levels could have served in the Iberian Peninsula as a refuge to some more exigent plants, such as *Rhynchospora fusca* and *Myrica gale.*

DISCUSSION

Physico-chemical data of 39 mires of northern Spain allowed us to classify these sites into four groups using PCO, giving results comparable to those achieved from the plant species analysis. Climate was the main factor in the plant ordination, with water chemistry second. These data indicated that the mires could be classified using the standard European criteria of climate and mineralization. Consequently, the Cantabrian mires were classified following SJÖRS (1950a, 1950b) into poor, intermediate and rich fens, depending on calcium levels, pH and alkalinity. The mires could also be divided into oceanic and continental mires using the climatic index .

The mires situated on old plutonic or metamorphic bedrock in the Segundera Mountains were the poorest and most continental of all the sites studied (Fig. 2, group 1). They were divided into a) basin mires with an extremely poor center and richer margins (poor fens), and b) small effluent basin or slope mires which were slightly richer due to percolation of water from the adjacent soil (frequently enriched by cattle wastes). In terms of plant species, the latter sites were comparable to the continental intermediate mires of the Cantabrian Mountains, situated mainly on conglomerates or impure quartzite (Fig. 4, group 2). These groups of poor to intermediate mires ranged from 0.2 to 2 mg/l Ca^{2+} in the Sierra Segundera and from 1 to 4 mg/l in the Cantabrian Mountains. Conductivity, pH and alkalinity values were generally lower in the Sierra Segundera mires. The more widely spread vascular plants were *Menyanthes trifoliata, Juncus bulbosus, Eriophorum angustifolium, Baldellia alpestris, Carex canescens, C. echinata, C. rostrata* and *Ranunculus peltatus*; these plants are capable of growth under a wide spectrum of conditions.

More specialized were *Isoetes velata, Myriophyllum alterniflorum, Subularia aquatica, Potentilla palustris, Carex limosa, Antinoria agrostidea,* and the alga *Nitella flexilis*, which grew in the poorest environments.

By contrast, *Viola palustris, Hypericum elodes, Carex demissa, Narthecium ossifragum, Potamogeton polygonifolius, Utricularia minor* and *Luzula multiflora* usually occurred in richer environments.

Of the mosses, *Warnstorfia exannulata, Aulacomnium palustre, Fontinalis antipyretica, Sphagnum flexuosum, S. angustifolium, S. cuspidatum, S. magellanicum, S. capillifolium* and *S. russowii* occurred at the poorest sites, while *Calliergon stramineum, Campylium stellatum, Sphagnum teres, S. subsecundum* and *S. subnitens* were found at the slightly richer ones.

However, no clear limit could be established between both types of communities because some mires of intermediate characteristics included plants of both groups. Moreover, no plant characteristic of a specific type mire could be recognized, because under favorable conditions the species are capable of colonizing certain places within other types of mires.

The mires situated on the coast of Lugo, Asturias and Cantabria (Fig. 2, group 2) had some characteristic features: the indices of oceanity were higher, indicating warmer temperatures and higher precipitation; the Na^{+} levels were also higher due to sea spray; finally, the levels of total phosphorus were lower because a faster degradation to soluble phosphorus. Moreover, the flora of these mires had some species in common, such as *Carex duriei, Erica mackaiana, Myrica gale, Drosera intermedia, Pinguicula lusitanica* and *Rhynchospora alba*. The mosses were *Sphagnum tenellum, S. pylaesii* and *Leucobryum glaucum*. Other plants were in common with the continental intermediate sites. Those data served to classify them as intermediate oceanic fens.

Finally, the richest mires were on limestones, marls or related rocks, but only four of these sites were studied in this work; thus, the data should be interpreted with caution. The levels of all ions reached considerably higher values than in other types of mires, and Ca^{2+} concentrations were too high to permit *Sphagnum* development; *Amblystegiaceae* and other groups were common under these conditions (GORHAM & JANSSENS, 1992). The most characteristic plants were *Chara* sp. pl., *Groenlandia densa, Carex lepidocarpa,* *C. flacca*, *Senecio aquaticus*, and the mosses *Palustriella commutata*, *Bryum pseudotriquetrum*, *Philonotis calcarea* and *Calliergonella cuspidata*. Less common were *Cirsium flavispina*, *Triglochin palustris* and *Centaurium somedanum*.

These data are in consonance with the classification of SJÖRS (1950 a and b), who established 4-5 as the limits of pH in poor fens of Fennoscandia. TOLONEN & HOSIAISLUOMA (1978) gave (summer) values of 3.9 in the Finnish poor mires. WELLS & ZOLTAI (1985) in Canada indicated values of 4.5-5.1 for poor or intermediate fens, and 3.8-4 for bogs. HAVAS (1961) gave a pH of 5 as the limit of oligotrophy. Finally, EUROLA & HOLAPPA (1985) and MALMER (1986) established that values of conductivity < 25 µS, calcium < 2 mg/l and total phosphorus < 50 µg/l indicate oligotrophy as regards bogs or poor fens. At the opposite extreme, the lower limits of the rich fens were established by GORHAM & *al.* (1987) at pH 6 and calcium concentrations of about 3-5 mg/l.

It should be emphasized that the chemical conditions of intermediate mire waters are not so constant. They are poorly buffered between pH 4.5 and 6.0, and slight shifts in the balance between bicarbonate and organic acids will result in large, sudden alterations in pH (GORHAM & JANSSENS, 1992). Thus, the cessation of a small minerotrophic input could generate strong falls in pH, constraining some adapted plants to colonize these transitional environments while other species are eliminated.

Some species seem to be more adapted to fluctuating conditions than to highly mineralized waters, such as the mosses *Sphagnum subsecundum*, *S. teres*, *S. fallax*, *S. subnitens*, *Calliergum stramineum*, *Campylium stellatum*, and the vascular plants *Hypericum elodes*, *Rhynchospora alba*, *Narthecium ossifragum*, *Viola palustris*, *Drosera intermedia* and *Menyanthes trifoliata* (Figs. 8 and 9). This species niche definition might better explain their ample chemical spectrum, which makes their use as indicator plants difficult (GORHAM & JANSSENS, 1992).

As a further consequence, we cannot agree with the proliferation of phytosociological community names applied to the intermediate mires. Their species generally have a wide spectrum of habitats, which renders them inadequate as indicator species.

Another interesting biological factor is the "biological inertia" that permits some plants to persist long after conditions suitable for their colonization and establishment have disappeared (GORHAM, 1957). Thus, a poor community could contain some minerotrophic species which could have survived under unfavorable conditions, such as the striking case of *Phragmites communis*, which grew in some N American and Scandinavian ombrotrophic mires (CHAPMAN, 1964a & 1964b, GORHAM & JANSSEN, 1992). These habitats might be deceptively classified as intermediate mires or described as a new phytosociological association, when in reality they can clearly be considered as ombrotrophic bogs. This problem is notorious in small Mediterranean mires, which are frequently merged with other ecosystems, and makes many of the phytosociological approaches to these environments unsuccessful.

Finally, the presence of relict species in the studied mires should be emphasized. Their extreme geographic situation, with very dry neighboring areas, and the continued destruction of the mire habitat represent serious threats to their persistence. The presence of *Carex limosa*, *Rhynchospora fusca*, *Drosera longifolia*, *Nuphar pumilum*, *Sphagnum subtile* and *S. majus* subsp. *norvegicum*, which are probably bordering on extinction, indicates the importance of study and classification of mires. Such efforts are needed if these endangered species and habitats are to be effectively conserved.

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