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A Floristic-Ecologic Classification of Five Mire Sites in the Montane-Subalpine Belt of South Tyrol (S Alps, Italy)

By

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With 8 figures

Key words: Mire typology, phytosociology, vegetation science. – Hydrochemistry. – Multivariate analyses.

Summary

GERDOL R., TOMASELLI M. & BRAGAZZA L. 1994. A floristic-ecologic classification of five mire sites in the montane-subalpine belt of South Tyrol (S Alps, Italy). – Phyton (Horn, Austria) 34 (1): 35–56, 8 figures. – English with German summary.

The rough morphology of the relief does not allow true raised peat bogs to develop in the Alps. Alpine peatlands are located on more or less inclined terrain and show series of transitional types from ombrosoligenous mires to fens, thus complicating the task of typifying mires and mire complexes. In this study five peatlands situated in the upper montane – lower subalpine vegetation belt of the South Tyrolian Alps (Italy) were considered as a representative sample of that range. Vegetation was studied by field relevés and mapped. Watertable depth as well as hydrochemistry (pH, electrical conductivity, Na^+, K^+, Ca^{2+}, Mg^{2+}) were monitored along transects at all sites.

By means of average linkage clustering (with Jaccard-index as similarity-coefficient) and comparison with material published up to now 9 different vegetation types belonging to 4 alliances (Piceion abietis / Bazzanio-Piceetum; Sphagnion magellanici / Pino mugo-Sphagnetum, Sphagnetum magellanici with 2 subassociations; Rhynchosporion albae / Caricetum rostratae, Caricetum limosae with 2 subassociations; Caricion davallianae / Schoenetum ferruginei, Caricetum davallianae) were distinguished. The peatlands analysed revealed as complexes of hydrologically different segments. In no case, however, could a clear delimintation be defined be-

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tween ombrotrophic and minerotrophic areas since the peat surface is never distinctly raised above the surrounding terrain.

Two main groups of peatlands could be distinguished. First, fen complexes heavily influenced by ground water and covered by a brown-moss sedge vegetation. These peatlands also include more or less extensive carpets of Sphagna that can be either distinctly minerotrophic or nearly ombrotrophic. Second, bog complexes mostly covered by a hummock-hollow mosaic having, if any, only a very loose contact with telluric water. A peripheric lagg is poorly differentiated at all of these latter sites. However, a narrow belt of wet fen often develops at the downslope edge. It can either directly rest on the mineral substrate or on humified acidic peat.

Plant communities defined by the BRAUN-BLANQUET approach are predictive with respect to mire habitat, especially when operating at a low hierarchical rank (subassociations). Even though most of those communities are by no means restricted to a given mire type, the whole vegetational pattern is well correlated with gross hydromorphological features.

Zusammenfassung

GERDOL R., TOMASELLI M. & BRAGAZZA L. 1994. Floristisch-ökologische Klassifizierung von fünf Mooren in der montan-subalpinen Stufe Süd-Tirols (S-Alpen, Italien). – Phyton (Horn, Austria) 34(1): 35–56, 8 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Aufgrund der Geländemorphologie kommt es in den Alpen nicht zur Ausbildung reiner Hochmoore im strengen Sinne. Stets in Hanglagen entwickelt, zeigen sie alle Übergänge zwischen ombrosoligenen und minerogenen Mooren, was ihre Typisierung erschwert. Für den vorliegenden Versuch einer floristisch-ökologischen Gliederung wurden fünf für die hochmontan-tiefsubalpine Stufe repräsentative Moore bzw. Moorkomplexe in den Sarntaler Alpen (Südtirol) ausgewählt. Die Geländestudien umfaßten die floristische Aufnahme nach der Methode von BRAUN-BLANQUET 1964 sowie Messungen über die Lage des Grundwasserspiegels entlang von Transekten. Untersuchungen hydrochemischer Parameter (pH, Leitfähigkeit, Na^+, K^+, Ca^{2+}, Mg^{2+}) ergänzen die Feldbeobachtungen. Die Vegetation der Moore wurde mit Unterstützung von Luftbildern kartiert.

Die Vegetationsgliederung mit Hilfe numerischer Methoden (Average linkage clustering mit dem Jaccard-Index als Ähnlichkeitskoeffizienten) führte nach dem Vergleich mit bisher publiziertem Material zur Unterscheidung von 9 Vegetationstypen, die sich klar 4 Verbänden zuordnen lassen (Piceion abietis / Bazzanio-Piceetum; Sphagnion magellanici / Pino mugo-Sphagnetum, Sphagnetum magellanici mit 2 Subassoziationen; Rhynchosporion albae / Caricetum rostratae, Caricetum limosae mit 2 Subassoziationen; Caricion davallianae / Schoenetum ferruginei, Caricetum davallianae). Die untersuchten Moore werden als Vegetationskomplexe gedeutet, deren Elemente unterschiedliche Ansprüche an Grundwasserstand und Wasserqualität haben. In keinem Fall konnte aber eine klare Abgrenzung zwischen rein ombrotrophen und minerotrophen Teilen gezogen werden, da der Torfkörper nirgends über das umgebende Gelände aufgewölbt ist.

Es können zwei Haupttypen unterschieden werden: Erstens Komplexe aus weniger nährstoffarmen, kalkreichen Nieder- und Übergangsmoorgesellschaften mit starkem Grundwassereinfluß und einer Vegetationsdecke, charakterisiert durch

Braunmoose und Seggen bzw. minerotrophe oder fast ombrotrophe *Sphagnum*-Decken. Zweitens nährstoffarme Moorkomplexe mit einem Bulten-Schlenken-Mosaik und undeutlich ausgebildetem Lagg. Der Kontakt zu tellurischem Wasser ist – falls vorhanden – sehr schwach. Direkt auf dem mineralischen Untergrund oder auf humifiziertem, sauren Torf ist am hangabwärtigen Rand häufig ein schmaler Streifen mit nasser Niedermoorvegetation ausgebildet.

Die auf floristischer Grundlage unterschiedenen Vegetationseinheiten – vor allem im Subassoziationsrang – korrelieren gut mit den untersuchten hydrochemischen Parametern. Keine der (Sub-)Assoziationen ist auf einen der Moorkomplextypen beschränkt. Diese eignen sich bei fehlenden hydrochemischen Untersuchungen besser zur Charakterisierung von Mooren als einzelne Pflanzengesellschaften oder Zeigerpflanzen (etwa "Mineralbodenwasserzeiger").

1. Introduction

The Alps, as well as all Central-European mountains, lie outside the main distributional area of ombrotrophic bogs (Hochmoore) in Europe (OSVALD 1925; KATZ 1948; EUROLA 1962). Raised bogs (Plateau-Hochmoore and Kermi-Hochmoore; see DIERSSEN 1982) in the region of the Alps sensu lato are mainly confined to the northern Praealps and the Jura, where they develop either in intermorainic depressions or on flat karst plateaux (RINGLER 1978; ROYER & al. 1978; GRÜNIG & al. 1986; FELDMEYER-CHRISTE 1990). By contrast, peatlands in the Alps sensu stricto are usually located on gently sloping terrains, especially saddles and valleys originated by glacial modelling. Although gross climate would be suitable for bogs to develop over extensive territories, the relief morphology hinders the formation of raised bogs. Hence, ombrosoligenous excentric bogs (ombrosoligene Hochmoore; RUDOLPH 1929) have been recognized since long ago as the dominant poor-mire type in the northern Alps (KAULE 1973, 1974).

In the southern Alps the Quaternary moraines penetrate into the uppermost sector of the Po plain, having a too dry and warm climate for allowing bog formation. On the other hand, bog-like peatlands are relatively frequent at higher elevations, particularly in the montane and in the lower subalpine vegetation belts. The only catalogue of peatlands in the southern Alps hitherto available (GÖTTLICH 1987, 1991) refers to the region of South Tyrol (Alto Adige, Italy). Among the almost 700 sites listed in that catalogue, only 12 were categorized as ombrotrophic. At least some of the latter cannot even be regarded as true bogs (GERDOL, unpublished).

Mire typology should be based on purely hydrotopographical criteria. However, as the peat bodies of alpine mires show only a modest elevation – if any – above the surrounding terrain, a satisfactory classification of those peatlands would require a number of time-consuming topographical surveys of mire surface and water table as well. On the other hand, a fairly large amount of data are available on mire vegetation in the southern Alps. They show that several peatlands in this region are covered by a vegetation closely resembling that of bogs, but often associated with fen communities in a more or less regular spatial pattern (GERDOL 1981, 1990; ANDREIS & RODONDI 1982; PEDROTTI 1982; GERDOL & TOMASELLI 1984, 1991; VENANZONI 1988; WÜRZ 1992). There seems to be, therefore, an intergradation of mire types from ombrosoligenous slope bogs to rich fens, through a continuous series of intermediate and poor fens sheltering more or less extensive islands of bog-like vegetation.

Aim of this paper is to test whether a consistent partitioning of that continuum can be produced through an integration of data concerning (1) surface topography, (2) water chemistry, and (3) floristic classification of vegetation.

2. Materials and Methods

2.1 Description of the Study Area

Research was confined to a small area in order to exclude the effects of large-scale phytogeographical trends as possible sources of floristic variation. Five mire sites, all comprised within a narrow elevational belt (ca. 1500-1750 m), were selected in the territory of Sarntaler Alpen (Monti Sarentini) in the Italian South Tyrol (Südtirol, Alto Adige). A preliminary field survey showed that these sites can be regarded as a representative sample for the main morphological types of peatlands occurring in the upper montane-lower subalpine vegetation belt in the southern Alps.

The climate is temperate-continental, with a mean annual temperature of ca. 5° C at 1500 m, and mean monthly temperatures ranging from -3° C in January to 14° C in July. Annual precipitation averages 900 mm and shows a distinct peak in summer (FLIRI 1975).

The mineral substrate mainly consists of ignimbrite dating back to Early Permian. The climax vegetation consists of Norway spruce *(Picea abies)* forests.

2.2 Field Work

Vegetation was studied at different periods during the summer months of 1986 and 1989, using the approach of BRAUN-BLANQUET 1964. The sampling plots, varying in size from a few square meters in the *Sphagnum* hummocks to 30 m^2 in the woodland vegetation of mire margins, were mostly placed along transversal transects (one or two per site). Although the choice of plots was subjective, the largest effort was made for every plot to represent a homogeneous stand and the sample to cover the entire set of vegetation patterns detected by visual inspection in the field.

The location of every plot was exactly marked by means of a woody stake, 1 m long, driven into the peat and cut off at the peat surface. Both water level and water chemistry were monitored at all plots, in the absence of precipitation, during a two-day campaign (22-23 July 1989). Hence, a reliable between-site comparison could be established. Unless water lay above surface, a hole was dug in the peat until the water table was reached. After ca. one hour the water level was measured from the stake, and both pH and electrical conductivity measured by portable instruments. The conductivity owing to hydrogen ions was substracted (SJÖRS 1952) to obtain corrected values. A water sample was then collected by means of a syringe, carefully avoiding peat compaction. The water was filtered, placed in 100mL acid-washed plastic bottles, and deep frozen until analysis. A topographic map as well as a series of peat-depth profiles were obtained for each site within a project of mire mapping by the Biological Laboratory of the Bozen (Bolzano) province.

2.3 Laboratory Work

The vegetation relevés were bulked into a floristic table and classified by average linkage clustering (ANDERBERG 1973), using the Jaccard index (WESTHOFF & VAN DER MAAREL 1978) as similarity coefficient. The units obtained by this cluster analysis were then compared with syntaxonomical types. The sources of nomenclature are: PIGNATTI 1982 for vascular plants, with the exceptions of *Carex nigra* (L.) RICHARD, *Melampyrum pratense* L. subsp. *paludosum* (GAUD.-B.) RONN. and *Picea abies* (L.) KARSTEN; CORLEY & al. 1981 for mosses; ANDRUS 1980 for *Sphagnum;* and GROLLE 1983 for hepatics.

The water samples were analysed for major cations (Na^+, K^+, Ca^{2+}, and Mg^{2+}) by atomic absorption spectrophotometry. Lanthanum was added when analysing calcium and magnesium in order to reduce anionic interference.

The topographical distribution of the vegetation types was mapped by surveying aerial photographs. The variations of the main environmental variables along the transects were also shown graphically. In addition, the relations between physicochemical variables and vegetation types were explored by multiple discriminant analysis. The package SPSSPC+ for IBM PC was employed to this regard (NORUSIS 1986).

For the abbreviations of the community names see chapter 4 or Tab. 1.

3. Topography and Hydrology

All of the mires develop in glacial landforms (either small valleys or saddles) and their sizes range from less than 1 ha to ca. 10 ha (Fig. 1-5). The mire surface is more or less distinctly undulating for being covered, to a variable extent, by *Sphagnum* carpets and/or hummocks. In no case, however, does it give rise to a pronounced mound. A detailed topographic survey at one of the sites (BRAGAZZA 1992) showed that even the elevational difference between forested ridges and deep hollows never exceeds 100 cm.

The strategy adopted in the sampling only permits to get a record of the hydrologic conditions at the sampling time, without accounting for the seasonal patterns of variation. The water table is slightly raised under *Sphagnum* hummocks which represent, as could be easily expected, the driest microhabitats at the peatlands examined. Most of the hollows, as well as the marginal belts had the water table above ground at the time of sampling (Fig. 1-5).

4. Vegetation

Nine clusters were recognized at a similarity value of ca. 0.40 (Fig. 6). All of them can be interpreted in syntaxonomical terms as associations or

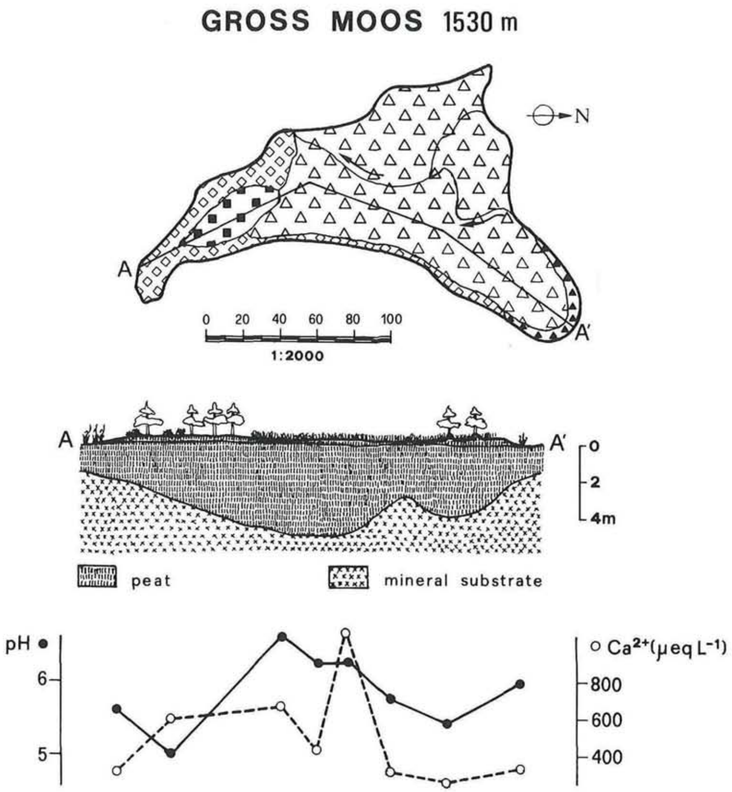

Fig. 1. Top: schematic vegetational map of Groß Moos. The vegetation types mapped are: Sphagnetum magellanici typicum (■), Schoenetum ferruginei (△), Caricetum davallianae (▲) and Caricetum limosae subass. of *Sphagnum subsecundum* (◇). Arrows indicate surface water-flows in streams.
Centre: hydrotopographical profile. The thin line indicates the watertable. (Vertical exaggeration 10x).
Bottom: hydrochemical transect.

subassociations. Following recent literature (DIERSSEN 1982; DIERSSEN & REICHELT 1988; OBERDORFER 1992a, 1992b), they are included in the classes Vaccinio-Piceetea, Oxycocco-Sphagnetea and Scheuchzerio-Caricetea nigrae. Whereas both of the former classes are represented in this data set an only one order each (Vaccinio-Piceetalia and Sphagnetalia magellanici, respectively), the latter has two orders (Scheuchzerietalia palustris and Caricetalia davallianae). The syntaxonomical arrangement (Tab. 1) is briefly outlined in the following and the floristic composition of the types is synthesized in Tab. 2.

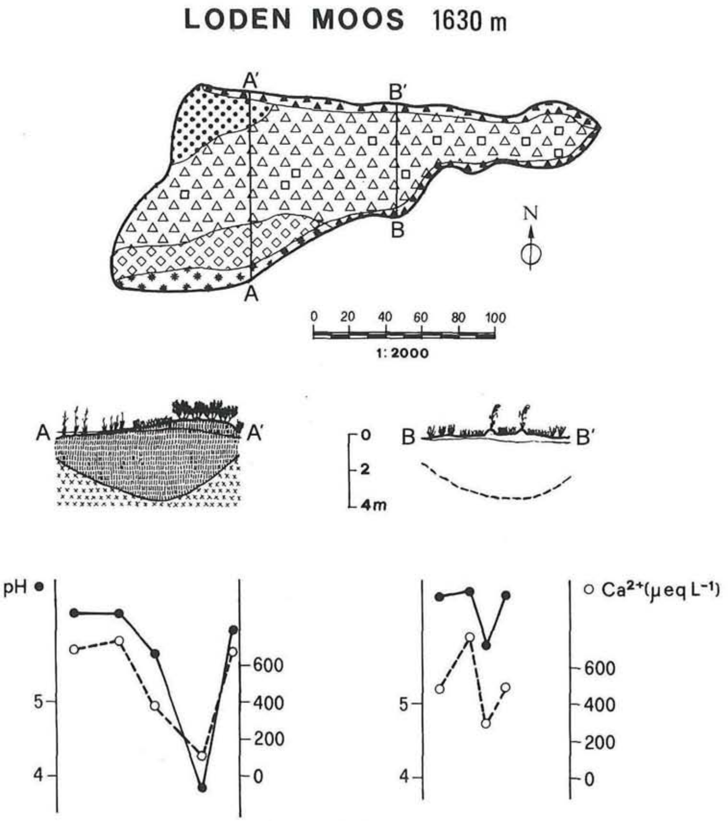

Fig. 2. Top: schematic vegetational map of Loden Moos. The vegetation types mapped are: Pino mugo - Sphagnetum (●), Sphagnetum magellanici sphagnetosum fusci (□), Schoenetum ferruginei (△), Caricetum davallianae (▲), Caricetum rostratae (✳) and Caricetum limosae subassociation of *Sphagnum subsecundum* (◇). (Intermixed symbols indicate mosaics). Centre: hydrotopographical profiles. The symbols for peat and mineral substrate are as in Fig. 1; the thin line indicates the water-table. Profile B - B' is largely hypothetical, for being reconstructed based on a single peat profile. (Vertical exaggeration 10x).
Bottom: hydrochemical transects.

Bazzanio-Piceetum (BP = abbreviation used here). Corresponds to a forest type having *Picea abies* as the dominant tree. The understory is rich in *Ericaceae*, especially *Vaccinium myrtillus*. The bottom layer has some mosses and Sphagna typic of peaty substrates *(Sphagnum nemoreum, S. russowii* and *Polytrichum strictum),* together with species more frequent on mineral soils *(Pleurozium schreberi, Sphagnum girgensohnii, S. quinquefarium, Polytrichum formosum* and *Calypogeia azurea).* Other

KLEIN MOOS 1510m

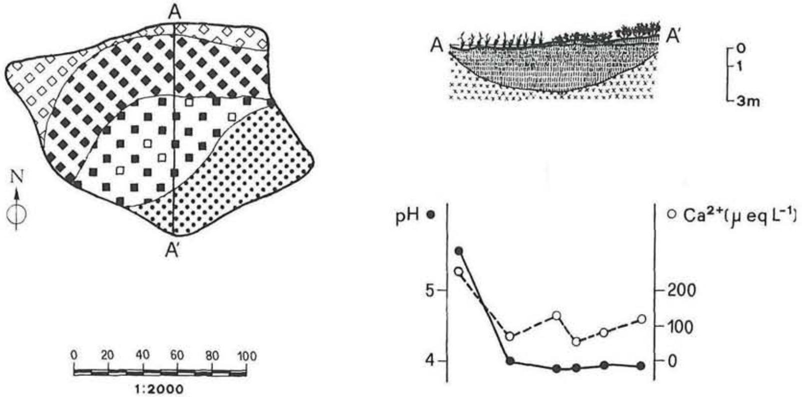

Fig. 3. Left: schematic vegetational map of Klein Moos. The vegetation types mapped are: Pino mugo - Sphagnetum (●), Sphagnetum magellanici typicum (■), Sphagnetum magellanici sphagnetosum fusci (□), Caricetum limosae subass. of *Sphagnum subsecundum* (◇) and Caricetum limosae subass. of *Sphagnum majus* (◆). (Intermixed symbols indicate mosaics). Right, above: hydrotopographical profile. The symbols for peat and mineral substrate are as in Fig. 1; the thin line indicates the watertable. (Vertical exaggeration 10x).
Right, below: hydrochemical transect.

HIRSCHENLACKE 1770 m

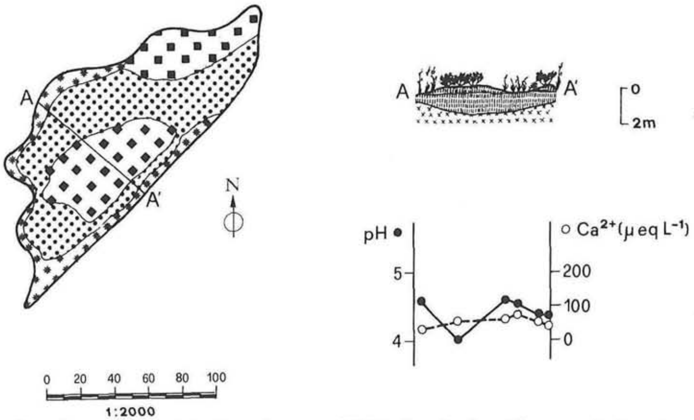

Fig. 4. Left: schematic vegetational map of Hirschenlacke. The vegetation types mapped are: Pino mugo - Sphagnetum (●), Sphagnetum magellanici typicum (■), Caricetum rostratae (✳) and Caricetum limosae subass. of *Sphagnum majus* (◆).
Right, above: hydrotopographical profile. The symbols for peat and mineral substrate are as in Fig. 1; the thin line indicates the watertable. (Vertical exaggeration 10x).
Right, below: hydrochemical transect.

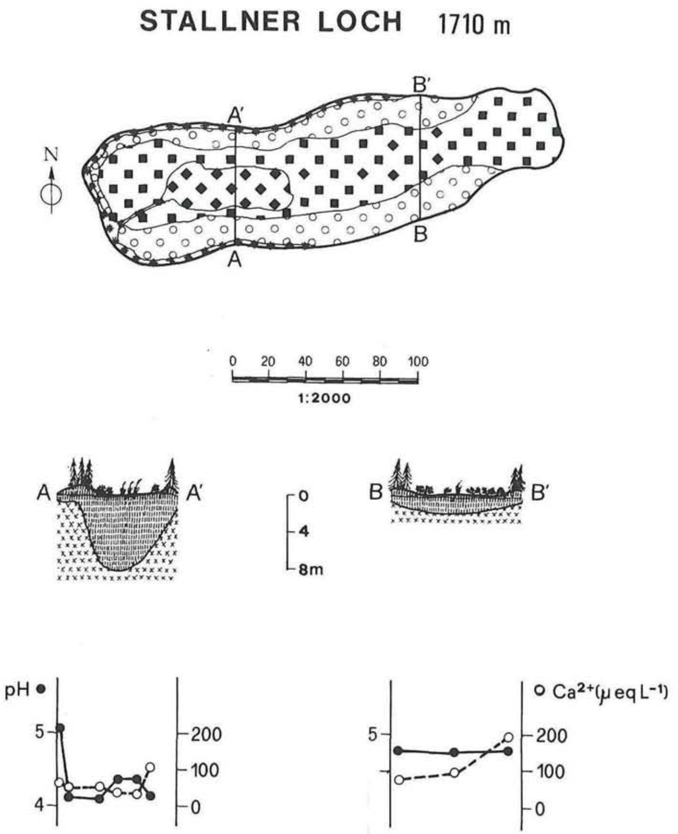

Fig. 5. Top: schematic vegetational map of Stallner Loch. The vegetation types mapped are: Bazzanio-Piceetum (○), Sphagnetum magellanici typicum (■), Caricetum rostratae (✳) and Caricetum limosae subass. of *Sphagnum majus* (◆). (Intermixed symbols indicate mosaics).
Centre: hydrotopographical profiles. The symbols for peat and mineral substrate are as in Fig. 1; the thin line indicates the water-table. (Vertical exaggeration 20x).
Bottom: hydrochemical transects.

species almost exclusive of mineral soils are found in the herbaceous layer *(Calamagrostis villosa* and *Melampyrum sylvaticum)*. Although the only character species of this association *(Bazzania trilobata)*, does not occur in our relevés (Tab. 2), the overall floristic composition fits well to that of the Bazzanio-Piceetum, and especially to the subassociation of *Vaccinium uliginosum*, widespread at the margin of peatlands in Central Europe (OBERDORFER 1992 b).

Pino mugo-Sphagnetum (PS). Corresponds to a scrub dominated by *Pinus mugo*. Even though floristically similar to the Bazzanio-Picee-

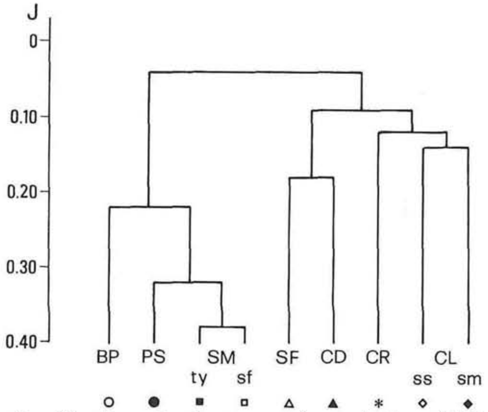

Fig. 6. Synthetic classification dendrogram of vegetation. (Abbrev. for vegetation types as in Tab. 1; J=Jaccard index).

Table 1

Syntaxonomical arrangement of the plant communities occurring in the five mires investigated, including the abbreviations used in the text as well as in Tab. 2 and Fig. 6.

- Vaccinio-Piceetea Br.-Bl. in Br.-Bl. & al. 1939
  - Piceetalia abietis Pawł. in Pawł. & al. 1928
    - Piceion abietis Pawł. in Pawł. & al. 1928
      - Vaccinio-Piceenion Oberd. 1957
        - BP – Bazzanio-Piceetum Br.-Bl. & Siss. 1939 in Br.-Bl. & al. 1939 subass. vaccinietosum uliginosi Oberd. 1992
- Oxycocco-Sphagnetea Br.-Bl. & Tx. 1943
  - Sphagnetalia magellanici (Pawł. 1928) Kästn. & Flössn. 1933
    - Sphagnion magellanici Kästn. & Flössn. 1933
      - PS – Pino mugo-Sphagnetum Kästn. & Flössn. 1933 em. Neuhäusl 1969 corr. Dierssen
      - SM – Sphagnetum magellanici (Malcuit 1929) Kästn. & Flössn. 1933
        - ty – subass. typicum
        - sf – subass. sphagnetosum fusci Dierssen in Oberd. & al. 1975
- Scheuchzerio-Caricetea nigrae (Nordh. 1936) Tx. 1937
  - Caricetalia davallianae Br.-Bl. 1949
    - Caricion davallianae Klika 1934
      - SF – Schoenetum ferruginei du Rietz 1925
      - CD – Caricetum davallianae Dutoit 1924
- Scheuchzerietalia palustris Nordh. 1936
  - Rhynchosporion albae W. Koch 1926
    - CR – Caricetum rostratae Rübel 1912 ex Osv. 1923
    - CL – Caricetum limosae Paul 1910 ex Osv. 1923 em. Dierssen 1982
      - ss – subass. of *Sphagnum subsecundum*
      - sm – subass. of *Sphagnum majus*

Table 2

Synthetic phytosociological table. The figures were obtained by multiplying the mean cover × frequency of every species in each type (abbrev. as in Tab. 1). Underlined values refer to characteristic and/or differential (d) species. Rare species not included.

	BP	PS	SM ty	SM sf	CR	CL ss	CL sm	SF	CD
N. of relevés	3	5	8	3	4	5	7	7	3
VACCINIO-PICEETEA									
Vaccinium myrtillus	57	16	+						
Picea abies	37	+	+						+
Vaccinium uliginosum	23	6		1					
Vaccinium vitis-idaea	10	8	5	9				+	+
Pleurozium schreberi	10	+							
Sphagnum girgensohnii	10				+				
Polytrichum formosum	7								
Larix decidua	1	+							
Calamagrostis villosa	1								
Melampyrum sylvaticum	1								
Homogyne alpina	+		+						
Rhododendron ferrugineum	+	2							
Sphagnum quinquefarium	+								
Pinus sylvestris		1	+	4				+	+
Pinus cembra		1	+	1					
OXYCOCCO-SPHAGNETEA									
Pinus mugo	11	46	+	+					
Melampyrum pratense paludosum (d)		±							
Sphagnum magellanicum	4	16	45	4			+		
Spagnum fuscum (d)		35	+	50					
Eriophorum vaginatum	4	28	11	3	1		+		
Polytrichum strictum	1	12	11	7					
Carex pauciflora		10	17	+	1		+	+	
Sphagnum rubellum		11	5	3					
Sphagnum russowii	9		9	9					
Vaccinium microcarpum	+	5	6	4					
Sphagnum nemoreum	37	5	+	2					
Mylia anomala	+	3		1					
Drosera rotundifolia		+	+	1			+	+	+
Cephalozia connivens		+		+					
Calypogeia sphagnicola			+						
Sphagnum compactum			+				2		
SCHEUCHZERIO-CARICETEA NIGRAE									
Scheuchzerietalia palustris									
Carex rostrata	+		7	2	50	26	14	3	18
Carex limosa			+		+	18	20		+
Sphagnum subsecundum (d)					1	6	+		1
Sphagnum majus (d)							8		
Cladopodiella fluitans			+				10		
Menyanthes trifoliata				+	1	5	3	1	1
Scheuchzeria palustris							6		
Drepanocladus fluitans					4	1			
Sphagnum lescurii						+	3		
Sphagnum papillosum					+		2		

	BP	PS	SM ty	SM sf	CR	CL ss	CL sm	SF	CD
N. of relevés	3	5	8	3	4	5	7	7	3
Potentilla palustris					1	+			
Calliergon giganteum					1				
Sphagnum platyphyllum						1			
Scorpidium scorpioides						1		+	
Rhynchospora alba							1		
Carex lasiocarpa						+		+	1
Sphagnum contortum						+		2	
Drosera x obovata							+		
Caricetalia davallianae									
Schoenus ferrugineus								9	
Carex davalliana								+	20
Campylium stellatum						2		12	14
Carex lepidocarpa								+	2
Tofieldia calyculata								1	+
Selaginella selaginoides								1	+
Pinguicula vulgaris								+	1
Bartsia alpina								1	
Eriophorum latifolium								+	+
Juncus alpino-articulatus						+		+	+
Carex hostiana								+	
Primula farinosa								+	
Parnassia palustris								+	
Carex oederi						+			+
Others									
Drepanocladus revolvens						2		16	1
Sphagnum warnstorfii						+		6	5
Drepanocladus exannulatus					3	+	3	+	4
Carex nigra		+	2	4	1	6		+	2
Eriophorum angustifolium			+	1		4	+	+	+
Carex stellulata		+	1	+	2	+	+	+	
Carex canescens					3				
Viola palustris					1	+			1
Trichophorum alpinum								1	+
Calliergon trifarium								1	
COMPANIONS									
Trichophorum caespitosum		+	3	+		+	1	44	1
Calluna vulgaris	7	26	6	23					
Sphagnum fallax	1	2	18	+	+	+			
Molinia coerulea			1	1				9	+
Potentilla erecta			1	1	+			3	4
Avenella flexuosa	7								
Utricularia minor						7			
Calypogeia azurea	1			+					
Valeriana dioica								+	

tum (Fig. 6), this type is included in the class Oxycocco-Sphagnetea owing to the lack of most species indicating mineral substrate (see above). *Pinus mugo* is considered as character species of this association, and *Melampyrum pratense* subsp. *paludosum* as differential. The species in the field layer as well as those in the bottom layer are largely in common with open hummocks (Sphagnetum magellanici; Tab. 2).

Sphagnetum magellanici (SM). Corresponds to *Sphagnum* carpets and hummocks free from trees and shrubs and belongs, like the Pino mugo-Sphagnetum, to the class Oxycocco-Sphagnetea. The field layer has a number of species typical of peaty substrates (*Carex pauciflora, Eriophorum vaginatum* and *Vaccinium microcarpum* being the most frequent of them), besides some *Ericaceae* also occurring in woodlands and heathlands *(Vaccinium myrtillus, V. uliginosum, V. vitis-idaea* and *Calluna vulgaris)*. Based on the floristic composition of the bottom layer, two subassociations can be distinguished in the Sphagnetum magellanici, clearly separated by cluster analysis (Fig. 6). *Sphagnum magellanicum,* although occurring in both of them, and thus being considered as character species at the association level (Tab. 2), has a clear preference for the Sphagnetum magellanici typicum (SMty). Also *Sphagnum russowii* and *S. fallax* are common in this subassociation, which corresponds to flat carpets and low hummocks. By contrast, high hummocks are dominated by *Sphagnum fuscum* which differentiates the subassociation sphagnetosum fusci (SMsf).

Both the Schoenetum ferruginei (SF) and the Caricetum davallianae (CD) are rich in fen species, most of which are regarded as characteristic of the order Caricetalia davallianae, such as *Campylium stellatum, Eriophorum latifolium, Tofieldia calyculata, Carex lepidocarpa, Selaginella selaginoides, Pinguicula vulgaris* and others (see Tab. 2). The Schoenetum ferruginei has *Schoenus ferrugineus* as character species, but *Trichophorum caespitosum* usually achieves dominance. The Caricetum davallianae has *Carex davalliana* as character species, mostly with high cover.

The Caricetum rostratae (CR) is characterized by *Carex rostrata* and belongs to the Scheuchzerietalia palustris. The floristic composition of this association is somewhat heterogeneous, and at least part of the relevés probably indicate some transition to the Caricetum nigrae, as suggested by the presence of *Carex canescens* which is regarded as a character species of the latter association (OBERDORFER 1992a).

Also the Caricetum limosae (CL), having *Carex limosa* as character species, belongs to the order Scheuchzerietalia palustris and has two subassociations, viz. that of *Sphagnum subsecundum* (CLss) and that of *Sphagnum majus* (CLsm). They are floristically well differentiated from each other for several species, besides the two main differential, showing a more or less clear preference for either the one or the other subassociation (Tab. 2): *Scorpidium scorpioides* and *Utricularia minor* are exclusive of the Caricetum limosae subass. of *Sphagnum subsecundum;* while *Scheuchzeria palustris, Cladopodiella fluitans, Sphagnum papillosum* and *Rhynchospora alba* are centred in the Caricetum limosae subass. of *Sphagnum majus.*

5. Relationships between Environment and Vegetation

The vegetation types obtained by floristic criteria are well discriminated also in terms of environmental variables, as shown by the high canonical correlations of the first two discriminant functions (I function = 0.96; II function = 0.83) and the relatively low percentage of misclassifications (23%).

The canonical coefficients of the discriminant functions, as well as the correlations between those functions and the environmental variables (Tab. 3), point to water table as the environmental factor inducing the largest amount of floristic variation in the vegetation examined, followed by pH. The latter also accounts for similar trends of electrical conductivity and, to a lesser extent, of calcium concentration. By contrast, the concentrations of the other cations are not responsible for any significant change in vegetation. Accordingly, the ordination of plots based on the first two sets of discriminant scores can be regarded as a biplot ordering along gradients of water availability and nutrient status (Fig. 7).

Table 3

Canonical coefficients of the first two discriminant functions and significant correlations with the environmental variables ($P < 0.05$).

	Can. coefficients		Correlations	
	I	II	I	II
Water-table depth	1.08		0.71	
pH		1.03		0.91
El. conductivity				0.78
Na^+	–		–	
K^+	–		–	
Ca^{2+}	–			0.55
Mg^{2+}	–		–	

The first discriminant axis clearly separates two groups: 1) the one, with negative values, including all plots of forested stands (BP), scrubs (PS), as well as open *Sphagnum* carpets and hummocks (SM); 2) the other, with positive values, including all plots of fens (SF and CD), pools and mud-bottoms (CR and CL).

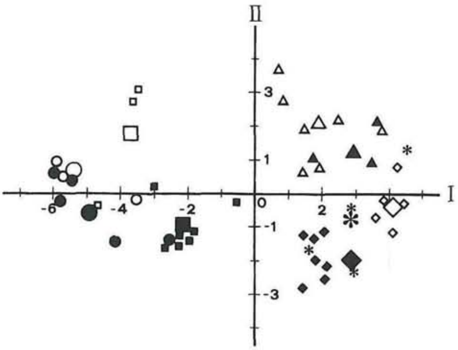

Fig. 7. Ordination of relevés based on the first two sets of discriminant scores. The first axis corresponds to a moisture gradient; the second axis to a nutrient gradient (see text).
(Symbols for vegetation types as in Fig. 6; large symbols indicate group centroids).

Water table is below surface in all of the vegetation types included in the first group, with mean depths decreasing from the BP to the SMty (Tab. 4). The vegetation types included in the second group are less discrete with respect to water-table depth (Fig. 7). At the time of sampling, the water table was below ground in fens and a few cm above ground in pools and mud-bottoms (Tab. 4).

Two parallel gradients of nutrient availability can be detected, the one within the vegetation of raised microsites and the other within that of fens and pools (Fig. 7). Both the SMty and the PS are restricted to acidic habitats having a low electrical conductivity. The mean Ca^{2+} concentration in

Table 4
Mean values (± standard error) of the environmental variables in the vegetation types (abbrev. as in Tab. 1).

	Water table (cm)	pH	El. cond. ($\mu S\ cm^{-1}$)	Na^+ ($\mu eq\ L^{-1}$)	K^+ ($\mu eq\ L^{-1}$)	Ca^{2+} ($\mu eq\ L^{-1}$)	Mg^{2+} ($\mu eq\ L^{-1}$)
BP	-46.0 ± 11.5	4.44 ± 0.14	21.0 ± 7.0	62.7 ± 36.1	17.3 ± 2.5	122 ± 68	40.3 ± 18.5
PS	-36.0 ± 11.2	4.02 ± 0.21	5.2 ± 4.0	34.2 ± 10.8	21.6 ± 11.1	76 ± 28	35.8 ± 15.8
SMty	-23.2 ± 5.8	4.31 ± 0.38	14.0 ± 10.1	50.6 ± 22.0	15.1 ± 10.6	147 ± 156	36.7 ± 9.1
SMsf	-38.0 ± 5.0	5.07 ± 1.00	28.0 ± 21.7	84.0 ± 10.4	30.0 ± 8.0	190 ± 122	29.0 ± 11.5
SF	-13.7 ± 6.3	6.28 ± 0.47	56.6 ± 17.8	72.1 ± 12.5	8.1 ± 8.0	633 ± 363	42.6 ± 9.3
CD	-5.3 ± 5.5	6.23 ± 0.40	51.0 ± 15.0	85.0 ± 7.8	11.0 ± 3.5	505 ± 172	53.7 ± 12.7
CR	+3.5 ± 4.7	5.11 ± 0.90	28.2 ± 28.9	65.5 ± 45.4	17.7 ± 5.3	206 ± 321	33.5 ± 10.6
CLss	+6.2 ± 6.6	5.59 ± 0.48	35.0 ± 18.2	66.4 ± 23.1	11.6 ± 8.6	331 ± 232	40.2 ± 9.4
CLsm	+1.6 ± 5.4	4.47 ± 0.28	11.1 ± 4.2	43.0 ± 16.3	13.9 ± 6.8	80 ± 54	32.4 ± 11.0

the open carpets is almost double that in scrubs (Tab. 4). The forested sites of the BP have a slightly less acidic water with somewhat higher conductivity, and calcium concentrations comparable to those in the SMty. The hummocks of the SMsf are located at the rich end of the gradient, for having less acidic water, with higher conductivity as well as greater calcium concentration. Also K^+ is distinctly enriched at those sites (Tab. 4).

The CLsm is typical of pools and mud-bottoms with acidic water poor in nutrients, as shown by the low mean electrical conductivity and Ca^{2+} concentration (Tab. 4), whereas the CLss occupies comparable habitats, but distinctly richer in nutrients. The CR is intermediate between them (Fig. 7). The fens are placed at the rich end of this second gradient (Fig. 7). Both the SF and the CD have subneutral water rich in calcium and with a moderately high electrical conductivity. All values are somewhat greater in the former association (Tab. 4).

6. Mire-Site Typology

There are major differences among the peatlands investigated, when examining both the distributional patterns of vegetation types within each site and the hydrochemical characteristics of mire water (Tab. 5).

Groß Moos (Fig. 1) and Loden Moos (Fig. 2) have a number of common features: mire water is only weakly acidic, moderately rich in nutrients and has relatively high Ca^{2+} concentrations. Both sites have a large portion of their surface covered by the Schoenetum ferruginei and are sur-

Table 5

Mean values (± standard error) of the main environmental variables at each site and presence/absence of plant communities (+++ = dominant; ++ = abundant; + = rare; (+) = occasional).

	Groß Moos	Loden Moos	Klein Moos	Hirschen-lacke	Stallner Loch
Water-table depth (cm)	-15±13	-13±14	-10±19	-17±24	-26±23
pH	5.86±0.53	5.98±0.97	4.48±0.71	4.32±0.24	4.58±0.28
El. conductivity ($\mu S\ cm^{-1}$)	48±19	48±22	14±10	9±4	16±7
Ca^{2+} ($\mu eq\ L^{-1}$)	523±366	524±226	135±66	55±14	82±50
Bazzanio-Piceetum					++
Pino mugo-Sphagnetum		+	++	++	(+)
Sphagnetum magellanici typicum	+		++	++	++
Sphagnetum mag. sph. fusci		+	+		
Schoenetum ferruginei	+++	+++			
Caricetum davallianae	+	++			
Caricetum rostratae		+	(+)	++	+
Caricetum limosae sub. ss	++	+	++		
Caricetum limosae sub. sm			+	+	++

rounded by a narrow belt of Caricetum davallianae. The deepest hollows are colonized by the Caricetum limosae subassociation of *Sphagnum subsecundum* (Tab. 5). *Sphagnum*-dominated vegetation (Sphagnetum magellanici) is confined to a reduced part of these sites, giving rise either to scattered hummocks or to larger carpets. A *Pinus mugo* scrub (Pino mugo-Sphagnetum) occurs only at Loden Moos.

The hydrochemistry of mire water does not vary appreciably along the transect examined at Gross Moos (Fig. 1), for the pH staying always above 5 and Ca^{2+} concentrations above 300 μeq L^{-1}, even in *Sphagnum* carpets. At Loden Moos, by contrast, the pH falls below 4 and the concentration of calcium does not exceed 100 μeq L^{-1} in the Pino mugo-Sphagnetum (Fig. 2).

Mire water is distinctly acidic and poor in nutrients and calcium at Hirschenlacke (Fig. 4) and Stallner Loch (Fig. 5) as well. Large areas at both peatlands are covered by *Sphagnum* hummocks and carpets, which either support a *Pinus mugo* cover (Pino mugo-Sphagnetum, Hirschenlacke) or are free from shrubs (Sphagnetum magellanici typicum, Stallner Loch), and by extensive hollows colonized by the Caricetum limosae subassociation of *Sphagnum majus*. In addition, Stallner Loch has a marginal strip of spruce forest (Bazzanio-Piceetum), developing over a shallow peat layer. The outermost belt forms at both sites a sort of narrow lagg lying on decomposed peat and having the Caricetum rostratae as distinctive vegetation type. Water chemistry in this lagg is quite similar to that in the inner sector, thus indicating poor contact with the mineral substrate. In only one case does pH rise up to 5 (Fig. 5).

Klein Moos (Fig. 3) has an acidic calcium-poor water over most of its area which is covered by a vegetational pattern quite similar to that at Hirschenlacke. This includes a scrub of *Pinus mugo* and a mosaic of *Sphagnum hummocks* (SMty and SMsf) and hollows (CLsm). The main distinctive feature at Klein Moos is the wet minerotrophic lagg developed at the downslope edge, colonized by the CLss. Here water-pH is ca. 6 and calcium concentration ca. 250 μeq L^{-1} (Fig. 3).

When classifying the whole set of data, related to both vegetation and hydrochemistry (see Tab. 5), the sites investigated are grouped into two clusters (Fig. 8) which can be regarded as the two principal mire complexes occurring in the study area.

The first group, including both Großes Moos and Loden Moos, corresponds to fen complexes and the second, including the remainder of the sites, to bog complexes. Two subgroups can be distinguished in the latter, one of which comprises the peatlands (Hirschenlacke and Stallner Loch) entirely covered by a vegetation resembling that of bogs and poor fens, and the other the peatland (Klein Moos) bordered by a downslope lagg sheltering a vegetation typic of moderate-rich fens.

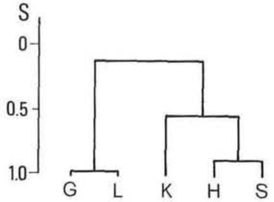

Fig. 8. Classification dendrogram of mire sites based on the data in Tab. 5. – The values of the physico-chemical variables were normalized as follows: $(x - x_{min}) / (x_{max} - x_{min})$ S = similarity ratio; G = Groß Moos, L = Loden Moos, K = Klein Moos; H = Hirschenlacke, S = Stallner Loch.

7. Discussion

A number of ecological gradients play a role in determining the vegetational patterns of boreal peatlands. Three of them have been recognized since long ago as of paramount importance for inducing variations in mire vegetation: 1) the mire expanse-mire margin gradient; 2) the poor-rich gradient; and 3) the gradient in depth to water table (SJÖRS 1948; DU RIETZ 1949; MALMER 1986). Furthermore, the peat-productivity gradient (MALMER 1962; ØKLAND 1989a) as well as regional floristic gradients (DAMMAN 1979; SJÖRS 1983; ØKLAND 1990; GIGNAC & al. 1991) can interact to a different extent with the former ones. As a consequence, several systems have been proposed for classifying mire vegetation, giving a prominent emphasis either to a single gradient or to a combination of more of them. They need not be discussed in detail for the purposes of this paper.

A classification of vegetation based on the floristic composition of plant communities, like that pursued by the Zürich-Montpellier school, should account for both ecological and phytogeographical aspects, the latter being in turn influenced by phytohistorical events. Most Scandinavian ecologists expressed reluctance about the possibility that clear-cut divisions within mire vegetation can be produced by the BRAUN-BLANQUET approach (MALMER 1985; ØKLAND 1989b). DIERSSEN & DIERSSEN 1985 pointed out that the vegetation units within the hierarchic syntaxonomical system should be comparable with respect to a single ecological gradient when considered at the same hierarchical level.

Our classification of mire vegetation obtained by cluster analysis, finds a good correspondence in the BRAUN-BLANQUET system, even though the syntaxonomical hierarchy cannot be exactly reproduced in a classification dendrogram. When operating at a low hierarchical level, as could be done in this study, the corresponding vegetational units prove to be discrete in terms of two major ecological factors, viz. distance to water table and nutrient status. The suggestion of DIERSSEN & DIERSSEN 1985 (see above) does not fully hold, however, since while within the class Oxycocco-Sphagnetea the subassociations account for differences along the gradient in depth to water table and the variants for differences along the poor-rich gradient, the reverse is true of the Scheuchzerio-Caricetea nigrae (DIERSSEN 1978). In fact, while the Sphagnetum magellanici typicum is clearly separated from the Sphagnetum magellanici sphagnetosum fusci with respect to watertable depth, and to a lesser extent also to pH, the subassociation of *Sphagnum subsecundum* and that of *S. majus* within the Caricetum limosae are discrete only in terms of water acidity and nutrient richness (Tab. 4; Fig. 7).

Although the peatlands examined do not differ greatly from each other on the basis of gross morphology, there are profound inter-site differences as far as both vegetation patterns and hydrochemistry are concerned. Especially the latter shows that most of these mires are complexes of hydrologically different areas, fed either by rain or by mineral water or by both at varying proportions. A precise definition of the "mineral soil water limit" (THUNMARK 1940) would require a periodic topographic survey of the water table which is still in progress in the study area. We cannot clearly state, at present, which of the mires examined – or which parts of them – are truly ombrotrophic. Nor could we expect a fruitful result when trying to infer such a limit from the distributional pattern of plants. The concept of "fen plant limit" (Mineralbodenwasserzeigergrenze; DU RIETZ 1954) is still under debate (MÜLLER 1976) since several species behaving as fen indicators in some regions are common elements of bog vegetations in others, as happens e.g. for *Eriophorum angustifolium* and *Schoenus nigricans* under oceanic climate (ALETSEE 1967). The very possibility of individuating a discontinuity in the nutritional gradient, based on a threshold value of a given hydrochemical variable revealed rather unsuccessful due to regional differences in precipitation chemistry. Even Ca^{2+} concentrations, which seemed to stay always below 50 $\mu eq\ L^{-1}$ in bog waters (WITTING 1947, 1948, 1949), have distinctly greater values in bogs from oceanic regions (SPARLING 1967) as well as from carbonate mountains (MARTINČIČ & PISKERNIK 1985; GERDOL 1990). Recent work showed a rather broad range of overlap between bogs and poor fens as far as mire-water chemistry is concerned. These two groups of peatlands proved to be much more similar to each other than the latter to rich fens (MALMER & al. 1992).

At least two of the mires investigated have most of their surface poorly influenced, if ever, by telluric water (Hirschenlacke and Stallner Loch). Both have, in addition, a narrow marginal lagg covered by a poor-fen vegetation. A similar condition was found at Klein Moos, but the downslope lagg has a direct contact with the mineral substrate, clearly mirrored in vegetation.

Both the vegetational patterns and the hydrochemical features agree in indicating the mineral water-table as the main source of nutrients for fen complexes. Both of the fen associations (viz. the Schoenetum ferruginei and the Caricetum davallianae) are restricted to minerotrophic sites. Among the hollow phytocoena the Caricetum rostratae is associated to habitats relatively poor in nutrients, whereas the Caricetum limosae subassociation of *Sphagnum subsecundum* characterizes nutrient-rich sites. By contrast, the Caricetum limosae subassociation of *Sphagnum majus* is restricted to extremely nutrient-poor habitats at sites having only occasional contacts, if any, with telluric water.

A *Sphagnum*-dominated vegetation can develop in a broad range of habitats. Especially the open carpets and hummocks (Sphagnetum magellanici) are found both at sites prevalently fed by rainwater (Klein Moos, Hirschenlacke and Stallner Loch) and in the clearly minerotrophic areas of fen complexes (Groß Moos and Loden Moos). Mire chemistry exactly reflects that pattern: pH is just above 4 and Ca^{2+} concentration always below 100 μeq L^{-1} in the former (Fig. 3–5), whereas both are much higher in the latter (Fig. 1–2). Mire water under the *Sphagnum* carpets and hummocks developing in fen complexes does not differ much hydrochemically from that in the surrounding fens. Only pH is somewhat lower, probably as a result of the well-known acidifying action of the Sphagna theirselves. By contrast, the Pino mugo-Sphagnetum always has an acidic calcium-poor water thus indicating ombrotrophy or at least a very poor addition of rainwater. This can be easily explained when dealing with the *Pinus mugo* scrubs settled on bog complexes (Fig. 3–5), but is rather astonishing when considering fen complexes (Fig. 2). Apparently, the areas covered by the Pino mugo-Sphagnetum form a hydrologically well-distinct sector within fen complexes behaving like a sort of miniature bog (BELLAMY & RIELEY 1967).

The marginal spruce forest (Bazzanio-Piceetum) is restricted to relatively xeric habitats in which there is only a modest accumulation of peat. Although certainly influenced by the mineral substrate, water is quite acidic and relatively poor in Ca^{2+}, probably because it has poor contact with bedrocks rich in calcium.

8. Conclusion

The main conclusion emerging from the present study is that the topographical differences among the mires investigated are little pronounced, even though the choice of sites was done so as to cover a broad range of vegetational variation extending from brown-sedge fens to *Sphagnum* hummocks and hollows. It seems, therefore, that a mosaic pattern of bog-like and fen-like vegetation be the far commonest situation in the study area. This widely justifies the use of the collective term "transitional mires" (Zwischenmoore, Übergangsmoore; PAUL & LUTZ 1941; ALETSEE 1967), including a large number of peatlands in the Alps.

Although a clear-cut division between fens and bogs can be only exceptionally established in this region, two main groups of peatlands can be nonetheless distinguished, viz. that of poor mires (bog complexes) and that of rich mires (fen complexes). Complexes of vegetation types are more instructive than both single plant communities and single plant species (fen indicators) for discriminating poor mires from rich mires in the absence of data on hydrochemistry and hydrotopography.

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