

# Ecological relationships between vegetation and soil-related variables along the mire margin–mire expanse gradient in the eastern Julian Alps, Slovenia

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In the NW part of Slovenia, at the southern border of the *Sphagnum*-mire area in Europe, the plant species diversity and vegetation structure of mires (sedge fen, spruce mire and dwarf-pine bog) and spruce forests were investigated using ordination techniques (detrended correspondence analysis, DCA). The mires studied occur at around 1200 metres above sea level. The correlation between plant distribution patterns and ecology, with particular reference to soil variables, was examined. Based on DCA ordination, the sedge fens were clearly distinguished from the dwarf-pine bogs and the spruce mires, as well as from the spruce forests on the mineral soils. A significant correlation between the first DCA axis and the plant species diversity was found. The Shannon diversity index and the species richness were highest in the sedge fen and on the mire-forest border zone. The first DCA axis was interpreted as a reflection of the gradients of the soil pH, the amount of calcium and the base saturation level. The first axis clearly differentiated the *Sphagnum* species (e.g. *S. girgensohnii*, *S. magellanicum*, *S. russowii*, *S. flexuosum*, *S. capillifolium*) from the moss species belonging mostly to Amblystegiaceae (e.g. *Drepanocladus cossonii*, *Campylium stellatum*, *Calliergon cordifolium*, *Cratoneuron decipiens*). The second DCA axis was interpreted in terms of the soil water content, total carbon content, C/N ratio and peat depth. It evidently differentiated the spruce forest on the mineral soil from the various mire ecosystems.

Key words: bryophytes, DCA ordination, diversity, mire, ecology, soil conditions, *Sphagnum*

## Introduction

Several recent reviews (e.g. Wheeler & Proctor 2000, Økland *et al.* 2001) focus attention on the

gradient relationships in north European mires. The vegetation and ecological gradients between different types of mires are important as criteria for classifying them. In the broadest sense, the



Fig. 1. Position of the Pokljuka plateau.

term bog should refer to acidic, low alkalinity peatlands, typically dominated by *Sphagna* and various ericaceous shrubs. Similarly, the term fen should broadly refer to somewhat less acidic, more alkaline peatlands, dominated by graminoids, brown mosses, taller shrubs, and coniferous and/or deciduous trees (Bridgham *et al.* 1996).

Bogs and fens in northern mires are usually easily differentiated in terms of water and peat chemistry (Bridgham & Richardson 1993, Wheeler & Proctor 2000). Most ecological and floristic variation within NW European mire vegetation is accounted for by three ecological gradients: the acid, base-poor vs. neutral, base- and bicarbonate-rich gradient; the gradient in fertility related to availability of limiting nutrient elements N and P; and the water level gradient (Wheeler & Proctor 2000).

Based on gradient studies on many Scandinavian (Swedish and Norwegian) and Finnish mires, Økland *et al.* (2001) reported considerable shifts in species compositions from the (mostly open) mire expanse to the mire margin (mostly with trees). This 'direction of variation in vegetation' is caused by a specific set of environmental factors.

The vegetation gradient can coincide with some important ecological gradients. A close link between pH/alkalinity/mineral cation concentrations and plant communities has been observed in some northern mires (e.g. Wassen *et al.* 1989, Vitt & Chee 1990, Gorham & Janssens 1992). Often,  $\text{Ca}^{2+}$  concentrations and the pH of surface water are used to define the boundaries

between different types of peatland (Malmer 1986).

Based on the water chemistry of surface waters, mires were clearly divided in a bipartite way by Du Rietz (1954). Gorham and Janssens (1992) examined bryophyte assemblages and surface-water pH across North America. Based on a distinct bimodal distribution of pH that coincided with Sphagnaceae at low pH and Amblystegiaceae at higher pH, they also suggested a bipartite separation into fen and bog. An intermediate transitional community distinction seemed possible, but the boundaries are only regionally applicable. The usefulness of elaborate phytosociological associations is usually limited to the region for which they were originally developed (Braun-Blanquet 1964, Gore 1983).

Due to different ecological influences and unique conditions at the southern border of the *Sphagnum*-mire distribution in Europe, a specific relation between mire vegetation and ecology could be expected. In Italy, at the southern border of the *Sphagnum*-mire distribution, some important studies of mire ecology and vegetation have been made (Bragazza 1994, 1996, 1997, Gerdol *et al.* 1994, Alber *et al.* 1996, Bragazza *et al.* 1998). Some well-preserved bogs also exist in Slovenia (Martinčič & Piskernik 1985). On the Pokljuka plateau, in NW Slovenia, there are also some smaller mires where studies of vegetation and ecology have been undertaken recently (Kutnar 2000a, 2000b, Kutnar & Martinčič 2001). Due to the different ecological influences, which are related to their transitional geographic position, these mires are very mosaic-like ecosystems that are characterised by very specific ecological conditions and vegetation.

In terms of diversity, the mire-site types situated on the border zones of different ecological influences are especially interesting (Korpela & Reinikainen 1996a, 1996b). Thus, the aim of this study was to determine the main ecological factors that control plant diversity and distribution along the mire margin–mire expanse gradient at the southern border of the *Sphagnum*-mire distribution. Because of their location at the edge of their natural range these peat bogs are especially endangered, which gives them added significance.

## Material and methods

### Study area

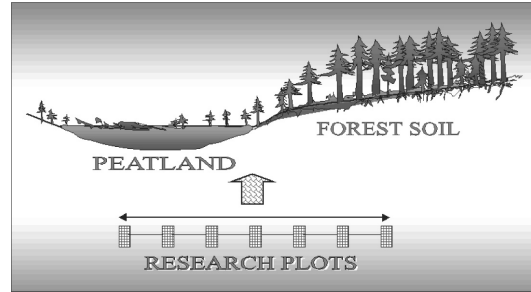
This study was performed on mires located on the Pokljuka high plateau (46°20'N, 13°59'E) on the eastern side of the Julian Alps in Slovenia (Fig. 1). The Pokljuka plateau ranges between 1000 m and 1500 m above sea level. Annual precipitation is between 1900 and 2700 mm, and average annual temperature is 1.4 to 3.2 °C. Snow cover lasts for about 170 days. Temperature inversions are frequent because of the dish-shaped relief. The parent material consists mainly of mixed glacial moraines (non-calcareous, limestone, dolomite). On this parent material different soil types are found: cambisols, podzols, gleysols, and histosols (Urbančič & Kutnar 1997, 1998, Kutnar 2000a).

Spruce forest almost completely dominates the Pokljuka plateau as a result of the severe alpine climate, the relief, and past forest management. Until the beginning of intensive iron production at the end of the 17th century this region was covered mainly by beech forest (*Fagus sylvatica*; Budnar-Tregubov 1958, Šercelj 1962, Culiberg *et al.* 1981), which was further reduced in the 19th century. As a result of its high usability, and for economic reasons, spruce was favored by the forest management. Anthropogenic influences in the past, such as charcoal burning, cutting wood and cattle grazing, changed the composition of the tree species from the original mixed forests of beech, silver fir (*Abies alba*) and Norway spruce (*Picea abies*) to pure spruce stands with only 1% of broad-leaved species and 1% of silver fir.

### Vegetation

On the Pokljuka plateau, different vegetation types of the predominant spruce forest were described by Zupančič (1999). The vegetation of spruce mires was investigated by Zupančič (1982), the dwarf-pine mires by Martinčič and Piskernik (1978, 1985), and the fen communities partly by Martinčič (1995).

Based on previous studies (Kutnar 2000b, Kutnar & Martinčič 2001), six main vegetation



**Fig. 2.** Set of research plots at the mire-forest transition zone. The first plots of sets are placed in the centre of mires, and the last plots are out of them (out of direct influences of the ground water). Each set includes plots on the peat-soils, and at least one plot (or more) on forest mineral-soils. The distance between plots in each set (mire) is constant, but according to dimension of mire, it varies from set to set. The plot-distance in sets (mires) ranges between 19 and 31 metres.

types were found in smaller mires and in the vicinity:

- A: ombro-oligotrophic dwarf-pine mire (*Pino mugi*–*Sphagnetum* associations);
- B: ombro-oligotrophic spruce mires (*Sphagno girgensohnii*–*Piceetum* var. *geogr. Carex brizoides*);
- C: oligotrophic spruce forests (*Rhytidiadelpho lorei*–*Piceetum typicum* and *sphagnetosum*);
- D: meso-oligotrophic spruce forests: transition to sedge fens (*Rhytidiadelpho lorei*–*Piceetum cardaminetosum*);
- E: meso-eutrophic sedge fens (*Sphagno-Caricetum rostratae* and plant communities dominated by *Carex davalliana* or by *Trichophorum alpinum*);
- F: mesotrophic transitions of sedge fens to spruce forests.

### Field sampling

The study was carried out on six small mires (less than 0.05 square kilometres) near the bogs of Šijec and Veliko Blejsko barje (Martinčič & Piskernik 1985) on the Pokljuka plateau. The 42 (six series of seven, 2 × 4 m) homogenous plots were placed systematically to determine plant distribution and diversity along the mire margin–mire expanse gradient (Fig. 2).

The vegetation of the research plots was surveyed according to the standard Central European method (Braun-Blanquet 1964). Cover estimates were made for the tree, shrub, herb and moss layer. The sources of the nomenclature were: Martinčič *et al.* (1999) for vascular plants; Corley *et al.* (1981) and Corley and Crundwell (1991) for mosses; Grolle and Long (2000) for liverworts. The source for the characterisation of the plant species according to the phytosociological units was Oberdorfer (1983, 1992).

From all 168 corners of the 42 research plots we took soil samples at depths of 0–10 cm. The living moss layers were not included. From these samples we produced 42 homogeneous composite soil samples.

### Analysis of soil samples

The soil samples were analysed at the laboratory of the Slovenian Forestry Institute in order to obtain the following characteristics: pH (H<sub>2</sub>O) using a pH-electrode measurement, at a ratio soil *vs.* deionized water = 10 g *vs.* 25 ml (ISO 1992a); total nitrogen content using modified Kjeldahl method (ISO 1993; *see also* Page 1982); total carbon content, using dry combustion (ISO 1994; *see also* Nelson & Sommers 1982); and exchangeable cations (Ca, Mg, K, Al, Fe, Mn, H). The cations were analysed with atomic absorption spectrophotometry using a barium chloride solution (ISO 1992b; *see also* Gillman 1979). On the basis of these measurements we also calculated the C/N ratio and the base saturation level:

$$BS = \frac{Ca + Mg + K}{\text{Sum of all exchangeable cations}} \times 100 (\%).$$

In late spring (20 May) and in mid-summer (11 August) we also took soil samples, at a depth of 5 cm, from the edges of the plots in order to measure the soil's water content (ISO 1992c; *see also* Reynolds 1970). The amount of water was calculated from the weight difference between the (wet) soil sample ( $S_w$ ) and the same soil sample dried at 105 °C ( $S_d$ ):

$$\text{WaterC} = \frac{S_w - S_d}{S_d} \times 100 (\%).$$

### Data analysis

Based on phytosociological relevés of sample plots, the Shannon diversity index (Shannon & Weaver 1949) and the species richness were calculated. For the data analyses, cover degrees were used according to van der Maarel's modification (1979). The main compositional gradients in the vegetation were extracted by detrended correspondence analysis (DCA) (Hill & Gauch 1980). The DCA was carried out with the PC-ORD program (McCune & Mefford 1999).

Spearman correlation coefficients between the DCA axes (plot scores) and the cover of vertical (tree, shrub, herb and moss) layers were calculated, and between the DCA axes and the plant species diversity (Shannon diversity index and species richness), too. We found a correlation between the DCA axes and the soil variables, and analysed the correlations between the soil variables. Analysis of variance (ANOVA) was used to test differences of soil parameters between vegetation types (Kutnar 2000b, Kutnar & Martinčič 2001).

### Results

We found a total of 170 species on the 42 research plots. In the DCA ordination (Fig. 3), the sample plots are represented items of vegetation groups (Kutnar 2000b, Kutnar & Martinčič 2001). In the ordination of 42 plots and 97 species (only the species that were represented in at least three plots, *see* Appendix) the eigenvalue of the first axis was 0.65, of the second axis 0.42 and of the third axis 0.16.

The vegetation groups — dwarf-pine mires, spruce mires, spruce forests, sedge fens and their transitions — are well separated in the plot ordination space (Fig. 3). Meso-eutrophic sedge fens and their transitions to spruce forests have high scores along the first axis. The variation along the first DCA axis is lower in plots with high DCA1 scores. The scores of the plots from other groups are lower along this axis. However, the second DCA axis clearly differentiates between these vegetation groups. Most of the spruce-forest plots have high scores while the dwarf-pine plots obtain low scores along the second

DCA axis. The spruce-mire plots occur around the mid-point of DCA2.

In the species ordination (Fig. 4) species typical of sedge fens (e.g. *Carex rostrata*, *C. davalliana*, *C. flava* agg., *Trichophorum alpinum*, *Pinguicula vulgaris*, *Eriophorum latifolium*, *Menyanthes trifoliata*, *Cardamine pratensis*, *Euphrasia rostkoviana*) obtained high DCA1 scores. These are mostly characteristic species of the *Scheuchzerio–Caricetea fuscae* class and the *Molinio–Arrenatheretea* class (Oberdorfer 1983, 1992). Some bryophyte species characteristic of sedge fens and transitions (e.g. *Drepanocladus cossonii*, *Campylium stellatum*, *Bryum pseudotriquetrum*, *Aulacomnium palustre*, *Homalothecium nitens*) also obtained high DCA1 scores. At high DCA1 values of species ordination numerous of species are represented. This ordination shows the highest species concentration to be in the area of sedge fens and their transition to spruce forests (see also Appendix).

The dwarf-pine-mire, spruce-mire and spruce-forest species have low scores along the DCA1 axis. The typical species of ombro-oligotrophic dwarf-pine mires (e.g. *Pinus mugo*, *Eriophorum vaginatum*, *Oxycoccus palustris*, *Carex pauciflora*, *Polytrichum strictum*) are at low values of the DCA2 axis. In addition to species that are mostly characteristic of the *Oxycocco–Sphagnetea* class there are also many *Sphagnum* species (e.g. *S. magellanicum*, *S. russowii*, *S. flexuosum*, *S. capillifolium*, *S. fallax*). These are often found on the plots of spruce mire (Appendix). The typical species of spruce mire (e.g. *Carex brizoides*, *Sphagnum girgensohnii*, *Polytrichum commune*) are close to the centre of the ordination space. Widely distributed species (e.g. *Picea abies*, *Vaccinium myrtillus*, *V. vitis-idaea*, *Maianthemum bifolium*, *Pleurozium schreberi*, *Hylocomium splendens*) are also centrally placed in the ordination space.

The characteristic species of spruce forests (e.g. *Lycopodium annotinum*, *Luzula luzuloides*, *Oxalis acetosella*, *Polytrichum formosum*, *Rhytidadelphus loreus*) and many other plants of the *Vaccinio–Piceetea* class obtain high scores along the DCA2 axis.

The first DCA axis correlates closely with the herb-layer cover (Table 1) while the second DCA

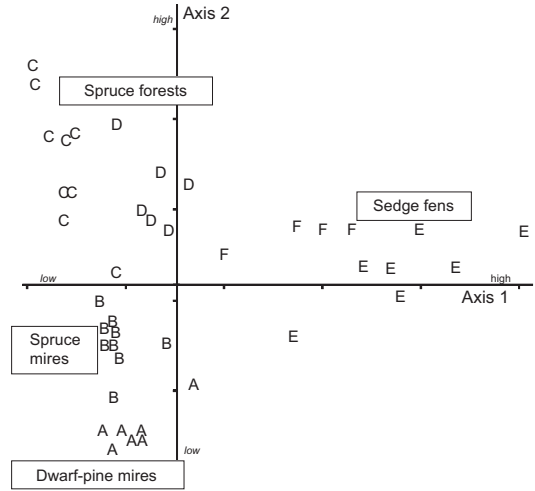
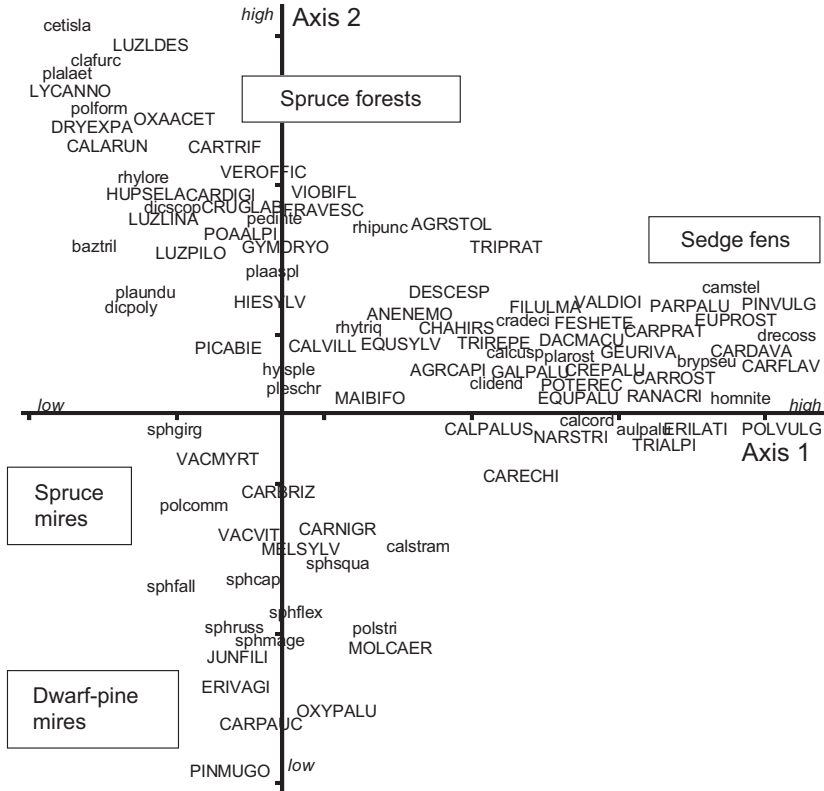


Fig. 3. DCA ordination of the 42 sample plots for axes 1 and 2. The letters A to F refer to six main vegetation types (as listed in chapter Vegetation on p. 179).

axis correlates with the tree-layer cover. Significant negative correlation was found between the second axis and the moss-layer cover.

The Shannon diversity index and the species richness were found to increase towards the sedge-fen plot (group E and group F). The first DCA axis correlates closely with the Shannon diversity index and the species richness (Table 1). We found the highest number of plant species at the transition of the sedge fens' vegetation to the spruce forest (34.0 species per plot), and on the sedge-fen plots (33.4 species per plot). However, we found the lowest species diversity (15.7 species per plot) on the plots covered by the dwarf-pine mire community. The average Shannon index of diversity was the highest for the sedge-fen plots ( $H' = 2.42$ ) and the lowest for plots of spruce forest of group C ( $H' = 1.52$ ). This is a consequence of the low number of plant species and the predominance of spruce.

The first DCA axis correlates closely with some soil variables (exchangeable Ca and Mn, pH and base saturation; Table 1). The peat-soil of sedge fens have a lot of base cations, especially calcium (Table 2). This element is a component of limestone, a commonly occurring mineral soil material in the vicinity of the research plots. The soil of the plots with lower scores along the



**Fig. 4.** DCA ordination of the 97 plant species for axes 1 and 2. Plant species (vascular plants in capital letters): *Agrostis capillaris* = AGRCAPI; *Agrostis stolonifera* = AGRSTOL; *Anemone nemorosa* = ANENEMO; *Aulacomnium palustre* = aulpalu; *Bazzania trilobata* = baztril; *Bryum pseudotriquetrum* = brypseu; *Calamagrostis arundinacea* = CALARUN; *Calamagrostis villosa* = CALVILL; *Calliergon cordifolium* = calcord; *Calliergon stramineum* = calstram; *Calliergonella cuspidata* = calcusp; *Caltha palustris* = CALPALUST; *Campylium stellatum* = camstel; *Cardamine pratensis* agg. = CARPRAT; *Cardamine trifolia* = CARTRIF; *Carex brizoides* = CARBRIZ; *Carex davalliana* = CARDAVA; *Carex digitata* = CARDIGI; *Carex echinata* = CARECHI; *Carex flava* agg. = CARFLAV; *Carex nigra* = CARNIGR; *Carex pauciflora* = CARPAUC; *Carex rostrata* = CARROST; *Cetraria islandica* = cetisla; *Chaerophyllum hirsutum* = CHAHIRS; *Cladonia furcata* = clafurc; *Climacium dendroides* = clidend; *Cratoneuron decipiens* = cradeci; *Crepis paludosa* = CREPALU; *Cruciata glabra* = CRUGLAB; *Dactylorhiza maculata* = DACMACU; *Deschampsia cespitosa* = DESCESP; *Dicranum polysetum* = dicpoly; *Dicranum scoparium* = discop; *Drepanocladus cossonii* = drecoss; *Dryopteris expansa* = DRYEXPA; *Equisetum palustre* = EQUPALU; *Equisetum sylvaticum* = EQUSYLV; *Eriophorum latifolium* = ERILATI; *Eriophorum vaginatum* = ERIVAGI; *Euphrasia rostkoviana* = EUPROST; *Festuca heterophylla* = FESHETE; *Filipendula ulmaria* = FILULMA; *Fragaria vesca* = FRAVESC; *Galium palustre* = GALPALU; *Geum rivale* = GEURIVA; *Gymnocarpium dryopteris* = GYMDRYO; *Hieracium sylvaticum* = HIESYLV; *Homalothecium nitens* = homnite; *Huperzia selago* = HUPSELA; *Hylocomium splendens* = hylsple; *Juncus filiformis* = JUNFILI; *Luzula paludosa* = LUZLINA; *Luzula luzuloides* = LUZLDES; *Luzula pilosa* = LUZPILO; *Lycopodium annotinum* = LYCANNO; *Maianthemum bifolium* = MAIBIFO; *Melampyrum sylvaticum* = MELSYLV; *Molinia caerulea* = MOLCAER; *Nardus stricta* = NARSTRI; *Oxalis acetosella* = OXAACET; *Oxycoccus palustris* = OXYPALU; *Parnassia palustris* = PARPALU; *Pedinophyllum interruptum* = pedinte; *Picea abies* = PICABIE; *Pinguicula vulgaris* = PINVULG; *Pinus mugo* = PINMUGO; *Plagiochila asplenoides* = plaaspl; *Plagiomnium rostratum* = plarost; *Plagiothecium laetum* = plalaet; *Plagiothecium undulatum* = plaundu; *Pleurozium schreberi* = pleschr; *Poa alpina* f. *vivipara* = POAALPI; *Polygala vulgaris* = POLVULG; *Polytrichum commune* = polcomm; *Polytrichum formosum* = polform; *Polytrichum strictum* = polstri; *Potentilla erecta* = POTEREC; *Ranunculus acris* = RANACRI; *Rhizomnium punctatum* = rhipunc; *Rhynchospora loreus* = rhylore; *Rhynchospora triquetra* = rhytriq; *Sphagnum capillifolium* = sphcapi; *Sphagnum girgensohnii* = sphgirn; *Sphagnum magellanicum* = sphmage; *Sphagnum flexuosum* = sphflex; *Sphagnum fallax* = sphfall; *Sphagnum russowii* = sphruss; *Sphagnum squarrosum* = sphsqua; *Trichophorum alpinum* = TRIALPI; *Trifolium pratense* = TRIPRAT; *Trifolium repens* = TRIREPE; *Vaccinium myrtillus* = VACMYRT; *Vaccinium vitis-idaea* = VACVITI; *Valeriana dioica* = VALDIOI; *Veronica officinalis* = VEROFFIC; *Viola biflora* = VIOMBIFL.

DCA1 axis has a lower content of calcium, a low base saturation and a low pH, however it also has a high concentration of aluminium, iron and hydrogen. The correlation between the DCA1 axis and these exchangeable cations is negative (Table 1).

The variation in the vegetation along the second axis is closely related to the soil-water content in May and August (Table 1). The significant negative correlation of the DCA2 axis with water content, with total carbon content and peat-soil depth is likely to reflect their intercorrelation (Tables 1 and 3). The total carbon content in the soil and the peat depth both increase with increasing water content. Consequently, the C/N ratio has a significantly negative correlation with the second DCA axis. Thus, the peat soils of the dwarf-pine mires and the spruce mires have a lot of carbon and a high C/N ratio (Table 2). In these conditions many characteristic plants of the deep peat-soil (e.g. *Oxycoccus palustris*, *Eriophorum vaginatum*, *Juncus filiformis*, *Sphagnum magellanicum*, *S. russowii*, *S. flexuosum*, *S. capillifolium*, *S. fallax*, *Polytrichum strictum*) are present (Fig. 4). The correlations between the DCA2 and magnesium, and the DCA2 and potassium are negative too (Table 1).

Based on ANOVA (Table 2), different types of mires and of spruce forest on mineral soil significantly differ from each other with respect to all soil parameters. There is also a significant difference in pH, cations (especially calcium), and base saturation between two types of spruce forest (groups C and D).

Due to predominant calcareous parent material on the Pokljuka high plateau, calcium is the dominant exchangeable basic cation. Therefore, the strong correlation between the exchangeable calcium and base saturation is expected (Table 3). The group of variables that are higher in the soil of sedge fens than in other vegetation groups (e.g. pH, exchangeable Ca, base saturation) are in positive correlation with each other. They do, however, correlate negatively with the exchangeable acid cations (Al, Fe and H).

The group of variables that are closely related to the second DCA axis (e.g. the water content in May and August, total C, C/N ratio, peat depth) correlate positively.

## Discussion

In this analysis we focus our attention on the distribution of the plant species and their relationships with soil variation. The ecological and vegetational groups (dwarf-pine mire, spruce mire, sedge fen, spruce forest) and their plant species were well separated in the DCA ordination space.

A number of ecological gradients play a role in determining the vegetation patterns of the peatlands. The identification of environmental gradients is very important in the study of niche relationships. Many authors (e.g. Karlin & Bliss

**Table 1.** Spearman rank correlations between DCA scores and (1) cover of vertical layers, (2) plant species diversity, (3) soil variables. Soil variables: WaterC-M = soil-water content in May, WaterC-A = soil-water content in August, pH = soil reaction, C<sub>tot</sub> = total carbon, N<sub>tot</sub> = total nitrogen, C/N = carbon/nitrogen ratio, Ca = exchangeable calcium, K = exchangeable potassium, Mg = exchangeable magnesium, Al = exchangeable aluminium, Fe = exchangeable iron, Mn = exchangeable manganese, H = exchangeable hydrogen, BS = base saturation, peat depth = depth of peat soil. \*\*\* =  $p \leq 0.001$ , \*\* =  $0.001 < p \leq 0.010$ , \* =  $0.010 < p \leq 0.050$ .

DCA axis	1	2	3
<b>1</b>			
Tree layer	-0.319*	0.562***	-0.138
Shrub layer	-0.078	-0.472**	-0.049
Herb layer	0.684***	-0.281	0.166
Moss layer	0.124	-0.735***	0.262
<b>2</b>			
Shannon <i>H'</i>	0.779***	-0.247	0.299
Species richness	0.785***	0.124	0.102
<b>3</b>			
WaterC-M	0.163	-0.923***	0.307*
WaterC-A	0.169	-0.834***	0.324*
pH	0.757***	0.333*	0.173
C <sub>tot</sub>	0.122	-0.901***	0.163
N <sub>tot</sub>	0.587***	-0.511***	0.231
C/N	-0.343*	-0.676***	-0.001
Ca	0.836***	-0.267	0.190
Mg	0.369*	-0.627***	0.212
K	0.182	-0.668***	0.177
Al	-0.837***	0.244	-0.204
Fe	-0.674***	-0.207	-0.021
Mn	0.713***	-0.095	0.137
H	-0.704***	-0.416**	-0.100
BS	0.825***	-0.129	0.226
Peat depth	0.212	-0.851***	0.138

1984, Martinčič & Piskernik 1985, Malmer 1986, Glaser *et al.* 1990, Gerdol 1995, Jeglum & He 1995, Bragazza & Gerdol 1996, Nordbakken 1996, Bragazza 1997, Wheeler & Proctor 2000, Økland *et al.* 2001) reported that some of the main factors controlling plant species and vegetation distribution in mires are the moisture gradient and the acidity/alkalinity gradient.

In our study the segregation of different plant species along the first axis reflects the acidity–alkalinity gradient. The DCA1 separation is consistent with Gorham and Janssen's (1992) bimodal distribution. In our study DCA1 clearly distinguishes *Sphagnum* species (e.g. *S. girgensohnii*, *S. magellanicum*, *S. russowii*, *S. flexuosum*, *S. capillifolium*) from other moss species belonging mostly to the Amblystegiaceae (e.g. *Drepanocladus cossonii*, *Campylium stellatum*, *Calliergon cordifolium*, *Cratoneuron decipiens*). The DCA1 axis clearly separates the meso-eutrophic sedge fens (some of them could be even eutrophic) from the ombro-oligotrophic dwarf-pine mire (bog) and the spruce mire, as well as from the spruce forests. The second DCA axis was closely related to soil-water, total-carbon and C/N-ratio gradients. According to the DCA2 scores the vegetation groups were progressively arranged as follows: dwarf-pine mire (bog) under the extreme conditions with a

high water content of the soil, the spruce mire; the sedge fen, and at the top of the ordination space the spruce forest.

H<sup>+</sup> ion activity, cation concentrations (especially calcium), and base saturation are important factors that determine the physiological tolerance of the mire plant species, and thus in determining the plant-community composition. The high species richness results from the heterogeneous ecological conditions, with the soil conditions being the most significant. Plant species richness is the highest in the sedge fens; these areas have peat-soil with a high pH, a high calcium content and a high base saturation. These are the main factors that accelerate the plant diversity of the mires and in surrounding spruce forest on the Pokljuka plateau. The species richness increases with decreasing of acid cations (Al, Fe and H). The dwarf-pine mires with peat-soil of low pH, low calcium content and low base saturation are dominated by the different *Sphagnum* species.

In spite of the fact that the spruce mire and the dwarf-pine mire were shown to be clearly separated from each other in a cluster analysis (Kutnar 2000b), the typical plant species of these two vegetation types are not placed far apart in the ordination space. The segregation of these mire clusters is mostly a result of the predominance of spruce (*Picea abies*) and dwarf

**Table 2.** Mean values (S.D.) of soil variables in the vegetation types. *N* = number of sample plots of each vegetation type. † Differences between vegetation types were tested with one-way ANOVAs. \*\*\* =  $p \leq 0.001$ , \*\* =  $0.001 < p \leq 0.010$ , \* =  $0.010 < p \leq 0.050$ . Symbols as in Table 1.

	Dwarf-pine mire A ( <i>N</i> = 7)	Spruce mire B ( <i>N</i> = 9)	Spruce forest C ( <i>N</i> = 9)	Spruce forest D ( <i>N</i> = 6)	Sedge fen E + F ( <i>N</i> = 11)	<i>p</i> <sup>†</sup>
WaterC-M	2030.2 (757.8)	1092.3 (305.5)	231.0 (243.5)	214.2 (89.3)	845.2 (386.3)	***
WaterC-A	963.1 (369.4)	733.9 (174.2)	114.5 (29.3)	154.8 (109.7)	630.8 (128.7)	***
pH	3.8 (0.3)	3.6 (0.3)	3.9 (0.1)	4.8 (0.8)	5.7 (0.6)	***
C <sub>tot</sub> (%)	43.1 (1.9)	41.8 (2.9)	15.5 (6.7)	18.4 (7.1)	37.0 (7.4)	***
N <sub>tot</sub> (%)	1.1 (0.2)	1.5 (0.3)	0.7 (0.2)	0.9 (0.2)	1.9 (0.4)	***
C/N	40.0 (6.0)	29.6 (4.7)	22.1 (4.5)	20.7 (4.7)	20.0 (4.1)	***
Ca (cmol(+)/kg)	16.5 (7.3)	14.5 (5.8)	5.3 (2.7)	30.1 (19.9)	84.2 (17.6)	***
Mg (cmol(+)/kg)	4.7 (2.6)	3.2 (0.7)	1.0 (0.4)	2.5 (1.4)	3.9 (2.5)	**
K (cmol(+)/kg)	1.5 (0.3)	1.7 (0.4)	0.6 (0.3)	0.5 (0.3)	1.5 (0.7)	***
Al (cmol(+)/kg)	3.8 (2.2)	4.8 (0.9)	8.7 (2.8)	2.9 (2.1)	0.6 (0.9)	***
Fe (cmol(+)/kg)	2.4 (1.2)	2.2 (1.6)	2.2 (1.3)	0.8 (0.8)	0.1 (0.1)	***
Mn (cmol(+)/kg)	0.02 (0.01)	0.02 (0.01)	0.01 (0.01)	0.06 (0.03)	0.08 (0.07)	**
H (cmol(+)/kg)	32.1 (12.0)	30.9 (8.9)	18.6 (4.6)	4.8 (4.5)	0.6 (1.5)	***
BS (%)	38.3 (20.1)	34.6 (12.3)	18.7 (7.8)	74.8 (17.8)	98.2 (4.0)	***
Peat depth (cm)	175.7(67.7)	100.0 (69.8)	0.0 (0.0)	0.0 (0.0)	107.3 (84.7)	***



**Table 3.** Spearman rank correlations between soil variables. \*\*\* =  $p \leq 0.001$ , \*\* =  $0.001 < p \leq 0.010$ , \* =  $0.010 < p \leq 0.050$ . Symbols as in Table 1.

	WaterC-M	WaterC-A	pH	C <sub>tot</sub>	N <sub>tot</sub>	C/N	Ca	Mg	K	Al	Fe	Mn	H	BS
WaterC-M	0.861***													
WaterC-A	-0.288	-0.209												
pH	0.870***	0.771***	-0.300											
C <sub>tot</sub>	0.516***	0.556***	0.289	0.635***										
N <sub>tot</sub>	0.659***	0.589***	-0.690***	0.612***	-0.047									
C/N	0.271	0.313*	0.710***	0.294	0.711***	-0.207								
Ca	0.581***	0.632***	-0.025	0.610***	0.479**	0.515***	0.463**							
Mg	0.661***	0.688***	-0.246	0.724***	0.582***	0.566***	0.321*	0.743**						
K	-0.232	-0.286	-0.651***	-0.288	-0.596***	0.153	-0.867***	-0.481**	-0.348*					
Al	0.228	0.098	-0.713***	0.143	-0.377*	0.468**	-0.660***	-0.169	-0.051	0.745***				
Fe	0.047	0.038	0.638***	0.092	0.401**	-0.309*	0.743***	0.217	0.075	-0.635***	-0.475**			
Mn	0.371*	0.274	-0.959***	0.378*	-0.259	0.720***	-0.688***	0.089	0.281	0.627***	0.775***	-0.621***		
H	0.115	0.174	0.780***	0.159	0.626***	-0.341*	0.958***	0.365*	0.183	-0.884***	-0.751***	0.755***	-0.781***	
BS	0.774***	0.757***	-0.214	0.791***	0.564***	0.482**	0.339*	0.590***	0.699***	-0.284	0.024	0.183	0.266	0.201
Peat depth														

pine (*Pinus mugo*). However, the DCA separation of many typical plants of these two mires is not so evident. The spruce mire and dwarf-pine mire have some common bryophyte species (e.g. *Sphagnum magellanicum*) that have a high average coverage in both vegetation types. Actually, these two mires form the mosaic-like mire complexes where the borders between them are diffuse. The initial phases of the spruce mires, with atrophied, shrub-form *Picea abies*, could be the scattered islands occurring among the predominant dwarf pines. It seems that the dwarf pine can grow in a bit more extreme, more ombrotrophic conditions, but the causes for alternation of spruce and dwarf pine in ombro-oligotrophic conditions have not been studied in detail yet.

There is a significant difference between two types of the spruce forest on mineral soil. The different forms of calcium-poor podzols predominate in the upland spruce forest (group C) characterised by low species richness. On the other hand, the species-rich spruce forest (group D) covers very heterogeneous soils with a high calcium content. Due to the level of some plots that are below the level of adjacent mires, the soils are under the influence of ground water or seasonal inundation. Hence, the gleysols are the predominating soil types of group D.

It can be assumed that due to the ecological multi-source origin of the flora and the location of the plots in very diverse ecological conditions, the mire-margin communities on the Pokljuka plateau in Slovenia show high species diversity. The plots were chosen in a systematic way so that they could include mixed elements of various mire conditions.

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**Appendix.** Vertical layer vegetation of the different vegetation types. Number of sample plots (*N*) of each vegetation type, frequency of occurrence (*n*), and mean cover value (in %) of 97 species in vegetation types (types E and F are joined) are presented.

	Dwarf-pine mire		Spruce mire		Spruce forest		Spruce forest		Sedge fen	
	A		B		C		D		E + F	
	(N = 7)		(N = 9)		(N = 9)		(N = 6)		(N = 11)	
	<i>n</i>	cover (%)	<i>n</i>	cover (%)	<i>n</i>	cover (%)	<i>n</i>	cover (%)	<i>n</i>	cover (%)
Tree and shrub layer										
<i>Picea abies</i>	7	12.9	9	43.3	9	58.7	6	79.2	9	13.1
<i>Pinus mugo</i>	6	52.6	1	15.0	–	–	–	–	–	–
Herb layer										
<i>Agrostis capillaris</i>	–	–	–	–	–	–	3	1.3	7	0.5
<i>Agrostis stolonifera</i>	–	–	–	–	–	–	2	0.5	2	0.5
<i>Anemone nemorosa</i>	–	–	–	–	–	–	6	5.0	8	3.3
<i>Calamagrostis arundinacea</i>	–	–	–	–	3	12.8	1	0.5	–	–
<i>Calamagrostis villosa</i>	–	–	2	7.8	2	1.8	3	5.3	1	62.5
<i>Caltha palustris</i>	–	–	1	15.0	–	–	2	15.0	8	21.9
<i>Cardamine pratensis</i> agg.	–	–	–	–	–	–	–	–	5	0.5
<i>Cardamine trifolia</i>	–	–	–	–	–	–	3	7.0	–	–
<i>Carex brizoides</i>	5	4.4	7	5.7	2	9.0	3	0.5	6	15.4
<i>Carex davalliana</i>	1	0.5	–	–	–	–	–	–	7	17.1
<i>Carex digitata</i>	–	–	–	–	1	0.5	2	1.8	–	–
<i>Carex echinata</i>	1	0.5	2	0.5	–	–	–	–	6	0.9
<i>Carex flava</i> agg.	–	–	–	–	–	–	–	–	7	7.4
<i>Carex nigra</i>	6	4.2	9	1.6	2	1.8	–	–	7	1.2
<i>Carex pauciflora</i>	6	6.6	3	0.5	–	–	–	–	1	0.5
<i>Carex rostrata</i>	1	0.5	–	–	1	0.5	–	–	8	35.4
<i>Chaerophyllum hirsutum</i>	–	–	–	–	–	–	4	5.4	5	15.8
<i>Crepis paludosa</i>	1	0.5	–	–	–	–	2	0.5	8	6.6
<i>Cruciata glabra</i>	–	–	–	–	–	–	4	1.1	–	–
<i>Dactylorhiza maculata</i>	–	–	–	–	–	–	1	0.5	8	0.8
<i>Deschampsia cespitosa</i>	–	–	–	–	–	–	3	1.3	3	1.3
<i>Dryopteris expansa</i>	–	–	1	0.5	2	1.8	1	0.5	–	–
<i>Equisetum palustre</i>	1	3.0	–	–	–	–	–	–	7	5.7
<i>Equisetum sylvaticum</i>	–	–	–	–	–	–	3	6.2	4	1.1
<i>Eriophorum latifolium</i>	–	–	–	–	–	–	–	–	9	4.0
<i>Eriophorum vaginatum</i>	5	19.2	6	3.8	–	–	–	–	–	–
<i>Euphrasia rostkoviana</i>	–	–	–	–	–	–	–	–	6	2.6
<i>Festuca heterophylla</i>	–	–	–	–	–	–	1	0.5	4	0.5
<i>Filipendula ulmaria</i>	–	–	–	–	–	–	1	0.5	2	1.8
<i>Fragaria vesca</i>	–	–	–	–	–	–	3	5.3	–	–
<i>Galium palustre</i>	–	–	–	–	–	–	–	–	5	0.5
<i>Geum rivale</i>	–	–	–	–	–	–	–	–	3	0.5
<i>Gymnocarpium dryopteris</i>	–	–	–	–	2	0.5	4	0.5	2	1.8
<i>Hieracium sylvaticum</i>	–	–	–	–	–	–	3	1.3	–	–
<i>Huperzia selago</i>	–	–	–	–	2	0.5	1	0.5	–	–
<i>Juncus filiformis</i>	2	7.8	1	0.5	1	0.5	–	–	–	–
<i>Luzula luzulina</i>	–	–	2	0.5	6	0.5	5	0.5	1	0.5
<i>Luzula luzuloides</i>	–	–	–	–	4	0.5	2	1.8	–	–
<i>Luzula pilosa</i>	1	3.0	3	0.5	8	2.1	6	0.9	2	0.5
<i>Lycopodium annotinum</i>	–	–	–	–	8	7.6	–	–	–	–
<i>Maianthemum bifolium</i>	2	7.8	2	1.8	1	0.5	5	6.8	6	1.3
<i>Melampyrum sylvaticum</i>	4	1.8	2	0.5	–	–	4	0.5	4	0.5
<i>Molinia caerulea</i>	1	3.0	–	–	–	–	–	–	1	3.0
<i>Nardus stricta</i>	1	0.5	–	–	–	–	1	0.5	5	1.0

Continues

## Appendix. Continued.

	Dwarf-pine mire		Spruce mire		Spruce forest		Spruce forest		Sedge fen	
	A (N = 7)		B (N = 9)		C (N = 9)		D (N = 6)		E+F (N = 11)	
	n	cover (%)	n	cover (%)	n	cover (%)	n	cover (%)	n	cover (%)
<i>Oxalis acetosella</i>	–	–	–	–	7	1.9	5	9.4	1	0.5
<i>Oxycoccus palustris</i>	7	5.4	1	0.5	–	–	–	–	3	0.5
<i>Parnassia palustris</i>	–	–	–	–	–	–	1	0.5	5	1.5
<i>Pinguicula vulgaris</i>	–	–	–	–	–	–	–	–	4	1.8
<i>Poa alpina</i> f. <i>vivipara</i>	–	–	–	–	1	0.5	5	0.5	–	–
<i>Polygala vulgaris</i>	–	–	–	–	–	–	–	–	3	2.2
<i>Potentilla erecta</i>	1	15.0	1	0.5	–	–	1	3.0	11	18.6
<i>Ranunculus acris</i>	–	–	–	–	–	–	–	–	7	6.1
<i>Trichophorum alpinum</i>	–	–	–	–	–	–	–	–	3	22.0
<i>Trifolium pratense</i>	–	–	–	–	–	–	1	0.5	2	1.8
<i>Trifolium repens</i>	–	–	–	–	–	–	1	0.5	2	0.5
<i>Vaccinium myrtillus</i>	7	34.8	9	48.7	6	31.8	6	27.3	6	5.8
<i>Vaccinium vitis–idaea</i>	7	27.9	8	10.0	3	1.3	5	10.8	8	3.3
<i>Valeriana dioica</i>	–	–	–	–	–	–	1	0.5	7	7.8
<i>Veronica officinalis</i>	–	–	–	–	–	–	3	0.5	–	–
<i>Viola biflora</i>	–	–	–	–	–	–	2	15.0	2	1.8
Moss layer										
<i>Aulacomnium palustre</i>	1	0.5	–	–	–	–	–	–	8	5.1
<i>Bazzania trilobata</i>	–	–	1	0.5	3	1.3	–	–	–	–
<i>Bryum pseudotriquetrum</i>	–	–	–	–	–	–	–	–	7	19.1
<i>Calliergon cordifolium</i>	–	–	–	–	–	–	–	–	3	5.3
<i>Calliergon stramineum</i>	–	–	–	–	–	–	–	–	6	5.8
<i>Calliergonella cuspidata</i>	1	0.5	1	0.5	–	–	–	–	2	0.5
<i>Campylium stellatum</i>	–	–	–	–	–	–	–	–	4	1.1
<i>Cetraria islandica</i>	–	–	–	–	3	2.2	1	0.5	–	–
<i>Cladonia furcata</i>	–	–	–	–	5	1.0	2	0.5	–	–
<i>Climacium dendroides</i>	–	–	–	–	–	–	3	0.5	7	3.3
<i>Cratoneuron decipiens</i>	–	–	–	–	–	–	–	–	3	2.2
<i>Dicranum polysetum</i>	1	0.5	6	0.9	6	12.8	1	0.5	–	–
<i>Dicranum scoparium</i>	–	–	2	0.5	2	7.8	6	0.9	–	–
<i>Drepanocladus cossonii</i>	–	–	–	–	–	–	–	–	4	17.3
<i>Homalothecium nitens</i>	–	–	–	–	–	–	–	–	4	8.4
<i>Hylocomium splendens</i>	1	0.5	4	1.1	3	0.5	3	12.8	3	2.2
<i>Pedinophyllum interruptum</i>	–	–	–	–	2	0.5	2	1.8	1	0.5
<i>Plagiochila asplenioides</i>	–	–	–	–	–	–	2	9.0	1	0.5
<i>Plagiomnium rostratum</i>	–	–	–	–	–	–	–	–	6	9.5
<i>Plagiothecium laetum</i>	–	–	–	–	3	0.5	–	–	–	–
<i>Plagiothecium undulatum</i>	–	–	2	0.5	1	0.5	–	–	–	–
<i>Pleurozium schreberi</i>	2	0.5	3	1.3	1	0.5	4	14.0	4	1.1
<i>Polytrichum commune</i>	1	3.0	9	10.6	1	3.0	–	–	1	0.5
<i>Polytrichum formosum</i>	–	–	–	–	9	2.4	3	1.3	–	–
<i>Polytrichum strictum</i>	4	8.4	1	0.5	–	–	–	–	4	1.1
<i>Rhizomnium punctatum</i>	–	–	–	–	2	0.5	1	0.5	2	7.8
<i>Rhytidiadelphus loreus</i>	–	–	2	1.8	7	0.9	3	1.3	–	–
<i>Rhytidiadelphus triquetrus</i>	–	–	1	0.5	3	1.3	5	18.7	6	19.8
<i>Sphagnum capillifolium</i>	4	11.0	6	4.2	–	–	–	–	3	5.3
<i>Sphagnum girgensohnii</i>	1	0.5	8	19.3	5	25.3	–	–	2	1.8
<i>Sphagnum magellanicum</i>	7	56.1	9	19.8	1	3.0	–	–	4	8.4
<i>Sphagnum flexuosum</i>	6	18.5	4	14.0	1	15.0	–	–	4	4.8
<i>Sphagnum fallax</i>	1	3.0	3	18.5	–	–	–	–	–	–
<i>Sphagnum russowii</i>	4	14.6	3	10.2	1	3.0	–	–	1	3.0
<i>Sphagnum squarrosum</i>	–	–	1	37.5	1	0.5	–	–	1	0.5