

Sphagnum species along environmental gradients in mires of the Sudety Mountains (SW Poland)

Bronisław Wojtuń*, Aleksandra Sendyk and Dagmara Martyniak

*Department of Ecology, Biogeochemistry and Environmental Protection, Wrocław University, ul. Kanonia 6/8, PL-50-328 Wrocław, Poland (*corresponding author's e-mail: bronislaw.wojturn@biol.uni.wroc.pl)*

Received 2 Sep. 2011, final version received 16 May 2012, accepted 16 May 2012

Wojtuń, B., Sendyk, A. & Martyniak, D. 2013: *Sphagnum* species along environmental gradients in mires of the Sudety Mountains (SW Poland). *Boreal Env. Res.* 18: 74–88.

We studied the regional ecology of 33 *Sphagnum* taxa in 37 mires and 141 stands in the Sudety Mountains, central Europe. Five ecological species groups were distinguished based on the occurrence of particular species in plant communities and mire stands, and their distribution patterns along water-chemistry gradients. The ordination analysis (CCA) suggests that the most important factors affecting *Sphagnum* species distribution and abundance in the Sudety mires were moss height above the water level, altitude as well as surface-water pH and conductivity. In ombrotrophic bogs, moss height above the water level was the primary controlling factor. Within minerotrophic mires the distribution of species was mostly limited by pH, conductivity and Ca concentration in surface water. *Sphagnum lindbergii*, *S. jenseni*, *S. warnstorffii* and *S. compactum* were mostly restricted to the higher elevations from 1405–1430 m a.s.l., whereas *S. rubellum*, *S. palustre* and *S. fimbriatum* were mainly located at 635–830 m a.s.l.

Introduction

Mosses of the genus *Sphagnum* occupy a wide variety of habitats, from peatlands, through margins of lakes, wet meadows, sedge mats, heaths and forests, moist slopes and sands, alpine swards, roadside ditches, to rocks covered by acidic humus and water-dripping cliffs. However, the most important habitats for most *Sphagnum* species are bogs, poor fens and intermediate fens, covering vast surfaces of land in boreal and subarctic zones of the northern hemisphere. In these habitats, peat mosses frequently dominate all other vegetation, both in respect of area covered and the amount of biomass formed (Vitt 2000, Rydin *et al.* 2006).

Regional ecological studies are needed because the response of plants may vary within their distribution area. Species may have different amplitudes in relation to environmental conditions in different parts of their geographic distribution as they differently respond to ecological factors under varying climatic conditions (Gignac *et al.* 1991, Bragazza 1997). These studies were performed mainly in North America (Vitt and Slack 1975, 1984, Horton *et al.* 1979, Andrus 1986, Gignac and Vitt 1990, Vitt *et al.* 1990, Gignac *et al.* 1991). In Europe, several studies deal specifically with *Sphagnum* ecology, however few analysed quantitatively effects of water-chemistry gradient on species distribution. These studies are known for the southern

and western Alps (Gerdol and Bragazza 1994, Bragazza 1997, 1999, Brusa 2001, Miserere *et al.* 2003). Only a few such studies from central Europe have so far been published (Zechmeister 1995, Dierßen 1983, 2001, Hájek *et al.* 2002, 2006). Depth to the water table, peat and surface water chemistry and light are largely responsible for the local distribution of *Sphagnum* on mires (Bragazza 1997, Gignac and Vitt 1990). Gerdol and Bragazza (1994) have also demonstrated the local distribution of *Sphagnum* species along an elevational gradient. However, the habitat limitations of individual species along local gradients are generally overshadowed by a more important factor, i.e. the climate (Gignac 1993).

As compared with other mountain ranges in Poland, the Sudety Mts. are special in the number and variety of mires that are dominated by *Sphagnum* mosses.

The objective of this investigation was to analyse the habitat ecology of *Sphagnum* species in mountain mires of the Sudety region. More specifically, we addressed the following four questions: (i) What are the most important ecological gradients affecting *Sphagnum* species distribution? (ii) What is the distribution pattern of *Sphagnum* species along the trophic mire gradient? (iii) What are the ecological amplitudes along the surface water-chemistry gradient for *Sphagnum* species? (iv) What are the preferences of *Sphagnum* taxa with regard to wetness, shade and altitude?

Material and methods

Study area

The studies were carried out in 37 mires located in the Polish part of the Sudety Mountains and the Kotlina Jeleniogórska basin (50°12'–50°53'N and 15°18'–16°51'E; elevations varies from 395 to 1430 m a.s.l., Fig. 1). The bedrock of the Sudety Mts. is mainly acidic, made up primarily of granites, gneiss and crystalline schists (Kondracki 2009). The average monthly temperature varies between –6.9 and –4.8 °C in January and from +9.0 to +14.8 °C in July; total annual precipitation varies between 997 and 1512 mm (Migała 2005). The considerable variety of cli-

mate conditions along the altitudinal gradient results in distinct vegetation belts in the Sudety Mountains. The montane belts (500–1250 m a.s.l.) are occupied by secondary spruce monocultures (lower forest belt) and natural spruce forest in the upper forest belt. The subalpine belt (up to 1450 m) in the most part is a mosaic of Sudetic dwarf pine shrubs, matt-grass meadows and subalpine mires which cover mostly flat and gently sloping summit plateaus. The alpine belt extends to 1603 m a.s.l. (Raj 2001).

Study sites

The most distinctive feature of the Sudety vegetation is the presence of mountain mires (Wolejko *et al.* 2005, Wojtuń 2006). Their distribution is uneven: the majority is found in the Western Sudety (Fig. 1). In the Eastern Sudety, one mire occurs: an ombrotrophic bog in the Śnieżnik Massif (mire 1). In the Central Sudety, the best developed mires occur in the Bystrzyckie Mts. and Stołowe Mts. In the former, it covers about 230 ha (mire 2) and is a complex of ombrotrophic part and transitional mire, surrounded by peaty spruce forest of the lower forest belt (750 m a.s.l.). The mire in the Stołowe Mountains (mire 3) is situated at the elevation of 715 m a.s.l. and has a surface of ca. 75 ha. Over most of the area conditions are nearly ombrotrophic with small, intermediate fen areas at the mire border. Small transitional mire (10 ha, 395 m a.s.l.), situated in the Kotlina Jeleniogórska basin (mire 4), covers waterlogged area in both meadow and forest complexes. Great diversity of morphological and hydrological mire types is found in the Western Sudety. In the lower forest belt of the Karkonosze mountains, there are several small transitional mires (mires 5–7). In the upper forest belts of the Karkonosze within the mountain spruce forest there are considerable areas occupied by transitional mires, which are soligenous sloping mires (mires 12–14, 16–18, 21, 22 and 24). In the elevated summit plateau area of the Karkonosze, large complexes of peat bogs developed, classified as subarctic-subalpine mires (mires 8–11, 15, 19, 20 and 23). These are ombro-minerotrophic complexes, in the most part wooded by mountain pine shrubs (Jenik and

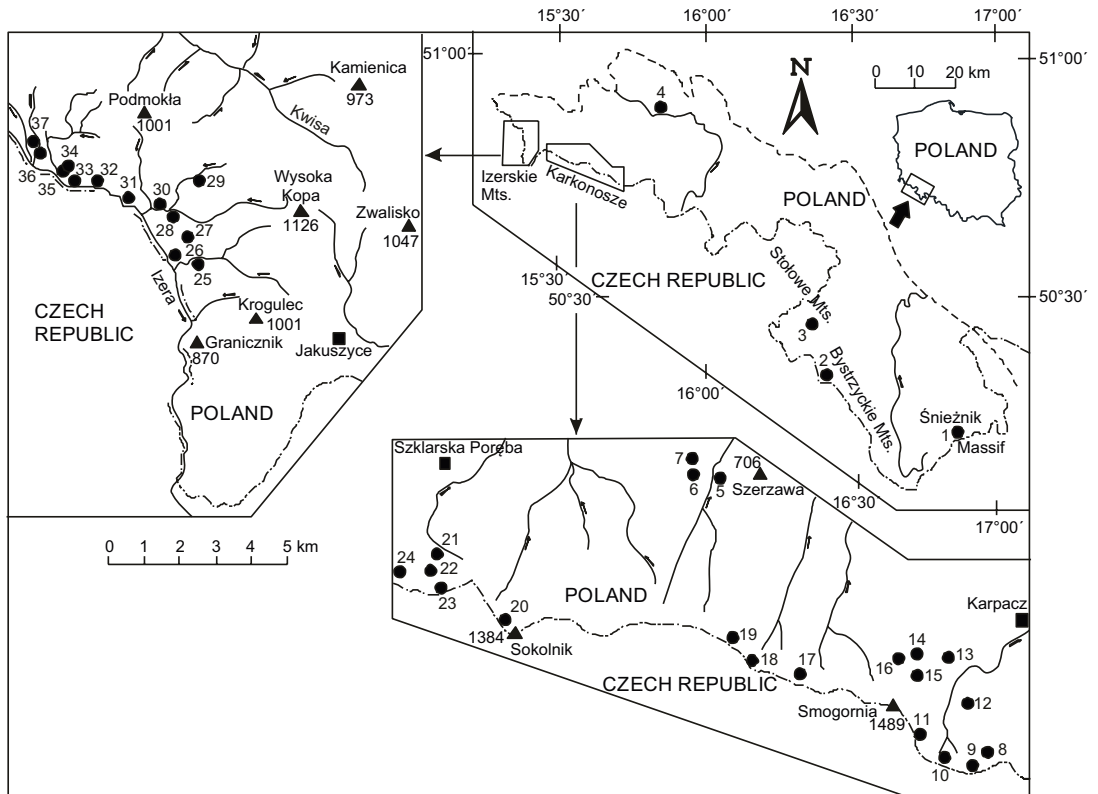


Fig. 1. Map of the Sudety Mountains showing the main mountain ranges and location of the mires studied (black dots). The dashed line indicates southern border of the study area.

Soukupová 1992). The majority of mires in the Izerskie Mts. occur within a mountain spruce forest belt at the elevation range 800–850 m a.s.l. They developed in the lower parts of slopes, on the meadow terraces of the Izer River valley where ombro-soligenous and soligenous sloping mires prevail. In terms of the current vegetation, they are mostly ombrotrophic bogs partially surrounded by transitional mires or fens (mires 26–28, 30, 32 and 37). In the largest part, the mire complexes of the Izer River valley are wooded, either by spruce or by mountain pine shrubs. Alongside the main Izer River, on waterlogged and often periodically inundated terraces, elongated valley fens developed (mires 25, 29, 31, 33–36). The flat surface of these fens is dominated by *Sphagnum*-sedge vegetation.

Mires and stands were chosen to represent the widest spectrum of habitats possible and to include all *Sphagnum* species present in the area. Within each of the mires, we selected stands that

we considered as representative units of vegetation, ecologically uniform and dominated by at least one *Sphagnum* species. The number of stands depended on the complexity and number of physiognomically distinct assemblages in the mire and in most cases corresponded to *a priori* community types. Thus the open, central part of a raised bog, its marginal part, with a relatively dense growth of the dwarf mountain pine, and the adjacent bog spruce forest were taken as separate stands. Moreover, in the open part of the bog, hummocks, moderately wet lawns, hollows and open waters were also treated separately. The number of stands present on mire varied from 1 to 18 (on average 4), with a total of 141 mire stands included in the study. The stands were defined in the field after a general survey of the mire. In each stand, the abundance of *Sphagnum* species was quantitatively recorded and nine environmental variables were measured.

Vegetation sampling

The stands were sampled using a random sampling technique (Slack *et al.* 1980, Vitt and Slack 1984). In each stand, a base line was laid out medially along the long axis of the stand in a uniform terrain, and squares were placed at random intervals along the baseline, on an undisturbed patch of vegetation. Additional squares were used to include all *Sphagnum* species. In most cases, 1 × 1 m squares were used but these were modified in size as necessary for hummock and hollow (25 × 25 cm), mountain pine rush (2 × 2 m) and spruce forest (5 × 5 m) stands. Variation in plot size does influence ordination patterns, including CCA and DCA (Otypková and Chytrý 2006). In general, five squares were sampled per stand; however, their number varied from 3 to 16, depending on the extent of the community. *Sphagnum* abundance was estimated visually as percentage cover.

Mire stands were classified into three groups based on vegetation and hydrology (source of water supply). Stands of ombrotrophic vegetation with individual areas dominated by *Pinus mugo*, *Picea excelsa*, *Eriophorum vaginatum*, *Baeothryon caespitosum*, *Carex limosa* and frequently associated with *Oxyccocus palustris*, *Andromeda polifolia*, *Calluna vulgaris*, *Vaccinium myrtillus*, *V. vitis-idaea*, *V. uliginosum*, *Drosera rotundifolia*, *Polytrichum strictum* and *Gymnocolea inflata* were designated as group 1. Stands with vegetation dominated by minerotrophic species such as *Carex rostrata*, *C. nigra*, *Eriophorum angustifolium*, *Juncus filiformis* and *Deschampsia caespitosa* and influenced by stagnating or slowly moving groundwater beneath the surface (in the field recognized by the absence of any moving water on the surface) were classified as group 2. All stands influenced by moving ground water on the surface, either from springs and others outflows or from streams and brooks, were classified as separate group 3. The group 3 vegetation, although often dominated by the above-mentioned minerotrophic species, is characterized by the presence in moderate quantities of additional species such as *Equisetum sylvaticum*, *E. palustre*, *E. fluviatile*, *Agrostis canina*, *Epilobium palustre*, *Galium palustre*, *Comarum palustre*, *Montia fontana*, *Swertia perennis*, *Stel-*

laria uliginosa, *Scirpus sylvaticus*, *Warnstorfia sarmentosa* and *Scapania undulata*. Recognition of the five ecological groups of *Sphagnum* species was based on the occurrence of species in plant communities and mire stands.

The nomenclature of vascular plants follows Mirek *et al.* (2002). Authority names and nomenclature of *Sphagna* in most cases follow Ochyra *et al.* (2003). The concept of *S. subtile* is that of Andrus (1979). The identity of critical species, i.e. *S. jensenii*, was confirmed by K. J. Flatberg and that of *S. subtile* by R. E. Andrus. The latter species, as well as *S. capillifolium* var. *tenerum* and *S. cuspidatum* var. *serrulatum* are rarely present in the literature, especially from Europe. Therefore, we provide a short description of how these taxa are distinguished. *Sphagnum subtile* combines characters of *S. capillifolium* and *S. rubellum*. Macroscopically it resembles *S. capillifolium*, however in stem leaf shape, it is similar to *S. rubellum*. They differ in leaf border: *S. subtile* has a very strong and apically well-developed border 40–60 µm broad, while in *S. rubellum* it does not exceed 40 µm. The diagnostic features *S. capillifolium* var. *tenerum* are found in the stem leaves: they are narrow and elongate, with the border distinctly denticulate at apex and have mostly S-shaped hyaline cells in the upper half of the leaf with elliptic commissural pores on the outer surface (Andrus 1980, Wojtuń 2006). *Sphagnum cuspidatum* var. *serrulatum* is easily identified in the field by its floating habit and habitat, which is always open water. The distantly serrulate margin of the leaves of the divergent branches and outer capitulum branches serve as the diagnostic character for this taxon (Crum 1984). This study is one of the first in Europe that describe ecology of these rare taxa.

Environmental variables and analyses

Surface water samples were collected during the growing season from natural depressions (pools, hollows and holes). From among a total of 141 stands, water was obtained for 125 of them. The water samples were collected into acid-washed polyethylene bottles; in the field the bottles were well rinsed with water to be sampled before the sample was collected. After collection, the sam-

ples were refrigerated as soon as possible and stored in a refrigerator at about 3 °C. Conductivity and pH were measured in the laboratory within 1–3 days of sample collection; pH was measured with an Orion 250A pH meter, and electrical conductivity (EC) with an N5711 conductivity bridge in non-filtered samples. Control measurements show that these parameters did not change significantly in the course of 3 days. The EC values were corrected to 25 °C and for H⁺ abundance (Sjörs 1950), and are given as corrected conductivity.

After filtration through a 2.7 µm Millipore filter, the samples were frozen and later analysed for Ca, Mg, K and Na concentrations with an inductively coupled argon plasma spectrophotometer (Varian). All analyses were done in duplicate. Shade was estimated as the sum of canopies of all trees and shrubs within a stand. The height of moss plants above the water surface was determined indirectly by assigning a sample square to one of the following microtopographic categories: 1 = open water, 2 = hollow, 3 = carpet, 4 = lawn and 5 = hummock (Chee and Vitt 1989). Indicator species and the distinguishing criteria of these microtopography categories follow Malmer (1985). Moss distance to the water level is affected by year-to-year and seasonal variation between spring runoff and summer drought conditions. Moreover, measurements of the water level are also affected by the rain events prior to sampling. Accurate water-level measurements would require sampling each study site several times over the year to record seasonal variation. Because of the distances between localities and a relatively large number of sites, only indirect measurements of depth above the water level were applied as in several regional studies (Nicholson *et al.* 1996, Gignac *et al.* 1991, plus others cited by Rydin and Jeglum 2006). The geographical co-ordinates of mires and their altitudes above the sea level were measured with a GPS Geoexplorer II receiver.

Data analysis

Differences in the mean values of chemical variables between mire-stand groups were evaluated

by one-way ANOVA followed by a post-hoc LSD test on log-transformed data to obtain a normal distribution of features (Zar 1999). Normality of the analysed data was checked by means of Shapiro-Wilk's *W* test, and the homogeneity of variances was checked by means of Levene's test. All calculations were done with Statistica ver. 9.0 (StatSoft Inc.).

A Canonical Correspondence Analysis (CCA) was used to relate variation in *Sphagnum* species abundances to the environmental variables (ter Braak 1986, Palmer 1993). This method of ordination was chosen after a preliminary DCA analysis of species data which yielded the long gradient axis (larger than 4 SD), i.e., 19.9 (Lepš and Šmilauer 2003). The CCA analysis was performed based on a 34 × 141 species-by-stands matrix. Nine environmental variables were analysed: pH, EC, Ca, Mg, K and Na in surface water as well as shade, altitude and height of mosses above the water level. All *Sphagnum* species were included in the computations and ordination. CCA was used with the following options: “no transformation of species data”, “no species and sample-weights specified” and “no downweighting of rare species”. Forward selection of explanatory variables was used in order to find the minimal subset of the best exploratory variables which account for the species data and to rank the importance of environmental variables for determining this data (Lepš and Šmilauer 2003). The statistical significance of the relationship between the species and the whole set of environmental variables in a constrained ordination model was evaluated using the Monte Carlo permutation test. This test was also used to judge the statistical significance of each selected variable in a regression model for forward selection. CCA analysis was computed using the CANOCO 4.5 program (ter Braak and Šmilauer 2002).

Results

Trophic groups of mire habitats

Based on the vegetation and hydrology, mire stands in the Sudety Mts. were generally classified into three major groups (Table 1). Group 1 consisted of stands characterised by the domi-

nance of plant communities of the class *Oxycocco-Sphagnetea* and hollow association of *Caricetum limosae* of the class *Scheuchzerio-Caricetea fuscae*. These stands were classified as ombrotrophic. In contrast, all stands characterised by the presence of plant communities from the class *Scheuchzerio-Caricetea fuscae* were generally recognised as minerotrophic, nourished by mineral soil groundwater. Plant communities of the stands in group 2 were dominated solely by *Carex rostrata*, *C. nigra*, *Eriophorum angustifolium*, *Juncus filiformis* and *Deschampsia caespitosa*. These stands represented poor-fen vegetation fed with stagnating or slowly moving groundwater. Stands in group 3 were nourished by moving groundwater and they were identifiable by the presence of species that suggest greater minerotrophy as compared with that in the stands of group 2.

These groups differ significantly with respect to pH, EC values and cation concentrations, and increase in Na concentrations is markedly visible (Table 1). Stands in group 1 had low pH, EC, Ca, Mg, K and Na values. Their pH and EC did not exceed 4.2 and 20 μS , respectively. Stands in group 2 were from poor fens and they had higher mean values of all the chemical variables as compared with those in group 1. Their pH was as low as 3.7 and only occasionally slightly exceeded 5.0. Stands in group 3 were from intermediate fens. Although stands in this group had the highest mean values of pH, EC, Ca, Mg, K and Na, they also showed the largest variation in these chemical variables of any of the groups in the Sudety mires. The majority of stands in group 3 had pH values between 5.0 and 6.7; however, some stands could have pH values as high as 7.1.

Ecological groups of species

Sphagnum species were classified into five ecological groups based on the occurrence of particular species in plant communities and mire stands, and their distribution patterns along water-chemistry gradients (Fig. 2 and Table 2).

Species of ombrotrophic habitats (group 1)

This group consists of eight taxa occurring nearly exclusively in raised bogs with only single small populations found in fens. They occur within a narrower trophic range and are mostly confined to water with very low pH (< 4.1) and conductivity ($\text{EC} < 16 \mu\text{S}$). Calcium concentration in their sites is mostly below 1.0 mg l^{-1} . With the exceptions of *S. compactum* and *S. tenellum*, which prefer lawns, the remaining taxa are found often (*S. rubellum*, *S. capillifolium* var. *capillifolium*, *S. magellanicum*) or exclusively (*S. capillifolium* var. *tenerum*, *S. fuscum*, *S. subtile*) on hummocks.

Species of ombrotrophic to poor fen habitats (group 2)

As compared with *Sphagna* of group 1, taxa in this group have a slightly wider range along water-chemistry gradient. Species in this group are mostly restricted to habitats with water with pH not exceeding 4.5, EC values less than 20 μS , and Ca concentration below 1.5 mg l^{-1} . The only exception is *S. lindbergii* which very rarely occurs in intermediate fen habitats with pH values 5.0–5.8. Although these taxa grow in

Table 1. pH, electrical conductivity (EC) and cation concentrations in surface waters collected from the mire stands in the Sudety Mountains (given are means \pm SD, n = number of stands per group). Groups with different superscript letters differ from each other at $p < 0.05$ (ANOVA and post-hoc LSD test).

Stand group	pH	EC (μS)	Ca (mg l^{-1})	Mg (mg l^{-1})	K (mg l^{-1})	Na (mg l^{-1})	n
1	4.04 \pm 0.10 ^a	12.6 \pm 3.2 ^a	0.75 \pm 0.30 ^a	0.18 \pm 0.07 ^a	0.25 \pm 0.12 ^a	0.65 \pm 0.32 ^a	38
2	4.35 \pm 0.32 ^b	24.2 \pm 7.8 ^b	1.50 \pm 0.58 ^b	0.33 \pm 0.18 ^b	0.33 \pm 0.22 ^a	1.54 \pm 0.58 ^b	63
3	5.75 \pm 0.78 ^c	42.2 \pm 21.9 ^c	3.10 \pm 2.58 ^c	0.55 \pm 0.33 ^c	0.44 \pm 0.29 ^b	1.97 \pm 0.84 ^c	24
ANOVA	$F_{2,122} = 139$, $p < 0.0001$	$F_{2,122} = 52$, $p < 0.0001$	$F_{2,122} = 28$, $p < 0.0001$	$F_{2,122} = 27$, $p < 0.0001$	$F_{2,122} = 6$, $p < 0.002$	$F_{2,122} = 45$, $p < 0.0001$	

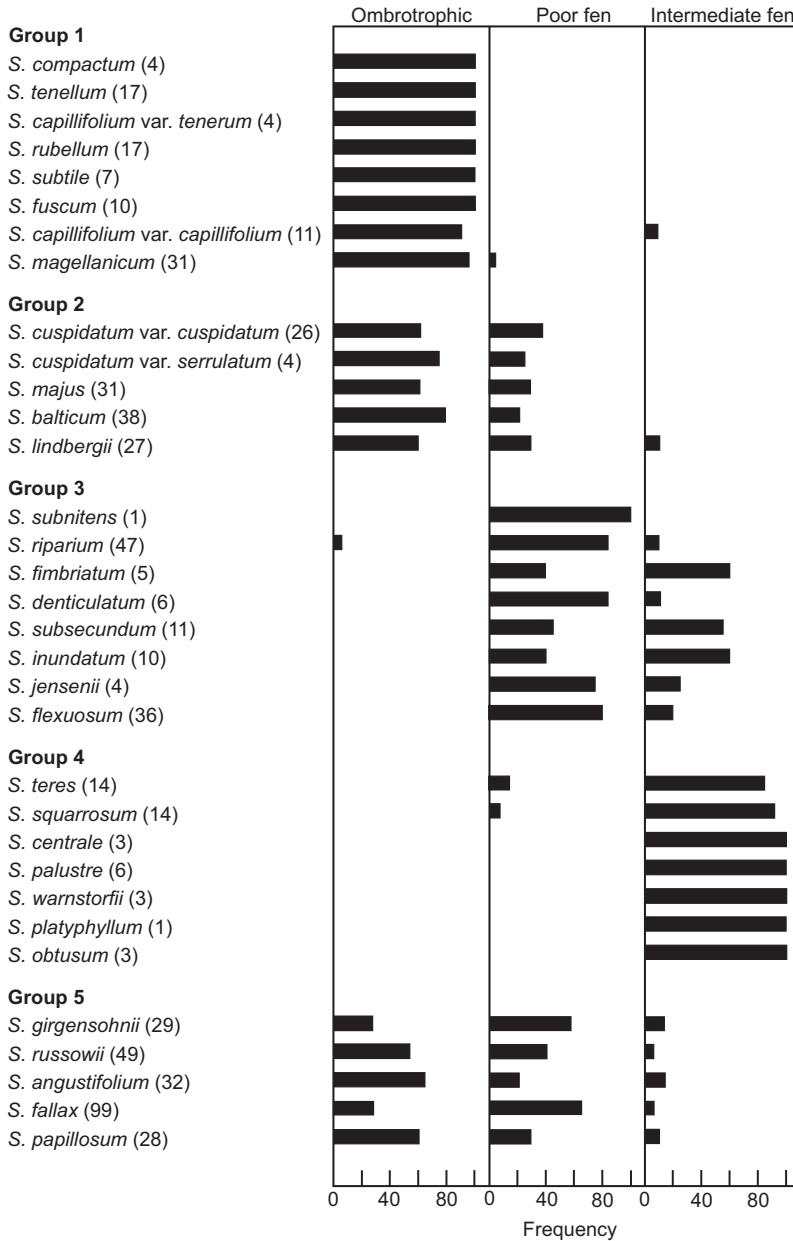


Fig. 2. Frequency of *Sphagnum* taxa along the ombrotrophic–poor-fen–intermediate-fen gradient in mires of the Sudety Mountains. Species are arranged into ecological groups. Number of in parentheses.

both raised bogs and poor fens, they are most prominent under ombrotrophic conditions. The taxa of this group prefer very wet habitats, such as carpets, hollows and open water.

Species of poor to intermediate fen habitats (group 3)

This largest group consists of eight species. The

species of this group are found in quite broad water-chemistry conditions. Although they occur mostly within a broad range of pH values (4.1–5.9) and EC (13–43 μS), they are not found in ombrotrophic conditions. The only exception is *S. riparium* which was very rarely found in such habitats. These *Sphagna* occupy moist microhabitats, usually within wet carpets. With the exception of *S. fimbriatum* and *S. subnitens*, species of this group are very often found in spring

Table 2. Environmental variables measured for 33 *Sphagnum* taxa in 37 mires of the Sudety Mountains (in parentheses are standard deviations, with the exception of WL for which ranges are given). Species are arranged in ecological groups (see Fig. 2). WL = index of the height of moss plants above the water surface, EC = electrical conductivity.

<i>Sphagnum</i> species	pH	EC ($\mu\text{S cm}^{-1}$)	Ca (mg l^{-1})	Mg (mg l^{-1})	K (mg l^{-1})	Na (mg l^{-1})	Altitude (m a.s.l.)	WL	Shade (%)	n
<i>compactum</i>	4.05 (0.06)	13.5 (1.2)	0.67 (0.42)	0.17 (0.11)	0.27 (0.17)	0.72 (0.56)	1254 (333)	3.5 (2-4)	0	4
<i>tenellum</i>	4.05 (0.09)	11.3 (2.7)	0.77 (0.23)	0.19 (0.07)	0.26 (0.11)	0.70 (0.35)	937 (226)	3.3 (2-4)	0	17
<i>capillifolium</i> var. <i>tenerum</i>	—	—	—	—	—	—	1385 (91)	4.7 (4-5)	19 (39)	4
<i>rubellum</i>	3.97 (0.11)	11.9 (2.1)	0.95 (0.19)	0.24 (0.07)	0.33 (0.16)	0.87 (0.37)	791 (42)	3.1 (2-4)	0	9
<i>subtile</i>	4.1	14.0	0.57	0.12	0.22	0.68	1405	4	0	1
<i>fuscum</i>	—	—	—	—	—	—	987 (264)	4.9 (4-5)	0	10
<i>capillifolium</i> var. <i>capillifolium</i>	4.97 (1.41)	22.4 (23.0)	0.85 (0.63)	0.35 (0.38)	0.37 (0.35)	1.43 (1.42)	902 (300)	3.7 (3-4)	17 (29)	3
<i>magellanicum</i>	4.10 (0.25)	14.9 (6.2)	1.04 (0.45)	0.24 (0.07)	0.28 (0.11)	0.93 (0.54)	927 (216)	3.3 (2-4)	17 (26)	16
<i>cuspidatum</i> var. <i>cuspidatum</i>	4.05 (0.16)	16.8 (7.3)	1.20 (0.57)	0.30 (0.20)	0.39 (0.26)	1.05 (0.71)	812 (189)	2.8 (1-4)	4 (13)	26
<i>cuspidatum</i> var. <i>serrulatum</i>	4.04 (0.09)	14.5 (5.0)	0.91 (0.51)	0.24 (0.13)	0.60 (0.47)	0.89 (0.38)	800 (51)	1	0	4
<i>majus</i>	4.23 (0.33)	16.1 (5.4)	0.85 (0.38)	0.19 (0.09)	0.23 (0.14)	0.90 (0.68)	1098 (267)	2.9 (1-4)	0.3 (2)	31
<i>balticum</i>	4.23 (0.47)	15.9 (6.8)	1.08 (0.55)	0.23 (0.10)	0.21 (0.06)	1.38 (0.42)	1012 (276)	3 (2-4)	1 (7)	4
<i>lindbergii</i>	4.37 (0.44)	16.7 (4.9)	0.81 (0.41)	0.16 (0.06)	0.18 (0.05)	1.84 (0.58)	1324 (138)	2.9 (1-4)	0	22
<i>subnitens</i>	4.27	21.6	0.88	0.15	0.42	1.74	1200	3	0	1
<i>riparium</i>	4.63 (0.76)	26.0 (12.1)	1.86 (1.69)	0.33 (0.13)	0.31 (0.14)	1.55 (0.70)	964 (206)	3 (1-4)	5 (12)	47
<i>fimbriatum</i>	5.41 (1.15)	58.5 (15.8)	4.98 (4.01)	0.82 (0.34)	0.54 (0.26)	1.86 (1.09)	690 (51)	3	0	5
<i>denticulatum</i>	4.80 (0.35)	27.4 (10.8)	1.86 (0.91)	0.36 (0.20)	0.26 (0.10)	1.72 (0.25)	1258 (123)	3	12 (18)	6
<i>subsecundum</i>	5.55 (1.04)	25.5 (8.2)	1.50 (0.69)	0.32 (0.15)	0.27 (0.08)	1.55 (0.32)	1241 (69)	3	5 (9)	11
<i>inundatum</i>	5.52 (0.97)	23.4 (2.6)	1.40 (0.34)	0.29 (0.08)	0.29 (0.07)	1.62 (0.28)	1247 (67)	3	5 (10)	10
<i>jensenii</i>	4.92 (0.49)	17.7 (3.5)	1.05 (0.25)	0.18 (0.04)	0.21 (0.06)	1.38 (0.42)	1369 (73)	3	0	4
<i>flexuosum</i>	5.06 (0.93)	31.5 (17.9)	2.23 (2.06)	0.41 (0.29)	0.37 (0.24)	1.73 (0.61)	1042 (245)	3	3 (9)	36
<i>teres</i>	5.87 (0.85)	43.7 (19.2)	3.36 (2.87)	0.58 (0.32)	0.40 (0.23)	1.86 (0.87)	1000 (282)	3	0.7 (2.7)	14
<i>squarrosum</i>	5.57 (0.98)	42.9 (24.6)	3.36 (3.10)	0.56 (0.34)	0.43 (0.25)	1.83 (0.85)	972 (259)	3	9 (16)	14
<i>centrale</i>	6.48 (0.74)	21.6 (2.5)	1.14 (0.31)	0.27 (0.08)	0.20 (0.05)	1.37 (0.38)	1210 (52)	3	3 (5.8)	3
<i>palustre</i>	5.40 (1.92)	47.6 (24.4)	3.29 (2.97)	0.75 (0.44)	0.60 (0.24)	1.92 (0.98)	667 (50)	3	6 (15)	6
<i>warnstorffii</i>	5.25 (0.39)	38.6 (14.7)	2.53 (1.05)	0.50 (0.25)	0.24 (0.02)	1.70 (0.19)	1352 (74)	3	0	3
<i>platyphyllum</i>	4.95	96.2	8.23	1.10	0.90	1.60	755	3	50	1
<i>obtusum</i>	6.94 (0.21)	23.7 (4.5)	1.04 (0.13)	0.32 (0.11)	0.25 (0.10)	1.15 (0.07)	1180	3	0	3
<i>girgensohnii</i>	4.69 (0.77)	30.2 (20.5)	2.47 (2.49)	0.39 (0.22)	0.29 (0.15)	1.37 (0.66)	1034 (254)	3.1 (3-4)	13 (20)	26
<i>russowii</i>	4.41 (0.42)	19.6 (9.1)	1.15 (0.69)	0.23 (0.13)	0.22 (0.08)	1.10 (0.62)	1209 (224)	3.3 (2-5)	11 (22)	38
<i>angustifolium</i>	4.73 (0.98)	27.2 (21.5)	1.86 (1.85)	0.42 (0.33)	0.37 (0.21)	1.37 (0.78)	944 (300)	3.1 (2-4)	7 (17)	22
<i>fallax</i>	4.49 (0.67)	24.3 (13.6)	1.63 (1.29)	0.34 (0.19)	0.33 (0.22)	1.46 (0.71)	958 (246)	3.0 (2-4)	6 (16)	92
<i>papillosum</i>	4.40 (0.69)	17.9 (8.3)	1.16 (0.63)	0.29 (0.23)	0.28 (0.12)	1.15 (0.57)	948 (303)	3.3 (2-4)	6 (18)	23

fens and other groundwater outflows, as well as along streams and brooks.

Species of intermediate fen habitats (group 4)

These species occupy habitats of the highest trophicity almost exclusively within transitional mires. As with the species of the previous group, they often grow along streams and brooks as well as in spring outflows under a strong influence of flowing, mineral groundwater. These species occur over rather a broad pH range (3.8–7.1), but they are most prominent at a range of 4.8–6.6. At low pH (less than 4.6) these *Sphagna* are found very rarely. However, they are found at a very broad range of electrical conductivity, from as low as 19 to about 100 μS , with a wide range of Ca concentrations, being as low as 0.95 mg l⁻¹ and reaching nearly 10 mg l⁻¹. With the exception of *S. teres*, which is widespread and frequent, the remaining *Sphagna* are among the rare and very rare species in the mires studied. The species of this group prefer wet habitats, such as carpets.

Species of broad ecological amplitude (group 5)

This group comprises five species. These species show a considerable ecological amplitude in respect to water chemistry conditions. They are tolerant to acidic, ombrotrophic and poor fen to less acidic, intermediate fen conditions. The species of this group occur over a very broad pH range of 3.7–7.1, EC range of 6.0–98 μS and 0.30–9.4 mg l⁻¹ of Ca. However, they are most prominent under low pH (< 5.2) and low cation concentrations (EC < 40 μS and Ca concentrations < 3.0 mg l⁻¹). Two species of this group, *Sphagnum fallax* and *S. russowii*, are the most abundant and widespread in the Sudety mires. The species of this group mostly prefer carpets and lawns, with the exception of *S. angustifolium* and *S. russowii* which also grow on hummocks.

Gradient analysis and species distribution

The CCA was used to determine the main envi-

ronmental gradients and their effects on the distribution of the individual *Sphagnum* species. The highest eigenvalues were obtained for the first three CCA axes: 0.60, 0.53 and 0.38, respectively. These axes together accounted for 67% of the variation in the species–environment relationship. The results of Monte Carlo permutation tests were highly significant ($p = 0.002$) for both the test on the first axis and the test on all the axes. The species–environment correlations were also higher for the first three axes (0.87, 0.82 and 0.76). This means that these three axes are very well correlated with the environmental data and these variables explain a relatively high proportion of the species data along each axis.

Based on the intraset correlations, the first axis is defined by chemical variables of surface water, particularly by pH, EC and Ca; the second by the height of moss plants above the water level; and the third axis by altitude. Shade, Mg, K and Na are not highly correlated with either the first or second and third axes. Forward selection showed that among nine environmental variables, the height above the water level and pH, followed by altitude and conductivity (having the highest λ_A values, i.e. 0.52, 0.51, 0.36 and 0.24, respectively), appear to be the most important factors which explain the pattern of species composition. The effect of Ca, Mg, K and Na decreases because they are closely correlated ($p < 0.001$) with EC, as expected.

The distribution of *Sphagnum* species positioned around the origo seems not to be limited by water chemistry parameters. Species, such as *S. fallax*, *S. girgensohnii*, *S. angustifolium*, *S. russowii* and *S. papillosum*, are found throughout the water-chemistry gradient (Fig. 3a). These *Sphagna* were classified into group 5 as the species of a broad trophic amplitude (Fig. 2 and Table 2). Although *S. subnitens* and *S. riparium* are also ordered amongst these widespread species, they have true optima there and are not distinguished from the species of group 5 (ter Braak 1986). The same may hold for *S. lindbergii* which is situated in close proximity to *S. fallax* in the CCA ordination diagram. The *Sphagnum* species of groups 1 and 2 are arranged on the negative side of the first axis. These species are confined to low pH and conductivity as well as cation values that are associated

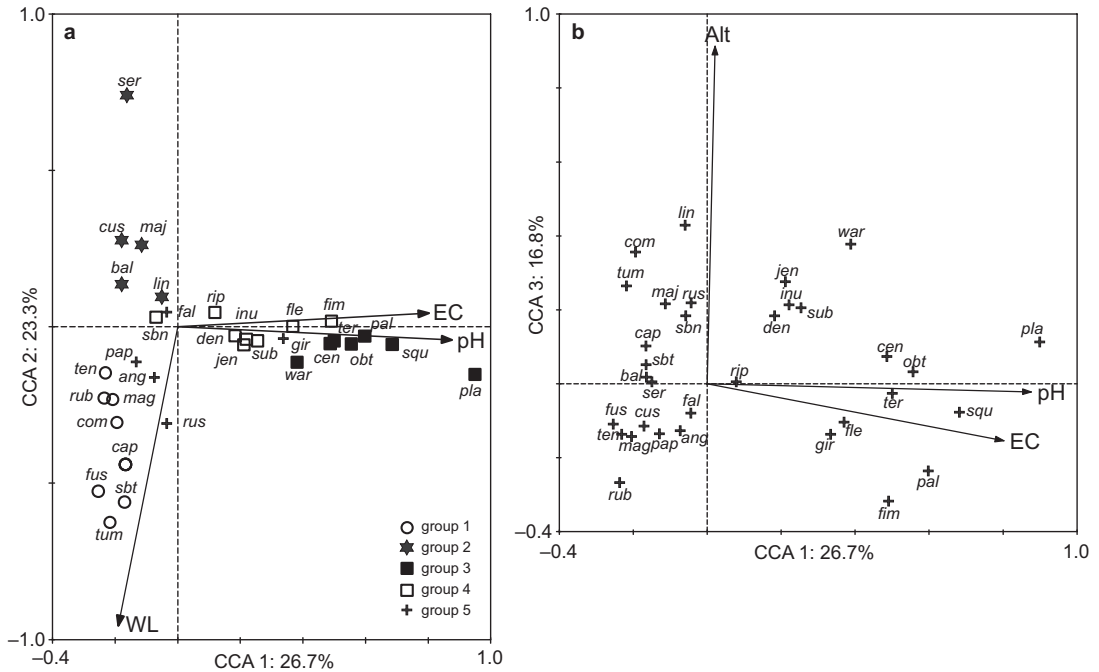


Fig. 3. CCA biplot ordination of *Sphagnum* species and variables for the Sudety Mountains. The environmental variables are denoted by arrows and their abbreviations are: WL = index of the height of moss plants above the water surface, EC = electrical conductivity, Alt = altitude. Species abbreviations are: ang = *angustifolium*, bal = *balticum*, cap = *capillifolium* var. *capillifolium*, cen = *centrale*, com = *compactum*, cus = *cuspidatum* var. *cuspidatum*, den = *denticulatum*, fal = *fallax*, fim = *fimbriatum*, fle = *flexuosum*, fus = *fuscum*, gir = *girgensohnii*, inu = *inundatum*, jen = *jensenii*, lin = *linbergii*, mag = *magellanicum*, maj = *majus*, obt = *obtusum*, pal = *palustre*, pap = *papillosum*, pla = *platyphyllum*, rip = *riparium*, rub = *rubellum*, rus = *russowii*, sbn = *subnites*, sbt = *subtile*, ser = *cuspidatum* var. *serrulatum*, squ = *squarrosum*, sub = *subsecudum*, ten = *tenellum*, ter = *teres*, tum = *capillifolium* var. *tenerum*, war = *warnstorffii*. For ecological groups of species in a see Fig. 2.

with ombrotrophic bog and poor fen habitats (Table 2). *Sphagna* having the highest negative values on the first axis, such as e.g. *S. tenellum*, *S. rubellum* and *S. fuscum*, were exclusively found in ombrotrophic habitats. Species having a somewhat broader trophic amplitude (e.g. *S. balticum*, *S. cuspidatum* and *S. majus*) which apart from ombrotrophic bogs were also found in poor fen habitats, are located closer to the 0 point of axis 1. There is some overlap between the species of groups 1 and 2. However, *Sphagna* of these two groups are dispersed along axis 2, indicating that they show distinct species pattern with respect to moisture gradient along this axis. Species, such as *S. capillifolium* var. *tenerum*, *S. fuscum* and *S. subtile*, found exclusively in the driest habitats, are positioned close to the negative end of that axis. *Sphagnum cuspidatum* var. *serrulatum*, occurring in the wettest habitats

(floating in water) is located at the opposite end of axis 2. Intermediate positions on the second axis are occupied by the species mostly found in lawns and dry carpets, e.g. *S. tenellum*, *S. papillosum* and *S. angustifolium* (Table 2).

The distribution of the *Sphagnum* species positioned on the positive side of the first axis is mostly limited by pH, EC and cation concentrations in surface waters. These species cover a wide portion of the water-chemistry gradient and are tightly grouped along axis 1. However, they occur in a relatively narrow range of the moisture gradient around 0 on axis 2. This indicates that moisture gradient is not an important factor limiting the distribution of these species, as they are mostly found in wet carpets. Species of group 4 are located at the right-hand-side end of axis 1. These *Sphagna* occurred almost exclusively in intermediate fen habitats (Fig. 2

and Table 2) having distinctly higher surface water pH, EC and cation concentrations than the remaining species in the mires studied. The exceptions are *S. squarrosum* and *S. teres* which are very rarely found in poor fens, although within this type of mire they prefer microhabitats with higher pH. *Sphagna* of group 3 have intermediate positions in the CCA biplot, between the species of group 5 and those of group 4. This indicates that these species, as compared with those of group 4, are generally found in habitats having lower pH and EC values. There is some overlap between groups 4 and 3. Species of the latter group covered a relatively wide portion of the minerotrophic part along the water-chemistry gradient. They are characterised by a quite broad tolerance of trophic conditions and are found not only in poor fen, but also extend into intermediate fen habitats. However, species of this group differ markedly in their ecological optima of the water-chemistry gradient. The position of each species relative to the 0 point on the first axis can be used to indicate this difference. *Sphagnum riparium*, which was most abundant in poor fen conditions, is positioned close to the 0 point. In contrast, *S. flexuosum*, which was decidedly more abundant in intermediate fen conditions, is located far to the right from the 0 point and close to the species of group 4.

Sphagnum species of the Sudety mires are clearly ordered from the bottom to the top of the ordination diagram along the third axis. This axis forms an altitudinal gradient (Fig. 3b and Table 2). Species, such as *S. lindbergii*, *S. warnstorffii*, *S. jensenii* and *S. compactum*, positioned at the upper end of the third axis, were mostly restricted in their occurrence to mires of the highest zone in the subalpine belt (1405–1430 m). Three species, namely *S. rubellum*, *S. fimbriatum* and *S. palustre*, are located at the opposite end of the third axis. This indicates that they occurred mostly at lower elevations, in the lower forest belt and foothills (635–830 m). Variation between most of the remaining species along the third axis exhibits clear tendencies based on their abundance along the altitudinal gradient. Thus, *S. cuspidatum*, *S. fallax*, *S. flexuosum*, *S. papillosum*, *S. tenellum*, *S. balticum*, *S. magellanicum*, *S. angustifolium*, *S. girgensohnii*, *S. squarrosum* and *S. riparium* are mostly

grouped on the negative side of the third axis. These species were most abundant below the upper forest limit and they became sporadic and sparse in the highest parts of the subalpine belt. *Sphagnum majus* and *S. russowii*, positioned on the positive side of axis 3, show the reverse pattern: they were more abundant in mires of the subalpine belt; however, they became less abundant below the upper forest limit. Less frequent species, e.g. *S. subtile*, *S. subnitens*, *S. centrale*, *S. obtusum* and *S. platyphyllum*, are difficult to assess for their altitudinal distribution pattern due to their rarity.

Discussion

Mire habitats

Sjörs (1950) recognised six major vegetation types correlated with the cation content and pH of surface waters in the mires of northern Sweden. These groups and corresponding pH ranges are as follows: bog or moss (3.7–4.2), extreme poor fen (3.8–5.0), transitional poor fen (4.8–5.7), intermediate fen (5.2–6.4), transitional rich fen (5.8–over 7.0) and extreme-rich fen (7.0–8.4). The pH ranges of *Sphagnum* stand groups in the Sudety Mts. (Table 1) are well comparable to Sjörs's mire types. The conformity is particularly apparent for groups 1 and 2 from the Sudety Mts., with bog and extreme poor fens, respectively. Although Sudety group 3 partly overlaps with transitional poor fen and intermediate fen, the majority of pH values (as indicated by lower and upper SD limits) are within the range of intermediate fens. Similar variation in chemistry along the bog–fen gradient with comparable ranges of pH and Ca were also reported from North America (Rydin and Jeglum 2006) and other parts of Europe (Tahvanainen *et al.* 2002, Tahvanainen 2004, Hájek *et al.* 2006).

Gradient analysis of *Sphagnum* species

The *Sphagnum* species in the mires studied demonstrate a variety of distributional patterns, with ecological amplitudes ranging from narrow to

broad, showing differences between species in the utilisation of habitat resources. Species of group 1 show the narrowest ecological amplitude of water chemistry variables, particularly pH, EC and Ca, being restricted mostly to ombrotrophic stands. Species of group 2 occupy broader ranges of water-chemistry gradients. This indicates that these species have slightly wider amplitudes of trophic conditions. In contrast, species of groups 3, 4 and 5, all reveal broad ecological amplitude along the water-chemistry gradient. However, they prefer different mire habitats (Fig. 2). Whereas *Sphagna* of group 4 are largely restricted to intermediate fen conditions, species of group 3 are also found in poor fen habitats. *Sphagna* of group 5 are the widest ranging and they are found throughout the ombrotrophic to intermediate fen conditions.

It is apparent that the distribution of *Sphagnum* species in the Sudety mires is mostly limited by three environmental factors: habitat moisture, altitude and surface-water chemistry (especially pH, electrical conductivity and calcium concentration). In ombrotrophic bogs, where *Sphagna* occur in narrow ranges of water chemistry parameters, moisture is the primary factor which controls the occurrence and distribution of species. In minerotrophic mires, where *Sphagna* usually occur in a relatively narrow range of habitat moisture, the distribution of species is mostly restricted by pH, conductivity and calcium concentration in water. These results are similar to those reported from other mires in Europe and North America. According to Vitt and Slack (1975), Vitt and Bayley (1984), Malmer (1986), Gignac (1992), Nicholson *et al.* (1996), Bragazza (1999), Tahvanainen (2004) and Andersen *et al.* (2011) four principal environmental gradients control the local distribution of mire bryophytes: ombrotrophic to minerotrophic, wet to dry, intensity of shade and local climate. Pakarinen and Ruuhijärvi (1978), Malmer (1985, 1986) and Økland (1990) also stressed a regional gradient in mire vegetation. However, several studies have shown that among these gradients, the ombrotrophic to minerotrophic and wet to dry are the most important factors affecting the distribution and abundance of *Sphagnum* species in mires (Vitt and Slack 1975, 1984, Vitt *et al.* 1975, Horton *et al.* 1979,

Clymo and Hayward 1982, Andrus 1986, Vitt *et al.* 1990, Gignac *et al.* 1991, Belland and Vitt 1995). The fact that the distribution of bryophytes in bogs is largely affected by factors other than water and peat chemistry has been reported by several authors. For example, Bragazza and Gerdol (1996) and Bragazza (1997, 1999), studying mires in the southern Alps, found that in oligotrophic conditions the moisture gradient is more important than the water-chemistry gradient in controlling the local distribution of individual *Sphagnum* species. Belland and Vitt (1995) showed that bryophyte vegetation patterns in continental bogs in western Canada are mainly determined by dryness, shade and, to a lesser extent, pH. Similarly, Karlin and Bliss (1984) noted that in mires of central Alberta the distribution of plant species (including *Sphagnum* mosses) in weakly minerotrophic peatlands results mainly from the peat moisture and biotic interactions. The data presented by Andrus *et al.* (1983), the comprehensive review by Rydin (1993) and Rydin and Jeglum (2006) also well illustrate the fact that in ombrotrophic mires with well-developed microtopography composed of hummocks (strings, peat mounds), lawns, hollows (depressions, pools), water table depth often plays much more important role in the *Sphagnum* species distributional pattern, than in fens, where such microtopography is generally lacking.

Sphagnum species of the Sudety mires are clearly ordered along an altitudinal gradient (Fig. 3b). *Sphagnum lindbergii*, *S. warnstorffii*, *S. jensenii* and *S. compactum* are mostly restricted in their occurrence to mires of the subalpine belt. Gerdol and Bragazza (1994) reported in mires of the southern Alps that *S. compactum* and *S. warnstorffii* are the only species whose prevalence increases with increasing elevation. Similarly, in the Swiss Alps, Feldmayer-Christe *et al.* (2001) stated that these two species mainly occur in the subalpine zone. However, *S. compactum* cannot be regarded as a mountain species, being common and widespread in lowland Europe (Daniels and Eddy 1985). In contrast, *S. warnstorffii* is more abundant in lowland and mountains of northern parts of Europe (subarctic and northern boreal zones), but further south, in central Europe it is mostly restricted to mountains

(Daniels and Eddy 1985, Hill *et al.* 1992). Three species of the Sudety mires, namely *S. rubellum*, *S. fimbriatum* and *S. palustre*, are located at the opposite end of the altitudinal gradient. This indicates that they occur mostly at lower elevations, in the lower forest belt and foothills. These species are also reported to occur mostly in the mountain belts below the upper forest limit in other European mountains (Gerdol and Bragazza 1994, Dierßen 2001, Feldmayer-Christe *et al.* 2001). Variation between most of the remaining species along the third axis exhibits clear tendencies based on their abundance along the altitudinal gradient. Thus, *S. cuspidatum*, *S. fallax*, *S. flexuosum*, *S. papillosum*, *S. tenellum*, *S. magellanicum*, *S. balticum*, *S. angustifolium*, *S. girgensohnii*, *S. squarrosum* and *S. riparium* are mostly grouped on the negative side of the third axis. These species are most abundant below the upper forest limit and they become sporadic and sparse in the highest parts of the subalpine belt. *Sphagnum majus* and *S. russowii*, positioned on the positive side of axis 3, show the reverse pattern: they are more abundant in mires of the subalpine belt, and they become less abundant below the upper forest limit. In mires of the Swiss Alps, Feldmayer-Christe *et al.* (2001) found that *S. cuspidatum*, *S. fallax*, *S. flexuosum*, *S. papillosum* and *S. magellanicum* show a somewhat limited altitudinal amplitude with half of the observations restricted to a range of about 400 m a.s.l.

However, as noted above, *Sphagnum* species composition in bogs differs regionally and most important are the differences between continental and oceanic areas (Pakarinen and Ruuhijärvi 1978, Malmer 1985, 1986, Rydin 1993). This is most apparent in the species sequence along a moisture gradient. In Canada, Horton *et al.* (1979) showed that the oceanic hollow-to-hummock sequence is *S. cuspidatum* to *S. rubellum* to *S. papillosum*, whereas in more continental areas of the Caribou Mountains, this *Sphagnum* sequence is replaced by the following: *S. jensenii* to *S. angustifolium* to *S. magellanicum*. Similarly, Malmer (1986) reported that in northwestern Europe the coastal oceanic hollow-lawn-hummock sequence, *S. cuspidatum* to *S. magellanicum* and *S. papillosum* to *S. rubellum*, is replaced in continental northeastern and boreal areas by

the sequence *S. lindbergii* and *S. majus* to *S. balticum* to *S. fuscum*. In ombrotrophic bogs of the Sudety Mts., hollows are dominated by *S. cuspidatum*, *S. lindbergii* and *S. majus*; for lawns *S. fallax*, *S. tenellum*, *S. compactum*, and sometimes *S. papillosum* and *S. angustifolium* are characteristic species, whereas *S. rubellum*, *S. magellanicum*, *S. angustifolium*, *S. russowii* and *S. fuscum* are most often found on hummocks. From a regional point of view the sequence of *Sphagnum* in the hollow to hummock series in Sudety bogs seems to be intermediate between continental and oceanic areas in Europe.

Acknowledgements: Sincere thanks are due to Prof. Aleksandra Samecka-Cymerman, Dr. Pekka Pakarinen and three anonymous reviewers for the critical proposals of the manuscript and helpful suggestions.

References

- Andersen R., Poulin M., Borcard D., Laiho R., Laine J., Vasander H. & Tuittila E.-T. 2011. Environmental control and spatial structures in peatland vegetation. *Journal of Vegetation Science* 22: 878–890.
- Andrus R.E. 1979. *Sphagnum subtile* (Russow) Warnst. and allied species in North America. *Systematic Botany* 4: 351–362.
- Andrus R.E. 1980. Sphagnaceae (peat moss family) of New York State. *New York State Museum Bulletin* 442: i–vi. 1–89.
- Andrus R.E. 1986. Some aspects of *Sphagnum* ecology. *Canadian Journal of Botany* 64: 416–426.
- Andrus R.E., Wagner D.J. & Titus J.E. 1983. Vertical zonation of *Sphagnum* mosses along hummock-hollow gradients. *Canadian Journal of Botany* 61: 3128–3139.
- Belland R.J. & Vitt D.H. 1995. Bryophyte vegetation patterns along environmental gradients in continental bogs. *Ecoscience* 2: 395–407.
- Bragazza L. & Gerdol R. 1996. Response surfaces of plant species along water-table depth and pH gradients in a poor mire on the southern Alps (Italy). *Annales Botanici Fennici* 33: 11–20.
- Bragazza L. 1997. *Sphagnum* niche diversification in two oligotrophic mires in the southern Alps of Italy. *The Bryologist* 100: 507–515.
- Bragazza L. 1999. Spatial patterns of plant species in poor mire in the Southern Alps (Italy). *Plant Biosystems* 133: 83–92.
- Brusa G. 2001. Il genere *Sphagnum* (Bryophyta) in provincia di Varese: fattori ecologici condizionanti la distribuzione. *Bollettino della Società ticinese di Scienze naturali* 89: 67–70.
- Chee W.L. & Vitt D. 1989. The vegetation, surface water chemistry and peat chemistry of moderate fens in central

- Alberta, Canada. *Wetlands* 9: 227–261.
- Clymo R.S. & Hayward P.M. 1982. The ecology of *Sphagnum*. In: Smith A.J.E. (ed.), *Bryophyte ecology*, Chapman & Hall, New York, pp. 229–289.
- Crum H.A. 1984. *Sphagnopsida, Sphagnaceae*. North American Flora, Series II, The New York Botanical Garden, New York.
- Daniels R.E. & Eddy A. 1985. *Handbook of European Sphagna*. Natural Environment Research Council, Institute of Terrestrial Ecology, Huntingdon.
- Dierßen K. 1983. Zur Verbreitung und Soziologie von *Sphagnum riparium* Ångstr. in Mitteleuropa. *Andrias* 2: 9–22.
- Dierßen K. 2001. *Distribution, ecological amplitude and phytosociological characterization of European bryophytes*. Bryophytorum Bibliotheca Band 56, J. Cramer, Berlin–Stuttgart.
- Feldmeyer-Christe E., Schnyder N. & Bisang I. 2001. Distributions and habitats of peat mosses, *Sphagnum*, in Switzerland. *Lindbergia* 26: 8–22.
- Gerdol R. & Bragazza L. 1994. The distribution of *Sphagnum* species along an elevational gradient in the southern Alps (Italy). *Botanica Helvetica* 104: 93–101.
- Gignac L.D. 1992. Niche structure, resource partitioning, and species interactions of mire bryophytes relative to climatic and ecological gradients in western Canada. *The Bryologist* 95: 406–418.
- Gignac L.D. 1993. Distribution of *Sphagnum* species, communities, and habitats in relation to climate. *Advances in Bryology* 5: 187–222.
- Gignac L.D. & Vitt D.H. 1990. Habitat limitations of *Sphagnum* along climatic, chemical, and physical gradients in mires of Western Canada. *The Bryologist* 93: 7–22.
- Gignac L.D., Vitt D.H., Zoltai S.C. & Bayley S.E. 1991. Bryophyte response surfaces along climatic, chemical, and physical gradients in peatlands of western Canada. *Nova Hedvigia* 53: 21–71.
- Hájek M., Hekera P. & Hájková P. 2002. Spring fen vegetation and water chemistry in the western Carpathian flysch zone. *Folia Geobotanica* 37: 205–224.
- Hájek M., Horsák M., Hájková P. & Dátě D. 2006. Habitat diversity of central European fens in relation to environmental gradients and an effort to standardise fen terminology in ecological studies. *Perspectives in Plant Ecology, Evolution and Systematics* 8: 97–114.
- Hill M.O., Preston C.D. & Smith A.J.E. (eds.) 1992. *Atlas of the Bryophytes of Britain and Ireland, volume 2. Mosses (except Diplolepidaceae)*. Harley Books, Colchester.
- Horton D.G., Vitt D.H. & Slack N.G. 1979. Habitats of circumboreal-subarctic sphagna: I. A quantitative analysis and review of species in the Caribou Mountains, northern Alberta. *Canadian Journal of Botany* 57: 2283–2317.
- Jeník J. & Soukupová L. 1992. Microtopography of sub-alpine mires in the Karkonoše Mountains, the Sudetes. *Preslia* 64: 313–326.
- Karlin E.F. & Bliss K.C. 1984. Variation in substrate chemistry along microtopographical and water-chemistry gradients in peatlands. *Canadian Journal of Botany* 62: 142–153.
- Kondracki J. 2009. *Geografia regionalna Polski*. PWN, Warszawa.
- Lepš J. & Šmilauer P. 2003. *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press, Cambridge.
- Malmer N. 1985. Remarks to the classification of mires and mire vegetation. Scandinavian arguments. *Aquilo, Serie Botanica* 21: 9–17.
- Malmer N. 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. *Canadian Journal of Botany* 64: 375–383.
- Migała K. 2005. *Piętra klimatyczne w górach Europy a problem zmian globalnych [Climatic belts in the European Mountains and the issue of global changes]*. Acta Universitatis Wratislaviensis 2718, Studia Geograficzne 78. [In Polish with English summary].
- Mirek Z., Piękoś-Mirkowa H., Zając A. & Zając M. 2002. *Flowering plants and pteridophytes of Poland. A checklist*. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.
- Miserere L., Montacchini F. & Buffa G. 2003. Ecology of some mire and bog plant communities in the Western Italian Alps. *Journal of Limnology* 62: 88–96.
- Nicholson B.J., Gignac L.D. & Bayley S.E. 1996. Peatland distribution along a north–south transect in the Mackenzie River Basin in relation to climatic and environmental gradients. *Vegetatio* 126: 119–133.
- Ochyra R., Żarnowiec J. & Bednarek-Ochyra H. 2003. *Census catalogue of Polish mosses [Katalog mchów Polski]*. Institute of Botany, Polish Academy of Sciences, Kraków. [In English with Polish summary].
- Otypková Z. & Chytrý M. 2006. Effects of plot size on the ordination of vegetation samples. *Journal of Vegetation Science* 17: 465–472.
- Økland R.H. 1990. Regional variation in SE Fennoscandian mire vegetation. *Nordic Journal of Botany* 10: 285–310.
- Pakarinen P. & Ruuhijärvi R. 1978. Ordination of northern Finnish peatland vegetation with factor analysis and reciprocal averaging. *Annales Botanici Fennici* 15: 147–157.
- Palmer M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* 74: 2215–2230.
- Raj A. 2001. *Karkonoski Park Narodowy*. “Mazury” Photographic and Publishing Agency, Jelenia Góra.
- Rydin H. 1993. Mechanisms of interactions among *Sphagnum* species along water-level gradients. *Advances in Bryology* 5: 153–185.
- Rydin H., Gunnarsson U. & Sundberg S. 2006. The role of *Sphagnum* in peatland development and persistence. In: Vitt D.H. & Wieder R.K. (eds.), *Boreal peatland ecosystems*, Ecological Studies vol. 188, Springer-Verlag, Berlin, pp. 49–65.
- Rydin H. & Jeglum J. 2006. *The biology of peatlands*. Oxford University Press, New York.
- Sjörs H. 1950. On the relation between vegetation and electrolytes in North Swedish mire waters. *Oikos* 2: 241–258.
- Slack N.G., Vitt D.H. & Horton D.G. 1980. Vegetation gradient of minerotrophically rich fens in western Alberta. *Canadian Journal of Botany* 58: 330–350.

- Tahvanainen T. 2004. Water chemistry of mires in relation to the poor-rich vegetation gradient and contrasting geochemical zones of the north-eastern Fennoscandian shield. *Folia Geobotanica* 39: 353–369.
- Tahvanainen T., Sallantausta T., Heikkilä R. & Tolonen K. 2002. Spatial variation of mire surface water chemistry and vegetation in northeastern Finland. *Annales Botanici Fennici* 39: 235–251.
- ter Braak C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167–1179.
- ter Braak C.J.F. & Šmilauer P. 2002. *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination. Version 4.5*. Microcomputer Power, Ithaca, NY.
- Vitt D.H. 2000. Peatlands: ecosystems dominated by bryophytes. In: Shaw A.J. & Goffinet B. (eds.), *Bryophyte Biology*, Cambridge University Press, pp. 312–343.
- Vitt D.H., Crum H. & Snider J.A. 1975. The vertical zonation of *Sphagnum* species in hummock–hollow complexes in northern Michigan. *The Michigan Botanist* 14: 190–200.
- Vitt D.H. & Slack N.G. 1975. An analysis of the vegetation of *Sphagnum*-dominated kettle-hole bogs in relation to environmental gradients. *Canadian Journal of Botany* 53: 332–359.
- Vitt D.H. & Bayley S. 1984. The vegetation and water chemistry of four oligotrophic basin mires in northwestern Ontario. *Canadian Journal of Botany* 62: 1485–1500.
- Vitt D.H. & Slack G. 1984. Niche diversification of *Sphagnum* relative to environmental factors in northern Minnesota peatlands. *Canadian Journal of Botany* 62: 1409–1430.
- Vitt D.H., Horton D.G., Slack N.G. & Malmer N. 1990. *Sphagnum*-dominated peatlands of the hyperoceanic British Columbia coast: patterns in surface water chemistry and vegetation. *Canadian Journal of Forestry Research* 20: 696–711.
- Wojtuń B. 2006. *Peat mosses (Sphagnaceae) in mires of the Sudetes Mountains (SW Poland): a floristic and ecological study*. Wydawnictwo Akademii Rolniczej, Wrocław.
- Wolejko L., Herbichowa M. & Potocka J. 2005. Typological differentiation and status of Natura 2000 mire habitats in Poland. In: Steiner G.M. (ed.), *Moore von Sibirien bis Feuerland*, Stapfia 85, zugleich Kataloge der OÖ, Landesmuseen Neue Serie 35, pp. 175–219.
- Zar H. 1999. *Biostatistical analysis*. Prentice Hall, Upper Saddle River, New Jersey.
- Zechmeister H.G. 1995. Ecology and distribution of *Sphagnum tenellum* (Brid.) Brid. and *S. compactum* DC in Austria. *Lindbergia* 20: 5–11.