

## Plant communities and environmental gradients in mires of the Ammergauer Alps (Bavaria, Germany)

### Pflanzengesellschaften und standörtliche Gradienten in Mooren der Ammergauer Alpen (Bayern, Deutschland)

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#### Abstract

In this study we present the plant communities, their abiotic site conditions and the main environmental gradients underlying variation in species composition of mire sites in three montane mires in the Northern Limestone Alps. For the phytosociological description of the mires we sampled species composition in 115 relevés. In order to characterize the site conditions of the most important plant communities we measured humification as well as water table depth, pH and electrical conductivity at 46 sites during a large part of the growing season. The main environmental gradients were identified by fitting environmental vectors and smoothed surfaces onto NMDS ordination. The most frequent communities on subneutral and neutral sites were the *Caricetum davallianae*, the *Amblystegio stellati-Caricetum dioicae* and the *Schoenetum ferruginei*, whereas acidic sites were mainly covered by the *Eriophoro-Trichophoretum cespitosi*. The most important factor for floristic variation between sites was pH. However, within bogs and fens, variation in species composition was mainly due to differences in water table depth.

**Keywords:** bog, Central Europe, fen, NMDS, poor-rich gradient, water table

**Erweiterte deutsche Zusammenfassung am Ende des Textes**

#### 1. Introduction

Ecological research on vegetational variation along environmental gradients in mires has mainly been carried out in Scandinavia (e.g. SJÖRS 1948, MALMER 1962a,b, 1986, TAHVANAINEN 2004, LAITINEN et al. 2008), North America (e.g. GLASER et al. 1990, VITT & CHEE 1990, VITT et al. 1995), Central Europe (e.g. GIES 1972, HÖLZER 1977, KAULE 1974, WAUGHMAN 1980, DIERBEN & DIERBEN 1984, SUCCOW & JOOSTEN 2001), Eastern Europe (e.g. HÁJEK et al. 2002, HÁJKOVÁ & HÁJEK 2003, 2004, ROZBROJOVÁ & HÁJEK 2009) and the Southern Alps (e.g. GERDOL 1995, BRAGAZZA et al. 1998, BRAGAZZA & GERDOL 1999a, b, 2002, MISERERE et al. 2003, GERDOL et al. 2010, 2011). The main focus of this research has

been on the niche differentiation of plant species and plant communities along gradients of water chemistry and water level, the relative importance of single gradients for compositional turnover, and where along these gradients the main floristic subdivisions occur (WHEELER & PROCTOR 2000, ØKLAND et al 2001, SJÖRS & GUNNARSSON 2002, HÁJEK et al. 2006). The four gradients considered to be of major importance are the *poor–rich gradient* (in a floristic sense), reflecting mainly differences in pH and base richness of the mire water and the peat (VITT & CHEE 1990, VITT et al. 1995, SJÖRS & GUNNARSSON 2002, BRAGAZZA et al. 2003, BRAGAZZA et al. 2005), the *water table gradient*, which is related to the microtopographical differentiation of the mire surface (SJÖRS 1948, ØKLAND 1990, NORDBAKKEN 1996a, b, BRAGAZZA & GERDOL 1996, SOTTOCORNOLA et al. 2009), the complex *mire margin–mire expanse gradient*, which is often paralleled by conspicuous physiognomic changes in mire vegetation (MALMER 1986, ØKLAND 1990, BRAGAZZA & GERDOL 1999a), and the *fertility gradient*, which is related to N and P availability and is sometimes supposed to be independent from the poor-rich gradient (WHEELER & PROCTOR 2000; but see ØKLAND et al. 2001, RYDIN & JEGLUM 2006).

Regarding the Northern Limestone Alps, only little is known about the local mires (KAULE 1974, 1976) despite the large variety of hydrological, morphological and ecological mire types that can be found in this geological and topographical diverse landscape (RINGLER 1978, 1981, SASS et al. 2010). Road construction and an increasing number of visitors in the Alps constitute potential threats to montane and alpine environments and mires (RINGLER 1981, RADEMACHER 2006, LANVERS et al. 2012). However, mire conservation and simultaneously a sustainable development of the mountain landscape are possible but this would require an ecological understanding of the local mires.

Therefore, the aims of the present study are to investigate in detail the plant communities of high altitude-mires in the German part of the Northern Limestone Alps and their abiotic site conditions, as well as the main environmental gradients related to variation in species composition between mire sites. We present a simple but broad spectrum of site-specific parameters in order to contribute to a better understanding of the relationship between site factors and vegetation in montane mires of the Alps.

## 2. Methods

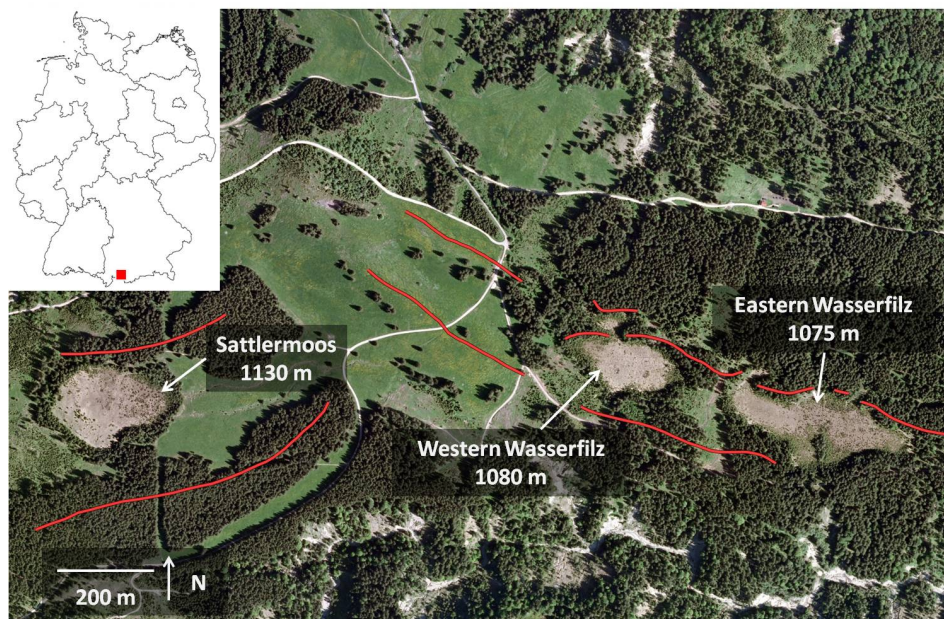
### 2.1 Study area

The study was conducted at three mires (Table 1) situated directly at the morphological fringe of the Alps in the “Ammergau Alpen”, a mountain range in the north-western part of the Northern Limestone Alps (Fig. 1). The climate is cool-temperate and slightly suboceanic with a high mean annual precipitation of 1750 mm that peaks during the summer months. Mean annual temperature is 5 °C, with a mean temperature of the warmest month (July) of 14 °C and -4 °C of the coldest month (January).

**Table 1.** Location of the mires investigated.

**Tabelle 1.** Lage der untersuchten Moore.

Mire	Abbrev.	Altitude	Northing	Easting	Size	Tubes
Sattlermoos	Sa	1130 m	47°36'4''	10°48'41''	3.4 ha	28
Western Wasserfilz	WW	1080 m	47°36'7''	10°49'30''	2.2 ha	12
Eastern Wasserfilz	EW	1075 m	47°36'4''	10°49'48''	3.8 ha	6



**Fig. 1.** Location of the study area in the Ammergauer Alps (digital orthophoto: BAYERISCHE VERMESSUNGSVERWALTUNG). Red lines indicate glacial moraines bordering the mires.

**Abb. 1.** Lage des Untersuchungsgebietes in den Ammergauer Alpen (digitales Orthofoto: BAYERISCHE VERMESSUNGSVERWALTUNG). Rote Linien zeigen den Verlauf der Moränenwälle, die die Moore begrenzen.

Climatic parameters were estimated using data from the nearest weather stations available provided by Deutscher Wetterdienst and assuming an increase in precipitation of 100 mm per 100 m (ELLENBERG & LEUSCHNER 2010), a decrease in temperature of 0.6 K per 100 m (KÖRNER 2003), and an average altitude of the study area of 1100 m. The underlying bedrock is basal till (Sattlermoos) and glacialfluvial gravel (Western and Eastern Wasserfilz). Along their northern and southern margins, the mires are flanked by glacial moraines consisting mainly of dolomite and limestone (HÖFLE & KUHNERT 1969, KUHNERT & OHM 1974). The Sattlermoos is a complex mire in saddle position with a sloping fen in its southwestern part that merges into an almost ombrogenous eastern part with a sloping margin. The Western and Eastern Wasserfilz are saddle mires with sloping margins at their western and eastern margins and consist mainly of bog vegetation. Therefore, we studied the two most frequent topographic mire types in the Northern Limestone Alps (RINGLER 1981). According to a local farmer and palynological and mire stratigraphical data by BLUDAU (1985), the mires have never been used for agriculture. The mires are currently in a near-natural state, but occasional browsing by wildlife was observed.

## 2.2 Vegetation sampling

Data on species composition was sampled in 115 plots in 2011. Plot size was 1 m<sup>2</sup> with the exception of forests and shrub communities. The latter were sampled in floristic homogenous plots of varying size, sufficient to gain a representative sample of the community. A plot size of 1 m<sup>2</sup> has also been used in previous fundamental studies of mire vegetation in southern Central Europe and the Alps (KAULE 1974, DIERBEN & DIERBEN 1984, STEINER 1992, LEDERBOGEN 2003), of which the first three studies represent the backbone of established phytosociological classifications of respective vegetation types (STEINER 1993a, b, DIERBEN 1998). We are in line with these authors that a plot size of 1 m<sup>2</sup> is suffi-

cient to picture the topographical structure of mire surfaces as well as the species composition of non-woody sites and therefore provide data that are easily comparable with existing relevés from surrounding regions. Species abundance was estimated according to REICHELT & WILMANN (1973) for the phytosociological data analysis (chapter 2.4). For the purposes of ordination, cover was also estimated according to a semi-quantitative scale (PFADENHAUER 1997): > 0–1%, 1–3%, 3–5%, 5–15%, 15–25%, 25–50%, 50–75%, and 75–100%. In addition, we estimated cover of trees (> 5 m), shrubs (0.5–5 m), ground, litter and moss layer. We followed WISSKIRCHEN & HAEUPLER (1998) for the nomenclature of ferns and flowering plants (except *Melampyrum pratense* subsp. *paludosum* (Gaud.-B.) Ronn, *Pinus mugo* Turra and *Pinus rotundata* Link), WIRTH (1995) for lichens, and FRAHM & FREY (2004) for mosses and liverworts (except *Drepanocladus cossonii* (Schimp.) Loeske, *Hamatocaulis vernicosus* (Mitt.) Hedenäs and the genus *Sphagnum*, which follows HÖLZER (2010)).

### 2.3 Environmental variables

In May 2011 we inserted 46 perforated plastic tubes that were positioned subjectively at selected locations to cover the most frequent mire sites and communities. Von Post humification (H) (VON POST 1922) of the peat was determined after drilling the hole for the tubes. Water table depth (WTD), water pH and water electrical conductivity (EC) were measured in regular intervals at six dates between early June and early September 2011. Reference point for WTD measurements was the soil surface beneath the moss and the litter layer or, in *Sphagnum*-rich stands, the capitula of the peat mosses. Water pH and EC were measured in the field with portable instruments with automatic temperature compensation for 25 °C. The pH value is a measure of acidity whereas EC is a measure of the ionic concentration and both show a strong correlation with Ca and Mg concentrations of the mire water (SJÖRS & GUNNARSSON 2002, HÁJEK et al. 2002). Chemical data from 15 tubes is missing for the last day due to a defective pH meter. Electrical conductivity was not corrected for hydrogen ions because this partially led to negative values at low pH and indicates that some of the measured pH values are probably too low, what can be attributed to strong differences in cation concentrations between the acidic mire water samples and the calibration solution (see also SJÖRS 1950). We abstained from calculating theoretical pH values and present uncorrected raw data for both, pH and EC (see also DIERBEN & DIERBEN 1984). Verbal descriptions of mire sites with respect to their acidity given in the text are based on the classification by SUCCOW & JOOSTEN (2001)

**Table 2.** Assignment of pH values to classes (SUCCOW & JOOSTEN 2001). Unit boundaries were increased by 0.5 in order to compensate for the different dilutions in which pH was measured (ROWELL 1997).

**Tabelle 2.** Einteilung von pH-Werten in Klassen (SUCCOW & JOOSTEN 2001). Die Grenzen der Einheiten wurden um 0,5 erhöht um Unterschiede durch die Messreagenzien zu kompensieren (ROWELL 1997).

pH	Class	Verbal description
< 2.9	acidic	extremely acidic
2.9 – 3.7	acidic	very strongly acidic
3.7 – 4.5	acidic	strongly acidic
4.5 – 5.3	acidic	moderately acidic
5.3 – 6.1	subneutral	weakly acidic
6.1 – 6.9	subneutral	very weakly acidic
6.9 – 7.7	(alkaline)	neutral
> 7.7	calcareous	base rich

(Table 2) of which we increased the unit boundaries by 0.5 (ROWELL 1997) in order to compensate for the different dilutions in which pH was measured (pH<sub>KCl</sub> in SUCCOW & JOOSTEN 2001). As a measure of the extent and frequency of water table fluctuations, we also calculated the groundwater fluctuation index WI (SCHOLLE & SCHRAUTZER 1993) using the formula

$$WI = \frac{XS \cdot |(G_{\min} - G_{\max})|}{M} \cdot A_p$$

where XS is the sum of absolute differences in WTDs between each pair of sampling dates divided by the total number of sampling dates,  $G_{\min}$  is the minimum and  $G_{\max}$  the maximum WTD, respectively, M is the whole time period within which the measurements were done in days, and  $A_p$  is the number of pairs of sampling dates between which the fluctuation of WTD was higher than XS in percent of all sampling dates. Following LEDERBOGEN (2003), the obtained values were assigned to five classes (Table 3). As we did not measure water nutrient contents or biomass production directly, we calculated weighted mean Ellenberg indicator values for N (ELLENBERG et al. 1992) for each site with cover values of ferns and flowering plants as weights, and used them as a measure of site fertility. This is possible because it has been demonstrated that Ellenberg N is a good and even better predictor of biomass production (which reflects site fertility) rather than of soil N content (MELMAN et al. 1988, HILL & CAREY 1997, SCHAFFERS & SÝKORA 2000). In the phytosociological tables, values for all variables were rounded to one decimal place, except EC values > 100  $\mu\text{S cm}^{-1}$ , which were rounded to the next integer.

**Table 3.** Assignment of groundwater fluctuation indices to classes (LEDERBOGEN 2003).

**Tabelle 3.** Einteilung von Wechselfeuchte-Indices in Klassen (LEDERBOGEN 2003).

Groundwater fluctuation index	Groundwater fluctuation class	Verbal description
0 – 10	I	no fluctuation
10 – 50	II	little fluctuation
50 – 100	III	fluctuation
100 – 150	IV	large fluctuation
150 – 200	V	very large fluctuation

## 2.4 Phytosociological classification

Vegetation relevés were grouped and assigned to existing phytosociological units following the BRAUN-BLANQUET (1964) approach. Consideration of species as character or differential species of phytosociological units follows STEINER (1992, 1993a, b), DIERBEN (1998), SEIBERT (1992) and OBERDORFER (2001). Relevés were assigned to existing units based on the presence, cover and number of respective character and differential species. That means, if e.g. character species of two associations were present, we assigned the relevé to the association of the more abundant species. Furthermore, groups of differential species that are valid for the study area could be identified in some cases and were used for the delineation of phytosociological units as well. We followed STEINER (1992, 1993a) for the nomenclature and subdivision of the *Phragmitetea* Tx. & Preising 1942 and the *Scheuchzerio-Caricetea fuscae* Tx. 1937, with the exception of the *Caricetum fuscae* Br.-Bl. 1915; DIERBEN (1998) and STEINER (1992, 1993b) for the *Oxycocco-Sphagnetetea* Br.-Bl. et Tx. 1943, and SEIBERT (1992) for the *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939.

## 2.5 Ordination

In order to find patterns of floristic variation among sites, species data was subjected to Nonmetric Multidimensional Scaling (NMDS; MINCHIN 1987). Prior to analysis, cover values were transformed to the midpoints of the corresponding cover classes. The effect of high cover values was reduced by square root transformation and subsequent Wisconsin double standardization. We used a Bray-Curtis distance matrix, because it generally shows a good rank order relationship with environmental distance (FAITH et al. 1987). The final ordination was run with several random starts and used two dimensions. We fitted linear trends (environmental vectors) for H, WI, and the median values of WTD, pH and EC onto the ordination, and assessed their significance with 999 permutations. As there may be a non-linear relationship between these variables and ordination space, we used generalized additive models with thin plate splines (WOOD 2003) to fit smoothed surfaces onto the ordination. Generalized cross-validation was used to estimate the degree of smoothness. The coefficient of determination ( $R^2$ ) is higher for surfaces when there is a non-linear relationship with the ordination result. Otherwise, the surface will form a plane and  $R^2$  will be equal for the surface and the environmental vector (see also VIRTANEN et al. 2006). We also produced environmental vectors and smoothed surfaces for Ellenberg N, but abstained from significance testing for this variable because it already inherits information on compositional dissimilarity between sites and therefore relationships with ordination results would be overestimated (ZELENÝ & SCHAFFERS 2012). Environmental data from one site (*Caricetum fuscae sphagnetosum flexuosi*; chapter 3.4) was excluded from the ordination because it apparently was influenced by peat extraction. The ordination was carried out using the vegan package (OKSANEN et al. 2012) in the R statistical language (R CORE TEAM 2012) and surfaces were produced with function “ordisurf” in vegan. The R code as well as the vegetation and the environmental data are available in the electronic appendix S1.

## 3. The plant communities and their abiotic site conditions

### 3.1 Tall-sedge communities (*Magnocaricion elatae* W. Koch 1926, Table 4)

The *Caricetum elatae* W. Koch 1926 (column 1) was only found once in the lagg fen of the Western Wasserfilz and showed fluctuations of the water table of > 40 cm. One stand of the *Caricetum paniculatae* Wangerin ex von Rochow 1951 (columns 2–4) had a non-fluctuating water table with a median WTD of -12.5 cm. The site had a median pH of 7.2 and a median EC of 217  $\mu\text{S cm}^{-1}$ . Being structurally and environmentally similar to the above mentioned communities, we also assigned stands dominated by *Carex elongata* (*Carex elongata*-community; columns 5 and 6) to the *Magnocaricion elatae*.

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**Foot of table 4 (next page):**

**Fuß von Tabelle 4 (nächste Seite):**

Only once and abundance < 2a in **1:** *Deschampsia cespitosa* subsp. *cespitosa* r, *Drepanocladus polycarpus* l, *Dryopteris carthusiana* +. **2:** *Agrostis stolonifera* l, *Aster bellidiflorus* +, *Cirsium palustre* +, *Galium mollugo* +, *Juncus effusus* r, *Lysimachia nemorum* r. **3:** *Cirsium oleraceum* r, *Climacium dendroides* l, *Cratoneuron decipiens* l, *Crepis paludosa* +, *Galium uliginosum* r, *Ranunculus montanus* r, *Veratrum album* subsp. *lobelianum* r. **4:** *Calliargon giganteum* 2m, *Mentha aquatica* l, *Molinia caerulea* r. **5:** *Calliargon cordifolium* l. **6:** *Aneura pinguis* l, *Carex echinata* +, *Epilobium obscurum* +, *Equisetum palustre* r, *Ranunculus repens* +, *Rhytidadelphus squarrosus* l, *Senecio alpinus* r, *Silene flos-cuculi* +.

**Table 4.** Relevés of the *Magnocaricion elatae* from the Ammergauer Alps.

**Tabelle 4.** Aufnahmen des *Magnocaricion elatae* aus den Ammergauer Alpen.

1 = Caricetum elatae, 2 = Caricetum paniculatae, 3 = Carex elongata-Community						
Association/Community	1	2			3	
Column	1	2	3	4	5	6
Mire	WW	Sa	Sa	WW	WW	EW
Plot size (m <sup>2</sup> )	1	1	1	1	1	1
Exposition	-	E	-	-	-	W
Slope (°)	-	5	-	-	-	1
Height herb layer (cm)	100	80	100	60	55	50
Cover herb layer (%)	95	90	95	80	95	90
Cover moss layer (%)	1	15	20	95	2	20
Cover litter layer (%)	95	60	15	2	90	1
Median WTD (cm)	-	-12,5	-	-	-	-
WI	-	3,9	-	-	-	-
Median pH	-	7.2	-	-	-	-
Median EC (µS cm <sup>-1</sup> )	-	217	-	-	-	-
Species no.	8	18	26	16	11	20
<b>CA 1</b>						
Carex elata	5	.	.	.	.	.
<b>CA 2</b>						
Carex paniculata	.	4	4	3	.	.
<b>CA 3</b>						
Carex elongata	.	.	.	.	5	2b
<b>A-O-C</b>						
Galium palustre subsp. palustre	1	r	1	+	1	1
Equisetum fluviatile	.	.	.	+	.	.
<b>Scheuchzerio-Caricetea fuscae</b>						
Viola palustris	.	+	.	2b	+	2a
Valeriana dioica	.	+	1	2a	.	.
Carex panicea	.	.	+	1	.	.
Potentilla palustris	.	.	.	.	2a	2b
Carex rostrata	.	.	.	.	+	2b
Agrostis canina	.	.	.	.	1	+
Carex nigra	.	.	.	.	+	+
Menyanthes trifoliata	.	.	.	2a	.	.
<b>Molinio-Arrhenateretea</b>						
Myosotis scorpioides subsp. scorpioides	+	+	+	+	1	1
Caltha palustris	r	.	+	2a	2a	2a
Festuca rubra	.	1	2a	+	.	.
Cardamine pratensis	.	.	+	1	1	.
Geum rivale	.	.	2b	r	.	.
Succisa pratensis	.	.	2b	.	.	.
Mentha longifolia	.	.	2b	.	.	.
Bistorta officinalis	.	.	2a	.	.	.
Primula elatior	.	2a	.	.	.	.
<b>Others</b>						
Equisetum sylvaticum	+	r	r	.	.	+
Plagiomnium elatum	.	2a	1	5	.	.
Calliergonella cuspidata	.	1	2m	.	.	2a
Chaerophyllum hirsutum subsp. hirsutum	.	2b	+	.	.	.
Potentilla erecta	.	1	1	.	.	.
Mentha arvensis	.	.	1	.	.	1
Plagiomnium cuspidatum	.	.	2a	.	.	.

### 3.2 Mire pools and hollows (*Rhynchosporion albae* W. Koch 1926)

#### 3.2.1 *Caricetum limosae* Osvald 1923 (Table 5 in the Beilage, columns 1–8)

This association occurs in hollows and pool edges with low site productivity along a wide range of pH and EC values in bogs and fens and therefore includes floristically heterogeneous stands (DIERBEN & REICHEL 1988, STEINER 1992, DIERBEN & DIERBEN 2008). The subassociation of *Scorpidium scorpioides* (columns 1–4; Fig. 2) grew in shallow fen pools with median WTD between +3.5 and +13 cm and no fluctuation of the water table. Sites were subneutral with median pH values between 5.7 and 6.5 and median EC values between 131 and 379  $\mu\text{S cm}^{-1}$ . The subassociation of *Sphagnum fallax* in the variant of *Sphagnum flexuosum* (column 5) was recorded only once in the acidic lagg fen of the Eastern Wasserfilz. Peat thickness at this site was 60 cm. The subassociation of *Sphagnum cuspidatum* (columns 6–8) had a median WTD of +1.5 cm on average with little to no fluctuation. Sites were strongly acidic with median pH 4.4. Median EC was 18.1 and 18.6  $\mu\text{S cm}^{-1}$ , respectively.



**Fig. 2.** Vegetation patterning in the Sattlermoos fen: In the foreground a pool with the *Caricetum limosae scorpidietosum*, behind that the *Caricetum dioicae* with tussocks of *Trichophorum cespitosum*, in the middle ground (brownish) the *Schoenetum ferruginei* and more upslope (brighter) in the background, the *Caricetum davallianae* (Photo: P. Stojakowits).

**Abb. 2.** Vegetationsgliederung im Flachmoorbereich des Sattlermooses: Im Vordergrund eine Schlenke mit dem *Caricetum limosae scorpidietosum*, dahinter das *Caricetum dioicae* mit Horsten von *Trichophorum cespitosum*, im Mittelgrund (bräunlich) das *Schoenetum ferruginei* und hangaufwärts im Hintergrund (heller) das *Caricetum davallianae* (Photo: P. Stojakowits).



### **3.2.2 *Sphagno tenelli-Rhynchosporetum albae* Oswald 1923 (Table 5 in the supplement, columns 9–17)**

The *Sphagno tenelli-Rhynchosporetum albae* occurred in slightly drier hollows. *Carex limosa* and *Scheuchzeria palustris* achieved low abundance or were absent from the communities. Instead, *Rhynchospora alba* was abundant in the herbaceous layer, sometimes accompanied by a second character species of this association, *Lycopodiella inundata*. In addition, this community was differentiated by some hummock and lawn species, and *Gymnocolea inflata* and *Trichophorum cespitosum* subsp. *cespitosum* were more prominent within these communities. Water table showed little to no fluctuation and median WTD ranged between -5 and -2.5 cm. Sites were strongly acidic with median pH between 4.3 and 4.5; median EC was 16–28  $\mu\text{S cm}^{-1}$ , indicating ombrotrophic to slightly minerotrophic conditions.

### **3.3 Mire communities of transitional mire sites (*Caricion lasiocarpae* Vanden Berghen in Lebrun et al. 1949, Table 6)**

The *Caricetum rostratae* Oswald 1923 (columns 1–2) unites floristically and structurally very heterogeneous communities (STEINER 1992). Thus, the relevés of this association had only few species in common, although both were recorded in lagg fens. Its subdivision was determined by the dominant mosses (STEINER 1992). The *Amblystegio scorpioidis-Caricetum diandrae* Oswald 1923 (column 3) was found in a wet lagg fen. *Hamatocaulis vernicosus* was the dominant bryophyte in the moss layer and allowed the assignment to the corresponding subassociation.

#### **3.4 Small-sedge poor fens (*Caricion fuscae* W. Koch 1926)**

Because of the carbonaceous bedrock, sedge dominated fen communities typical for sites with low amounts of basic cations (*Caricion fuscae*) are scarce in the study area and are only represented by a few stands of the *Caricetum fuscae* Br.-Bl. 1915 (Table 7).

One stand of the subassociation of *Sphagnum flexuosum* was found on a floating mat with no fluctuation of the water table and a median WTD of -1.3 cm. The mire water was moderately acidic with median pH 5.2 and showed a median EC of 21.6  $\mu\text{S cm}^{-1}$ . However, as this floating mat occurred in a small pool that apparently had been cut, care has to be taken concerning the interpretation of measured environmental variables. We therefore excluded these variables from the ordination (chapter 4).

The subassociations of *Sphagnum fallax* and *S. angustifolium* (columns 1 and 5) were only found once, adjacent to sloping bog margins. The facies of *Sphagnum centrale* (column 6) occurred close to a glacial moraine that supplies this mire site with more alkaline and nutrient rich ground water.

#### **3.5 Small-sedge rich fens (*Caricion davallianae* Klika 1934)**

##### **3.5.1 *Amblystegio stellati-Caricetum dioicae* Oswald 1925 (Table 8)**

Because of environmental and floristic overlaps with the *Caricetum fuscae* on base-poor sites on the one hand, and with the *Caricetum davallianae* Dutoit ex Koch 1928 on base-rich sites on the other hand, as well as because of its floristic heterogeneity, there are general problems with the delineation, synsystematic placement and naming of the *Amblystegio stellati-Caricetum dioicae* (see DIERBEN 1982, STEINER 1992, 1993a, WITTIG 1999).

**Table 6.** Relevés of the *Caricion lasiocarpae* from the Ammergauer Alps.

**Tabelle 6.** Aufnahmen des *Caricion lasiocarpae* aus den Ammergauer Alpen.

Association: 1 = Caricetum rostratae, 2 = Amblystegio scorpioidis-Caricetum diandrae			
Subassociation: 1 = Calliergon cordifolium, 2 = typical, 3 = Hamatocaulis vernicosus			
Association	1		2
Subassociation	1	2	3
Column	1	2	3
Mire	WW	EW	WW
Plot size (m <sup>2</sup> )	1	1	1
Exposition	-	ESE	-
Slope (°)	-	2	-
Height herb layer (cm)	65	60	35
Cover herb layer (%)	60	100	45
Cover moss layer (%)	85	10	80
Cover litter layer (%)	10	5	2
Species no.	7	20	21
<b>CA 1</b>			
Carex rostrata	3	3	.
<b>CA 2</b>			
Carex diandra	.	+	2a
<b>d SA 1</b>			
Calliergon cordifolium	5	.	.
<b>d SA 3</b>			
Hamatocaulis vernicosus	.	.	4
<b>A-O-C</b>			
Potentilla palustris	2a	2a	1
Menyanthes trifoliata	.	.	2b
Carex echinata	.	.	+
Viola palustris	.	1	1
Carex nigra	.	2a	.
Carex limosa	.	.	2a
Calliergon giganteum	.	.	2b
<b>Others</b>			
Galium palustre subsp. palustre	+	1	+
Plagiomnium elatum	.	2a	2m
Caltha palustris	+	2b	.
Equisetum fluviatile	.	r	r
Mentha arvensis	.	2a	.
Ranunculus aconitifolius	.	2a	.
Bistorta officinalis	.	2a	.
Potentilla erecta	.	.	+

Only once and abundance < 2a in **1**: *Agrostis canina* 1, *Equisetum sylvaticum* r. **2**: *Valeriana dioica* +, *Agrostis stolonifera* 1, *Ranunculus repens* +, *Crepis paludosa* r, *Myosotis scorpioides* subsp. *scorpioides* 1, *Silene flos-cuculi* +, *Lysimachia nemorum* 1, *Stellaria alsine* 1. **3**: *Carex panicea* +, *Bryum pseudotriquetrum* 1, *Pedicularis palustris* subsp. *palustris* 1, *Aneura pinguis* 1, *Carex flava* +, *Parnassia palustris* 1, *Cardamine pratensis* 1, *Calliergonella cuspidata* 1, *Molinia caerulea* 1.

**Table 7.** Relevés of the *Caricetum fuscae* from the Ammergauer Alps.

**Tabelle 7.** Aufnahmen des *Caricetum fuscae* aus den Ammergauer Alpen.

1 = Sphagnum fallax, 2 = Sphagnum flexuosum, 3 = Sphagnum angustifolium, 4 = facies of Sphagnum centrale						
Subassociation/facies	1	2			3	4
Column	1	2	3	4	5	6
Mire	EW	WW	EW	EW	EW	EW
Plot size (m <sup>2</sup> )	1	1	1	1	1	1
Exposition	NNE	-	W	ESE	-	S
Slope (°)	3	-	4	5	-	5
Height herb layer (cm)	30	50	35	30	50	40
Cover herb layer (%)	35	40	40	60	60	35
Cover moss layer (%)	100	100	98	90	100	100
Cover litter layer (%)	0,2	1	3	0,2	1	1
Median WTD (cm)	-	-1,3	-	-	-	-
WI	-	1,1	-	-	-	-
Median pH	-	5,2	-	-	-	-
Median EC (µS cm <sup>-1</sup> )	-	21,6	-	-	-	-
Species no.	11	6	13	10	22	22
<b>CA</b>						
Carex nigra	.	+	2a	+	.	r
Viola palustris	.	.	+	.	2b	1
Agrostis canina	.	.	2a	.	1	1
Carex echinata	1	.	.	2a	1	1
Carex canescens	.	r	.	.	.	.
<b>d SA 1</b>						
Sphagnum fallax	5	.	.	.	.	.
<b>d SA 2</b>						
Sphagnum flexuosum	.	5	4	4	.	.
<b>d SA 3</b>						
Sphagnum angustifolium	.	.	.	2b	5	2m
<b>d SA 4</b>						
Sphagnum centrale	.	.	3	.	.	5
<b>A-O-C</b>						
Carex rostrata	+	2a	1	+	+	1
Menyanthes trifoliata	2b	3	+	3	2a	2b
Calliergon stramineum	.	.	1	.	2m	1
Scheuchzeria palustris	+	.	.	.	1	.
Eriophorum angustifolium	.	.	.	+	+	.
<b>Others</b>						
Potentilla erecta	1	.	r	.	2a	1
Equisetum palustre	r	.	r	.	1	r
Molinia caerulea	1	.	.	1	1	2a
Anthoxanthum odoratum	.	.	.	.	1	1
Bistorta officinalis	.	.	2b	.	.	.
Vaccinium oxycoccus	1	.	.	+	1	.
Equisetum fluviatile	r	.	.	.	+	.
Aulacomnium palustre	.	.	.	.	+	+
Dactylorhiza fuchsii subsp. fuchsii	r	.	.	.	+	.

Only once and abundance < 2a in **2**: Galium palustre subsp. palustre +. **3**: Senecio ovatus subsp. ovatus r, Stellaria alsine l. **4**: Eriophorum vaginatum +. **5**: Drosera rotundifolia l, Nardus stricta +, Rhynchospora alba +, Succisa pratensis +, Trichophorum cespitosum subsp. cespitosum r. **6**: Carex limosa r, Lysimachia nemorum +, Plagiochloa asplenioides l, Rhytidiadelphus squarrosus l, Rhytidiadelphus subpinnatus l, Sphagnum magellanicum l, Sphagnum warnstorffii l, Willemetia stipitata +.

The typical facies (columns 1–3) is characterized by a mix of acidity indicating species from the *Caricion fuscae* and the *Oxycocco-Sphagnetea* with more base demanding species. The occurrences of the character species *Carex pulicaris* and other basiphytic species differentiated these communities against the floristically similar *Caricetum fuscae* (STEINER 1992, 1993a). We found this facies in the Eastern Wasserfilz where it occurred in a fen beneath the poorly developed marginal slope of the ombrotrophic part of the mire, from which it receives some acidic discharge.

**Table 8.** Relevés of the *Amblystegio stellati-Caricetum dioicae* campylietosum from the Ammergauer Alps.

**Tabelle 8.** Aufnahmen des *Amblystegio stellati-Caricetum dioicae* campylietosum aus den Ammergauer Alpen.

Facies	typical			Trichophorum cespitosum				Trichophorum alpinum			
	1	2	3	4	5	6	7	8	9	10	11
Column											
Mire	EW	EW	EW	Sa	Sa	Sa	Sa	WW	WW	WW	WW
Plot size (m <sup>2</sup> )	1	1	1	1	1	1	1	1	1	1	1
Exposition	N	SSE	E	N	N	N	N	N	N	N	-
Slope (°)	3	3	1	5	5	2	2	1	1	1	-
Height herb layer (cm)	30	50	35	25	35	20	25	40	25	25	20
Cover herb layer (%)	90	90	80	70	60	70	45	75	65	80	60
Cover moss layer (%)	60	80	90	90	100	90	95	50	50	5	65
Cover litter layer (%)	40	5	1	15	10	45	80	80	75	75	90
Median WTD (cm)	-	-	-	-	-	-	-	-5,5	-6	-	-
WI	-	-	-	-	-	-	-	13	17,6	-	-
Median pH	-	-	-	-	-	-	-	5,7	6	-	-
Median EC (µS cm <sup>-1</sup> )	-	-	-	-	-	-	-	35,7	49,9	-	-
Species no.	31	34	34	29	34	35	29	19	23	22	21
<b>CA</b>											
<i>Carex pulicaris</i>	.	+	+	+	1	1	2a	.	+	1	.
<i>Carex demissa</i>	.	.	.	+	+	+	.	.	r	+	1
<b>Oxycocco-Sphagnetea</b>											
<i>Drosera rotundifolia</i>	.	.	r	.	1	1	+	1	1	+	1
<i>Vaccinium oxycoccus</i>	.	r	1	+	+	+	1	1	.	.	1
<i>Aulacomnium palustre</i>	.	2m	2a	.	.	.	.	.	.	.	.
<i>Sphagnum angustifolium</i>	.	2a	.	.	.	.	.	.	.	.	.
<b>Caricion fuscae</b>											
<i>Carex echinata</i>	1	1	+	.	.	.	.	+	+	+	.
<i>Agrostis canina</i>	2a	2a	1	.	.	.	.	.	.	.	.
<i>Calliergon stramineum</i>	1	.	1	.	.	.	.	.	.	.	1
<i>Viola palustris</i>	1	+	+	.	.	.	.	.	.	.	.
<i>Epilobium palustre</i>	+	1	.	.	.	.	.	.	.	.	.
<b>d 1</b>											
<i>Mentha arvensis</i>	2a	2a	.	.	.	.	.	.	.	.	.
<i>Cirsium palustre</i>	.	1	2a	.	.	.	.	.	.	.	.
<i>Galium uliginosum</i>	.	1	1	.	.	.	.	.	.	.	.
<i>Myosotis nemorosa</i>	+	.	1	.	.	.	.	.	.	.	.
<i>Anthoxanthum odoratum</i>	.	+	1	.	.	.	.	.	.	.	.
<i>Willemetia stipitata</i>	1	.	+	.	.	.	.	.	.	.	.
<i>Ranunculus montanus</i>	+	1	.	.	.	.	.	.	.	.	.
<b>d 1+2</b>											
<i>Menyanthes trifoliata</i>	3	2b	2a	r	+	+	.	.	.	.	.
<i>Sphagnum warnstorffii</i>	.	2a	5	.	.	1	1	.	.	.	.
<i>Carex rostrata</i>	.	1	.	+	1	r	.	.	.	.	.

Facies	typical			Trichophorum cespitosum				Trichophorum alpinum					
				+	+	.	.	.	.	.	.	.	.
Juncus articulatus subsp. articulatus	.	1	.	+	+	.	.	.	.	.	.	.	.
<b>d 2</b>													
Aster bellidiastrum	.	.	.	2a	2a	+	2a	.	r	.	.	.	.
Gentiana asclepiadea	.	.	.	+	+	+	1	.	.	.	.	.	.
Carex davalliana	.	.	.	2a	+	.	+	.	.	.	.	.	.
Schoenus ferrugineus	.	.	.	+	.	2a	+	.	.	.	.	.	.
Linum catharticum subsp. catharticum	.	.	.	r	1	1	.	.	.	.	.	.	.
Eriophorum angustifolium	r	.	.	.	.	+	1	.	.	.	.	.	.
Fissidens adianthoides	.	.	.	1	.	.	+	.	.	.	.	.	.
<b>d 2+3</b>													
Trichophorum cespitosum subsp. cespitosum	.	.	+	3	2b	2b	2b	+	2a	+	+	.	.
Trichophorum alpinum	.	.	.	+	+	1	+	2b	2a	2b	2a	.	.
Drepanocladus cossonii	.	.	.	2a	2a	2m	1	2m	2m	1	2a	.	.
Primula farinosa	.	.	.	+	1	1	1	1	1	1	2a	.	.
Parnassia palustris	.	.	.	1	1	1	1	1	1	1	1	.	.
Tofieldia calyculata	.	.	.	+	+	1	1	1	+	1	+	.	.
<b>Scheuchzerietalia</b>													
Drosera intermedia	.	.	.	.	+	1	r	+	1	1	1	.	.
Sphagnum subsecundum	.	.	.	.	.	1	1	1	2m	.	1	.	.
Rhynchospora alba	.	.	.	.	.	r	.	+	1	+	2b	.	.
Scheuchzeria palustris	.	.	.	.	.	+	.	.	+	.	r	.	.
<b>A-O-C</b>													
Campyllum stellatum	2m	3	1	4	5	5	5	3	3	2m	4	.	.
Carex panicea	+	2a	2b	.	+	+	.	1	+	1	.	.	.
Eriophorum latifolium	.	+	.	+	2a	2a	+	+	+	.	.	.	.
Pinguicula vulgaris	.	.	.	.	r	1	.	.	1	+	1	.	.
Valeriana dioica	2a	2b	1	.	r	.	.	.	.	.	.	.	.
Carex hostiana	.	.	.	+	1	+	.	.	.	2b	.	.	.
Bryum pseudotriquetrum	1	2m	.	.	1	.	.	.	.	.	.	.	.
Drepanocladus revolvens	.	.	.	.	.	1	.	.	.	.	1	.	.
Aneura pinguis	1	.	.	.	.	.	1	.	.	.	.	.	.
Carex lepidocarpa	r	.	.	.	.	1	.	.	.	.	.	.	.
Carex flava	r	.	1	.	.	.	.	.	.	.	.	.	.
<b>Others</b>													
Molinia caerulea	2b	2a	+	2a	1	2a	2a	2a	2b	3	1	.	.
Potentilla erecta	1	2a	1	+	1	1	1	1	1	1	1	.	.
Succisa pratensis	2b	.	2b	r	+	+	2a	.	r	.	+	.	.
Picea abies seedl.	.	.	.	r	+	+	+	+	+	+	.	.	.
Plagiomnium elatum	3	2a	1	.	1	.	.	.	.	.	.	.	.
Calliergonella cuspidata	2m	2m	1	.	1	.	.	.	.	.	.	.	.
Equisetum palustre	r	1	1	.	r	.	.	.	.	.	.	.	.
Leontodon hispidus subsp. danubialis	.	.	.	+	.	.	1	.	.	+	.	.	.
Homalothecium nitens	.	.	1	1	.	.	.	.	.	.	.	.	.
Acer pseudoplatanus seedl.	.	.	.	.	.	r	r	.	.	.	.	.	.
Dactylorhiza fuchsii subsp. fuchsii	r	.	.	.	.	.	.	.	.	r	.	.	.
Prunella vulgaris	.	2a	.	.	.	.	.	.	.	.	.	.	.

Only once and abundance < 2a in **1**: Atrichum undulatum 1, Crepis paludosa r, Plagiothecium denticulatum 1, Potentilla palustris r, Ranunculus acris subsp. acris +, Rhytidiadelphus squarrosus 1. **2**: Equisetum fluviatile +, Hypnum cf pratense 2m, Myosotis scorpioides subsp. scorpioides 1, Silene flos-cuculi r, Thuidium philibertii 1, Trifolium repens 1. **3**: Agrostis stolonifera r, Briza media r, Carex nigra +, Epipactis palustris +, Galium palustre subsp. palustre +, Lotus corniculatus subsp. corniculatus 1, Nardus stricta r. **4**: Carex flacca 1, Polygala amarella r. **5**: Cratoneuron commutatum var. falcatum +, Hypnum lindbergii 1. **6**: Leiocolea bantriensis 2m. **7**: Ctenidium molluscum 1, Thuidium tamariscinum +. **8**: Scorpidium scorpioides +. **10**: Riccardia multifida 1. **11**: Calluna vulgaris +.

The facies of *Trichophorum cespitosum* (columns 4-7) was dominated by this species, and differed by plants that were observed in the *Schoenetum ferruginei* Du Rietz 1925 (chapter 3.5.2) and the *Caricetum davallianae* (chapter 3.5.3), and moreover lacked species of the *Caricion fuscae*. This facies was restricted to the Sattlermoos (Fig. 2), where it occurred on 7 m thick peat in an intermediate position between the sloping fen in the southwest and the bog in the eastern part of the mire. Some difficulties emerged for the assignment of communities rich in *Trichophorum cespitosum*, because there may be only gradual environmental, compositional and structural transitions to the *Drepanoclado intermedii-Trichophoretum cespitosi* sensu auct. non Nordhagen 1928 and *Trichophorum*-rich montane forms of the *Caricetum davallianae*. However, we did not assign the respective relevés to the *Drepanoclado intermedii-Trichophoretum cespitosi* because they completely lacked its differential species *Bartsia alpina* and *Selaginella selaginoides* (DIERBEN & DIERBEN 1984, STEINER 1992), while the respective character species (*Carex pulicaris*, *C. demissa*) of the *Amblystegio stellati-Caricetum dioicae* were present. Moreover, we did not assign these relevés to the *Caricetum davallianae* for three reasons: first, because of the occurrence of *Carex pulicaris* and *C. demissa*, second, because bog and poor fen species (belonging to the class *Oxycocco-Sphagnetea* and the order *Scheuchzerietalia palustris* Nordhagen 1936) were more frequent, and, third, because the aspect of these communities was dominated by *Trichophorum cespitosum*, which is not the case in the *Caricetum davallianae*.

The facies of *Trichophorum alpinum* (column 8-11) was negatively differentiated against the latter facies. The aspect was dominated by *T. alpinum* while *T. cespitosum* only played a minor role. This facies was restricted to the Western Wasserfilz, where it grew in a sloping fen and on small remaining peat islands within erosion channels in the central part of the mire. Median WTDs were -6 and -5.5 cm and the water table showed only little fluctuation. Mire water was weakly acidic with median pH values of 5.7 and 6, respectively, and had median EC values of 35.7 and 49.9  $\mu\text{S cm}^{-1}$ .

### 3.5.2 *Schoenetum ferruginei* Du Rietz 1925 (Table 9)

The physiognomy of these stands was governed by the tussocks of *Schoenus ferrugineus* (Fig. 2). Its litter was hardly mineralized and covered large proportions of the stands. Under these conditions, character species of the *Oxycocco-Sphagnetea* occurred frequently in the relevés. Median WTD ranged between -10.5 and -4.5 cm, and the water table showed little fluctuations. Mire water was weakly to very weakly acidic with median pH values between 6.3 and 6.7; median EC was 113–158  $\mu\text{S cm}^{-1}$ . In the study area, the *Schoenetum ferruginei* occurred on > 5 m thick peat in the Sattlermoos adjacent to the *Amblystegio stellati-Caricetum dioicae*, the *Caricetum davallianae*, and also, where the uppermost 5 cm of peat were eroded, to the *Eriophoro-Trichophoretum cespitosi* (Zlatnik 1928, Rudolf et al. 1928) Rübél 1933.

### 3.5.3 *Caricetum davallianae* Dutoit ex Koch 1928 (Table 10 in the supplement)

This association (Fig. 2) is usually found in neutral to base-rich (calcareous) spring fens or sloping fens with a shallow (< 1 m) or non-existent peat layer (GÖRS 1998, KORTENHAUS 1987, HERTER 1990, STEINER 1992, EGGENSBERGER 1993), but in the study area, peat thickness in this association ranged between 1 and 7 m. The presence of *Trichophorum cespitosum* is characteristic for montane communities of this association (STEINER 1992). The typi-

**Table 9.** Relevés of the *Schoenetum ferruginei campylietosum* from the Ammergauer Alps.

**Tabelle 9.** Aufnahmen des *Schoenetum ferruginei campylietosum* aus den Ammergauer Alpen.

Column	1	2	3	4	5
Mire	Sa	Sa	Sa	Sa	Sa
Plot size (m <sup>2</sup> )	1	1	1	1	1
Exposition	N	-	N	NE	-
Slope (°)	1	-	1	2	-
Height herb layer (cm)	35	35	30	35	25
Cover herb layer (%)	75	75	50	65	60
Cover moss layer (%)	55	60	15	70	80
Cover litter layer (%)	50	40	90	85	85
Median WTD (cm)	-7	-4,5	-10,5	-	-
WI	42,8	11,5	45,3	-	-
Median pH	6,3	6,3	6,7	-	-
Median EC (µS cm <sup>-1</sup> )	158	113	121	-	-
Species no.	31	25	19	22	26
<b>CA</b>					
Schoenus ferrugineus	4	3	3	3	2b
<b>Oxycocco-Sphagnetea</b>					
Drosera rotundifolia	.	1	r	+	+
Vaccinium oxycoccus	.	.	r	+	.
Aulacomnium palustre	.	+	.	.	.
<b>A-O-C</b>					
Campylium stellatum	2m	4	2a	4	4
Trichophorum cespitosum subsp. cespitosum	+	+	+	r	2b
Drepanocladus cossonii	1	2m	+	1	1
Parnassia palustris	1	1	+	1	+
Tofieldia calyculata	1	1	1	+	1
Trichophorum alpinum	+	+	+	+	1
Primula farinosa	+	1	.	1	+
Menyanthes trifoliata	+	2a	.	.	+
Carex rostrata	+	1	.	.	1
Eriophorum latifolium	.	2a	.	r	+
Fissidens adianthoides	2m	.	1	.	1
Pinguicula vulgaris	+	r	.	.	+
Aneura pinguis	.	.	1	+	.
Carex hostiana	.	1	.	r	.
<b>Others</b>					
Molinia caerulea	2a	2a	2a	2a	2a
Potentilla erecta	1	1	1	1	1
Picea abies seedl.	+	+	+	+	1
Succisa pratensis	2b	+	2a	.	+
Leontodon hispidus subsp. danubialis	r	1	+	+	.
Aster bellidiastrum	1	.	1	1	1
Cirsium palustre	+	.	+	+	.
Calliergonella cuspidata	2a	1	.	+	.
Gentiana asclepiadea	r	r	.	.	1
Plagiomnium elatum	+	.	.	.	+
Hypnum lindbergii	1	.	.	.	1
Ctenidium molluscum	2b	.	.	.	1
Leiocolea bantriensis	+	2m	.	.	.
Riccardia multifida	.	+	.	.	2m
Homalothecium nitens	2a	.	.	.	.

Only once and abundance < 2a in **1**: *Carex davalliana* r, *Carex flacca* r, *Carex panicea* +, *Thuidium philiberti* 1, *Valeriana dioica* +. **2**: *Equisetum palustre* +. **3**: *Phyteuma orbiculare* subsp. *orbiculare* r. **4**: *Lophocolea bidentata* 1, *Picea abies* juv. r, *Pleurozium schreberi* +. **5**: *Bryum pseudotriquetrum* 1, *Moerckia hibernica* 1.

cal sites showed little to no fluctuation of the water table, median WTD ranged between -9 and -5.3 cm, and the amplitude of water table fluctuation was between 6.5 and 13 cm. Water reaction was very weakly acidic to neutral with median pH between 6.5 and 7. Median EC ranged between 171 and 322  $\mu\text{S cm}^{-1}$  in more upslope positions.

### 3.6 Hummocks and lawns in bogs (*Sphagnion magellanici* Kästner et Flößner 1933)

#### 3.6.1 *Sphagnetum magellanici* (Malcuit 1929) Kästner et Flößner 1933 (Table 11 in the supplement, columns 1–10)

With increasing altitude (at around 900 m in the foreland adjacent to the study area; KAULE 1976), the *Sphagnetum magellanici* gets replaced by the *Eriophoro-Trichophoretum cespitosi* (chapter 3.6.2) and occurs only in a few sites. The latter is differentiated against the *Sphagnetum magellanici* by the presence of *Trichophorum cespitosum* (DIERBEN & DIERBEN 2008; *Carex pauciflora* cannot be regarded as a good differential species in our records) and – within the study area – also by *Sphagnum rubellum*. In the subassociation of *Rhynchospora alba* (columns 1–3), median WTD was around -12 cm, and there was little to no water table fluctuation. Mire water was moderately acidic with median pH between 4.5 and 4.9; median EC values were 17.7–18.9  $\mu\text{S cm}^{-1}$ . The typical subassociation (columns 4–6) occurred on slightly higher lawns with very vital *Sphagnum magellanicum*. We found such communities only in the Eastern Wasserfilz. The *Vaccinium uliginosum*-stage (columns 7 and 8) occurred under drier site conditions at an intermediate position between the relatively shrub- and treeless mire expanse and the Spruce forests on the sloping margins of the bogs.

Shrubby individuals of *Picea abies* grew on high hummocks in the Western Wasserfilz. Corresponding to STEINER (1992), we assigned these communities to the *Picea abies*-phase of the subassociation of *Pleurozium schreberi* (columns 9 and 10).

#### 3.6.2 *Eriophoro-Trichophoretum cespitosi* (Zlatnik 1928, Rudolf et al. 1928) Rübél 1933 (Table 11 in the supplement, columns 11–38)

The *Eriophoro-Trichophoretum cespitosi* is the characteristic association of hummocks and lawns within the ombrotrophic to weakly minerotrophic parts of montane to subalpine mires (DIERBEN & DIERBEN 2008). Otherwise being floristically similar to the *Sphagnetum magellanici*, the physiognomy of these stands is characterized by the presence of *Trichophorum cespitosum*.

The subassociation of *Rhynchospora alba* (columns 11–15) occurred in lawns with median WTD between -12 and -8.3 cm and little to non fluctuating water table. Mire water was strongly to moderately acidic with median pH between 4.3 and 5.2. Median EC ranged between 17.7 and 25  $\mu\text{S cm}^{-1}$ .

The subassociation of *Scheuchzeria palustris* (columns 16–19) occurs under slightly drier conditions with median WTD between -15.5 and -10.8 cm and little to non-fluctuating water table. All sites were strongly acidic with median pH 4.4. Median EC ranged between 19.4 and 20.9  $\mu\text{S cm}^{-1}$ .

In the typical subassociation (columns 20–29), median WTD ranged between -21 and -11 cm. Again, there was little to no fluctuation of the water table. Mire water was strongly to moderately acidic with median pH between 4.2 and 4.7 and had a median EC between 19.4 and 27.2  $\mu\text{S cm}^{-1}$ .



The subassociation of *Sphagnum fuscum* (columns 30 and 31) had a median WTD of -16.8 cm and water table showed little fluctuation. Mire water was moderately acidic with median pH 4.9 and had a median EC of 18.1  $\mu\text{S cm}^{-1}$ .

The subassociation of *Cladonia arbuscula* (column 32) had a median WTD of -21.3 cm and little fluctuation of the water table. Mire water was strongly acidic with median pH 4.4 and had a median EC of 22.3  $\mu\text{S cm}^{-1}$ .

The *Vaccinium uliginosum*-stage of the *Eriophoro-Trichophoretum cespitosi* (columns 33–38) grows at drier site conditions between the relative shrub- and treeless mire expanse and the spruce forests on the sloping margins of the bogs. Water table showed little fluctuation and median WTD was between -21 and -17 cm. Mire water was strongly acidic with median pH at 4.2 and had a median EC between 30.2 and 35.3  $\mu\text{S cm}^{-1}$ .

### 3.6.3 *Pino mugo-Sphagnetum* Kastner et Flobner 1933 corr. Dieren 1978 (Table 12)

This association comprises bog shrub and forest communities with *Pinus mugo* and/or *Pinus rotundata* (STEINER 1992, 1993b, DIERBEN 1998). *Pinus mugo* occurs with scattered single individuals or in small groups in the central parts of the studied mires or forms dense thickets in the upper parts of the sloping mire margins.

### 3.7 Spruce forests (*Piceion abietis* Pawlowski in Pawlowski et al. 1928)

This alliance was only represented with the *Bazzanio-Piceetum* Br.-Bl. et Sissingh in Br.-Bl. et al. 1939 (Table 13) which comprises Spruce (*Picea abies*) forests in the lower parts and Spruce scrubs in the upper parts of the sloping mire margins, respectively. Therefore, species typical for lawns and hummocks (*Oxycocco-Sphagnetum*) occur more frequently and at higher abundance in the Spruce scrub communities. We detected a median WTD of -27 cm in one Spruce forest community with little fluctuation of the water table. Mire water was strongly acidic with median pH of 4.3 and showed a median EC of 37.3  $\mu\text{S cm}^{-1}$ . In one Spruce scrub community, median WTD was -20.5 cm and water table showed no fluctuation. Mire water was also strongly acidic with a similar median pH of 4.4; median EC was slightly lower with 25.4  $\mu\text{S cm}^{-1}$ .

## 4. Floristic variation and environmental gradients

### 4.1 Ordination results

The NMDS ordination largely confirmed our classification (Fig. 23). Bog associated plant communities were found on the right side of the plot and small sedge fen communities in the central parts, whereas the plant communities of tall sedge fens and transitional fens were located at the left part of the plot. Even at the level of associations and subassociations (the latter not shown but see electronic appendix S1 for own calculations) the ordination showed a good correspondence with the classification. However, some associations (e.g. *Schoenetum ferruginei*) could not be clearly separated from others by the NMDS.

Fitted environmental vectors and smoothed surfaces of all variables except WI were significantly ( $P = 0.001$ ) correlated with the ordination result (Table 14) and showed some clear tendencies regarding variation in species composition (Fig. 4). Overall, differences in pH

**Table 12.** Relevés of the *Pino mugo-Sphagnetum pleurozietosum* from the Ammergauer Alps.

**Tabelle 12.** Aufnahmen des *Pino mugo-Sphagnetum pleurozietosum* aus den Ammergauer Alpen.

Column	1	2	3	4	5	6	7
Mire	Sa	Sa	Sa	EW	WW	WW	EW
Plot size (m <sup>2</sup> )	12	8	4	6	4	3	25
Exposition	E	-	-	ESE	N	N	ENE
Slope (°)	5	-	-	2	4	1	5
Height tree layer (cm)	-	-	-	-	-	-	600
Height shrub layer (cm)	200	150	200	200	70	100	300
Height herb layer (cm)	30	30	25	45	60	40	50
Cover tree layer (%)	-	-	-	-	-	-	15
Cover shrub layer (%)	70	45	70	70	75	70	45
Cover herb layer (%)	55	30	30	30	15	20	70
Cover moss layer (%)	30	95	45	70	30	80	80
Cover litter layer (%)	60	10	50	20	90	20	15
Species no.	20	19	16	19	16	21	25
<b>CA</b>							
<i>Pinus rotundata</i>	.	.	.	.	.	.	2a
<b>DA</b>							
<i>Pinus mugo</i>	4	3	4	4	4	3	3
<i>Pleurozium schreberi</i>	2a	1	1	1	1	2a	2a
<i>Pinus mugo</i> seedl.	.	+	+	r	1	+	+
<i>Vaccinium myrtillus</i>	2b	.	1	2a	+	2a	2b
<i>Vaccinium uliginosum</i> subsp. <i>uliginosum</i>	2b	1	1	2a	.	.	3
<i>Melampyrum pratense</i> subsp. <i>paludosum</i>	1	.	1	.	.	.	+
<b>A-O-C</b>							
<i>Eriophorum vaginatum</i>	1	1	1	1	1	1	2a
<i>Sphagnum magellanicum</i>	2m	5	2a	3	3	4	4
<i>Vaccinium oxycoccus</i>	1	1	1	1	2m	1	1
<i>Dicranum bergeri</i>	1	1	1	2m	1	.	2m
<i>Polytrichum strictum</i>	2m	2m	1	2a	1	.	2m
<i>Andromeda polifolia</i>	.	1	1	1	1	+	+
<i>Sphagnum angustifolium</i>	2a	2m	2b	2m	.	+	2a
<i>Aulacomnium palustre</i>	1	1	1	.	.	.	2m
<i>Calypogeia sphagnicola</i>	1	1	.	.	.	2m	2m
<i>Drosera rotundifolia</i>	.	1	.	+	1	1	.
<i>Cephalozia connivens</i>	.	.	.	1	.	1	1
<i>Mylia anomala</i>	.	1	.	.	2m	1	.
<i>Sphagnum nemoreum</i>	.	2b	3	2a	.	.	.
<i>Picea abies</i>	.	.	.	.	.	2b	r
<i>Carex pauciflora</i>	.	1	.	r	.	.	.
<b>Others</b>							
<i>Calluna vulgaris</i>	1	2a	2b	1	1	1	1
<i>Picea abies</i> seedl.	.	+	+	r	.	+	+
<i>Molinia caerulea</i>	1	.	.	.	1	1	1
<i>Picea abies</i> juv.	+	.	.	r	.	.	.
<i>Bazzania trilobata</i>	2m	.	.	.	.	.	1
<i>Cephalozia loitlesbergeri</i>	.	.	.	.	2m	1	.
<i>Potentilla erecta</i>	.	.	.	.	+	+	.
<i>Trichophorum cespitosum</i> subsp. <i>cespitosum</i>	.	2a	.	.	+	.	.

Only once and abundance < 2a in **1**: *Betula pubescens* subsp. *pubescens* juv. r, *Sorbus aucuparia* subsp. *aucuparia* juv. r, *Vaccinium vitis-idaea* 1. **4**: *Dicranum scoparium* 2m, *Sphagnum rubellum* 2m. **6**: *Calypogeia azurea* 2m, *Menyanthes trifoliata* r, *Sphagnum fuscum* 1, *Sphagnum quinquefarium* 1. **7**: *Calliergon stramineum* 1, *Calypogeia muelleriana* 2m, *Carex nigra* +, *Carex rostrata* +, *Hylocomium splendens* 1.

**Table 13.** Relevés of the *Bazzanio-Piceetum* from the Ammergauer Alps.

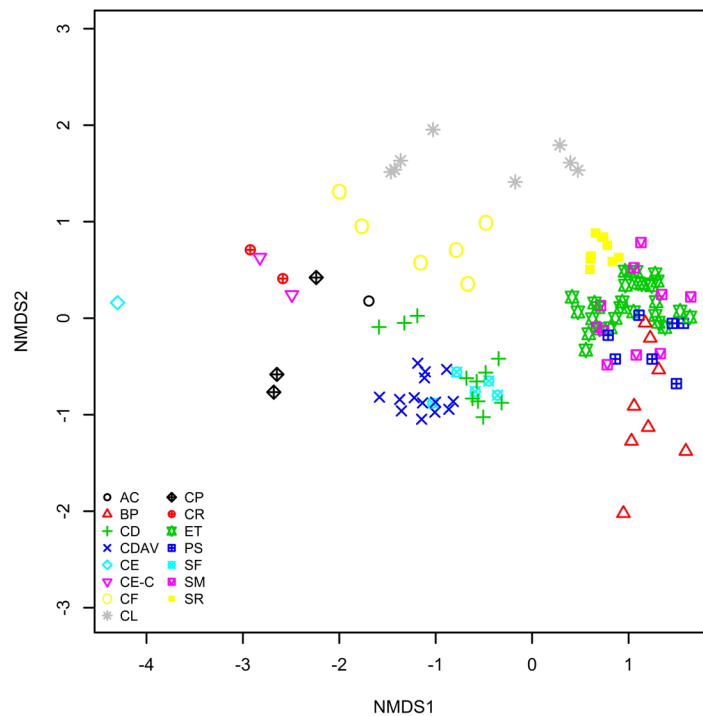
**Tabelle 13.** Aufnahmen des *Bazzanio-Piceetum* aus den Ammergauer Alpen.

Variant	Forest					Scrub		
	1	2	3	4	5	6	7	8
Column								
Mire	WW	Sa	WW	EW	EW	WW	EW	Sa
Plot size (m <sup>2</sup> )	80	40	60	45	55	60	40	45
Exposition	SE	ESE	SW	W	SSE	W	SSE	ESE
Slope (°)	40	25	25	15	15	5	5	5
Height tree layer (cm)	2000	1500	1200	1500	800	-	-	-
Height shrub layer (cm)	500	500	500	300	500	400	200	300
Height herb layer (cm)	30	25	55	50	40	50	45	40
Cover tree layer (%)	75	80	30	55	15	-	-	-
Cover shrub layer (%)	0,5	15	35	15	90	40	45	45
Cover herb layer (%)	35	15	50	35	25	85	85	85
Cover moss layer (%)	90	85	95	95	100	80	100	80
Cover litter layer (%)	30	15	15	10	10	60	10	1
Median WTD (cm)	-	-27	-	-	-	-20,5	-	-
WI	-	21,6	-	-	-	9,5	-	-
Median pH	-	4,3	-	-	-	4,4	-	-
Median EC (µS cm <sup>-1</sup> )	-	37,3	-	-	-	25,4	-	-
Species no.	29	24	35	35	31	24	21	22
<b>CA</b>								
Picea abies Shrub	+	2a	3	1	5	3	3	3
Picea abies Tree	4	5	3	4	2a	.	.	.
<b>Piceion</b>								
Bazzania trilobata	2m	2a	2m	2m	2m	.	.	.
Sphagnum quinquefarium	2b	2a	2a	.	.	.	.	.
Plagiothecium undulatum	+	.	2m	2m	.	.	.	.
<b>O-C</b>								
Rhytidiadelphus loreus	2m	2m	1	1	2m	.	.	.
Listera cordata	r	.	.	+	1	.	.	.
Vaccinium myrtillus	3	2a	3	2b	2b	2a	2a	2b
Picea abies seedl.	1	1	1	1	+	1	+	.
Vaccinium vitis-idaea	.	2m	1	1	.	1	.	2m
Picea abies juv.	.	.	.	.	+	.	+	1
Ptilium crista-castrensis	.	.	1	.	.	1	.	.
<b>d var</b>								
Vaccinium uliginosum subsp. uliginosum	.	.	2a	.	.	4	4	4
Calluna vulgaris	.	.	1	.	.	2m	1	2a
Trichophorum cespitosum subsp. cespitosum	.	.	.	.	.	.	r	+
<b>Oxycocco-Sphagnetea</b>								
Sphagnum magellanicum	2m	2m	3	2b	4	4	4	3
Calypogeia sphagnicola	2m	1	1	1	2m	.	.	2m
Eriophorum vaginatum	.	.	1	+	+	1	2a	2a
Polytrichum strictum	.	2m	2m	.	2m	2m	2m	2m
Sphagnum angustifolium	.	.	2a	2a	2a	2a	2m	2b
Vaccinium oxycoccus	.	.	1	1	1	1	2m	1
Aulacomnium palustre	.	.	.	1	2m	2m	2m	1
Andromeda polifolia	.	.	.	.	+	1	1	1
Carex pauciflora	.	.	.	.	.	.	1	+
Dicranum bergeri	.	.	.	.	.	.	1	1
Drosera rotundifolia	.	.	.	.	+	.	.	+
Sphagnum nemoreum	.	.	2b	.	.	.	.	.
<b>Others</b>								
Pleurozium schreberi	2m	2m	2m	1	2m	2a	2b	2a
Molinia caerulea	1	1	1	1	1	1	.	1

Variant	Forest					Scrub		
<i>Calypogeia azurea</i>	2m	2m	2m	2m	2m	2m	.	.
<i>Dicranum scoparium</i>	2m	2b	1	2m	2m	1	.	.
<i>Hylocomium splendens</i>	2m	1	2m	2m	2a	1	.	.
<i>Melampyrum pratense</i> subsp. <i>paludosum</i>	.	.	2m	1	1	1	2m	1
<i>Dicranodontium denudatum</i>	2m	2m	2m	2m	2m	.	.	.
<i>Polytrichum formosum</i>	4	2b	2m	2m	2m	.	.	.
<i>Carex rostrata</i>	.	.	.	+	+	+	1	.
<i>Polytrichum commune</i>	1	.	.	.	.	2m	1	.
<i>Carex nigra</i>	.	.	1	1	.	1	.	.
<i>Sorbus aucuparia</i> subsp. <i>aucuparia</i> juv.	+	r	1	.	.	.	.	.
<i>Tetraphis pellucida</i>	.	2m	.	2m	2m	.	.	.
<i>Thuidium tamariscinum</i>	1	1	.	1	.	.	.	.
<i>Carex echinata</i>	.	.	+	1	1	.	.	.
<i>Cephalozia loitlesbergeri</i>	.	2m	1	.	.	.	.	.
<i>Fagus sylvatica</i> juv.	r	r	.	.	.	.	.	.
<i>Lepidozia reptans</i>	.	.	.	1	2m	.	.	.
<i>Leucobryum glaucum</i>	1	1	.	.	.	.	.	.
<i>Maianthemum bifolium</i>	.	.	1	1	.	.	.	.
<i>Plagiochila asplenioides</i>	+	.	.	.	1	.	.	.
<i>Potentilla erecta</i>	r	.	1	.	.	.	.	.

Only once and abundance < 2a in **1**: *Athyrium filix-femina* r, *Lycopodium annotinum* 1, *Rhizomnium punctatum* 2m, *Thelypteris limbosperma* r. **3**: *Cephalozia bicuspidata* 2m, *Cladonia pyxidata* 1. **4**: *Barbilophozia attenuata* 2m, *Cephalozia connivens* 1, cf *Riccardia palmata* 1, *Menyanthes trifoliata* 1, *Sphagnum centrale* 2m. **5**: *Dactylorhiza fuchsii* subsp. *fuchsii* 1. **6**: *Ptilidium ciliare* 1. **7**: *Pinus mugo* r. **8**: *Dicranum fuscescens* 2m.

between sites had the strongest and an almost linear relationship with distance in ordination space and therefore floristic dissimilarity between sites. Along this gradient, there was a conspicuous separation of acidic bog sites on the right, and subneutral to neutral fen sites including tall sedge communities on the left side of the diagram. Median WTD showed a weaker linear relationship with the ordination but represented a roughly orthogonal axis to pH. Therefore, within each of the two groups separated by pH, large parts of the floristic variation could be attributed to differences in WTD, separating sites that have low WTD at the lower right region of the NMDS plot from sites with high WTD at the upper parts of the plot, respectively. As there was a strong correlation with pH (Pearson's  $r = 0.83$ ), median EC also showed a relatively strong relationship with ordination and generally increased from right to left. Bog sites differed only little with respect to EC, whereas small and tall sedge fen communities were distributed along a steep gradient of EC (Fig. 7). Site fertility, as indicated by Ellenberg N values, showed a moderately strong relationship with the ordination for both, environmental vectors and surfaces. Generally, fertility tended to be slightly higher at more base rich sites and at drier sites when pH was low, respectively. Peat humification (H) had a similar linear  $R^2$  to Ellenberg N, but its response surface was less related to the ordination result. In general, acidic mire sites had less humified peat than more base rich sites. WI showed by far the weakest relationship with the NMDS for both, linear and surface  $R^2$ . The weak pattern suggests that sites with lower WTD had lower fluctuation of the water table.



**Fig. 3.** NMDS plot of all sites from the Ammergauer Alps (stress = 14.6%). Phytosociological assignment of relevés is overlain (AC = *Amblystegio-Caricetum diandrae*, BP = *Bazzanio-Piceetum*, CD = *Caricetum dioicae*, CDAV = *Caricetum davallianae*, CE = *Caricetum elatae*, CE-C = *Carex elongata*-community, CF = *Caricetum fuscae*, CL = *Caricetum limosae*, CP = *Caricetum paniculatae*, CR = *Caricetum rostratae*, ET = *Eriophoro-Trichophoretum*, PS = *Pino-Sphagnetum*, SF = *Schoenetum ferruginei*, SM = *Sphagnetum magellanici*, SR = *Sphagno-Rhynchosporium*).

**Abb. 3.** NMDS-Plot aller Aufnahmen aus den Ammergauer Alpen (Stress = 14.6%). Die pflanzensoziologische Zuordnung der Aufnahmen ist darüber gelegt (AC = *Amblystegio-Caricetum diandrae*, BP = *Bazzanio-Piceetum*, CD = *Caricetum dioicae*, CDAV = *Caricetum davallianae*, CE = *Caricetum elatae*, CE-C = *Carex elongata*-community, CF = *Caricetum fuscae*, CL = *Caricetum limosae*, CP = *Caricetum paniculatae*, CR = *Caricetum rostratae*, ET = *Eriophoro-Trichophoretum*, PS = *Pino-Sphagnetum*, SF = *Schoenetum ferruginei*, SM = *Sphagnetum magellanici*, SR = *Sphagno-Rhynchosporium*).

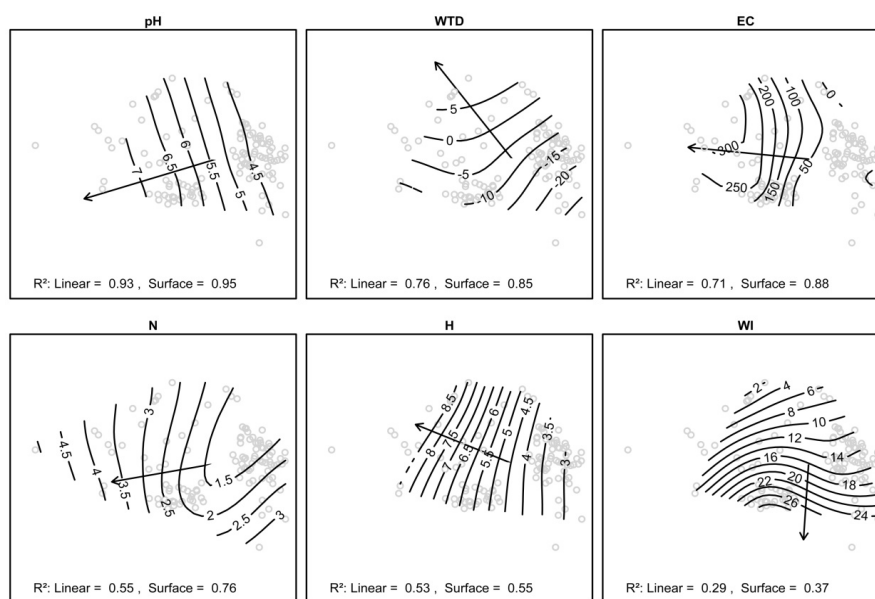
## 4.2 Discussion

Although there was a generally good correspondence of the ordination results with our classification, some phytosociological units could not be as clearly separated by the NMDS as suggested by the vegetation tables. Adopting the distances in ordination space as a classification criterion, the relevés of the *Schoenetum ferruginei* would have to be assigned to both, the *Caricetum davallianae* and the *Amblystegio stellati-Caricetum dioicae*. The floristic similarity between the relevés reflects the intermediate environmental and spatial position of the *Schoenetum ferruginei* between the two other associations in the study area (Fig. 2). Furthermore, the high cover of *Schoenus ferrugineus*, which is the significant physiognomic feature of these communities, is strongly down-weighted during the NMDS computation (see methods). The same is true for the differentiations of the scrub facies of the *Bazzanio-*

*Piceetum* against the *Pino mugo-Sphagnetum* on the one hand, and both of them against the *Vaccinium uliginosum*-stages of the *Sphagnetum magellanici* and the *Eriophoro-Trichophoretum* on the other hand, which are based on the high cover of *Picea abies* or *Pinus mugo* shrubs and trees in the phytosociological classifications (DIERBEN 1998, STEINER 1992, 1993b).

The main gradient underlying floristic variation between different mire sites was an acidity–alkalinity gradient, which was even more important than that of WTD, which is also in line with other studies (e.g. HÁJKOVÁ & HÁJEK 2004, BRAGAZZA et al. 2005). However, to detect this pattern it is important to cover a wide range of mire sites with respect to pH. Otherwise, one would come to a contrasting conclusion regarding the relative importance of pH and WTD (BRAGAZZA & GERDOL 1999a). As there was a strong relation between EC and pH, EC was also a good predictor of floristic variation between sites.

The main floristic subdivision in our dataset occurred between ombrotrophic (as indicated by the absence of even borderline minerotrophy indicating species) and weakly minerotrophic bog sites with median pH  $\leq 5$  and median EC  $\leq 30 \mu\text{S cm}^{-1}$  and fen communities on sites with median pH  $\geq 5.2$  and median EC mainly  $\geq 35 \mu\text{S cm}^{-1}$  (mostly  $\geq 100 \mu\text{S cm}^{-1}$ ; Figs. 4 and 6). Of course, the underrepresentation of poor fen communities (*Caricetalia fuscae* W. Koch 1926) in the study area and in our environmental dataset supports this clear split and results in a bimodal frequency distribution of measured pH values with a lack of pH values at around 5.5 (Fig. 5). This bimodality expresses two main buffering systems, with water being buffered by humic substances at pH  $\leq 5.5$  and by bicarbonates above that point (WHEELER & PROCTOR 2000).



**Fig. 4.** NMDS of all sites from the Ammergauer Alps with fitted environmental vectors and smoothed surfaces. Arrows indicate direction with most rapid change of the environmental variable.

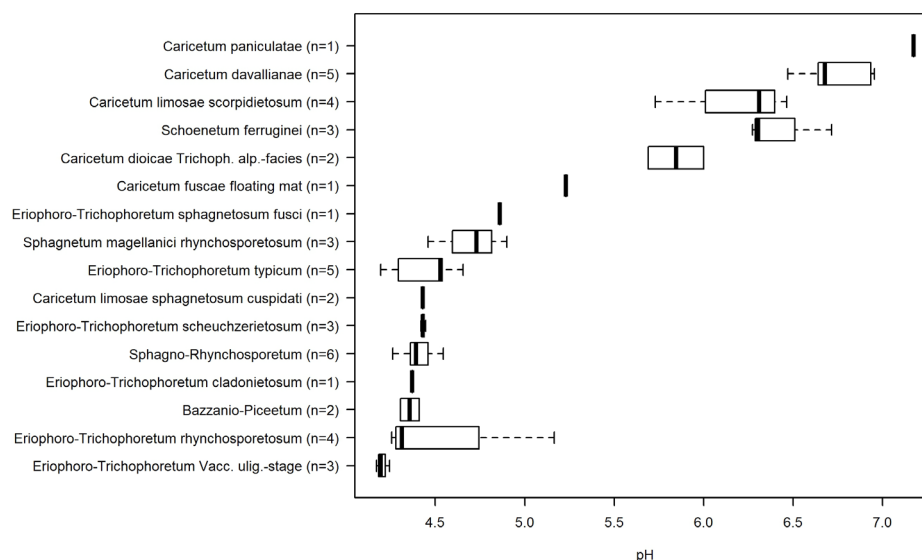
**Abb. 4.** NMDS aller Aufnahmen aus den Ammergauer Alpen mit angepassten Umweltvektoren und geglätteten Oberflächen. Pfeile zeigen in die Richtung der stärksten Änderung der jeweiligen Umweltvariable.

**Table 14.** Test statistics of environmental vectors and smoothed surfaces.

**Tabelle 14.** Teststatistik von Umweltvektoren und geglätteten Oberflächen.

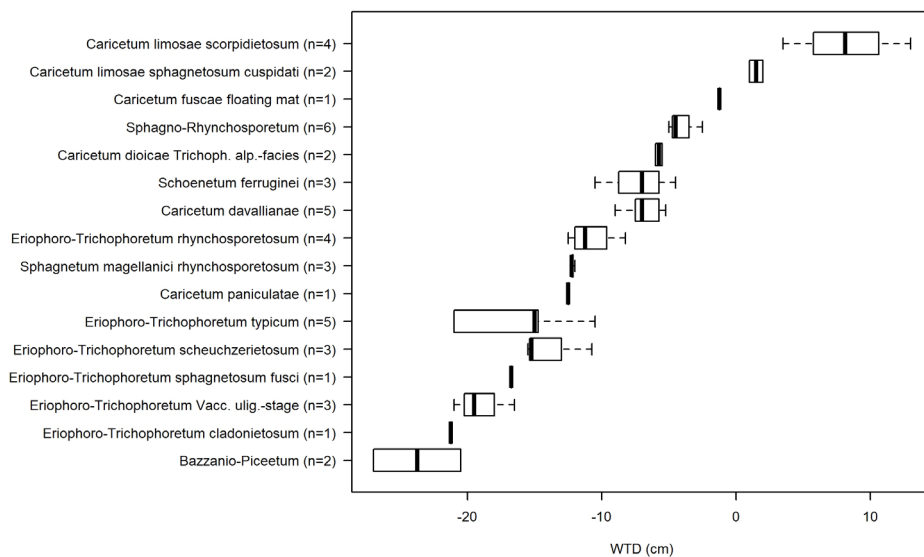
	Vectors			Surfaces			F	d.f.
	R <sup>2</sup>	P-value		R <sup>2</sup>	P-value			
EC	0.71	0.001	***	0.88	< 0.001	***	36.61	8.56
H	0.53	0.001	***	0.55	< 0.001	***	10.17	3.77
pH	0.93	0.001	***	0.95	< 0.001	***	101.4	6.83
WI	0.29	0.004	**	0.37	> 0.001	**	04.61	4.67
WTD	0.76	0.001	***	0.85	< 0.001	***	32.55	6.02
Ellenberg N	0.55	0.001		0.76	< 0.001		39.43	7.96

Nonetheless, WTD still played an important role in determining patterns of compositional variation. As has also been demonstrated in other studies (NORDBAKKEN 1996a, b, BRAGAZZA & GERDOL 1996, SOTTOCORNOLO et al. 2009), this was particularly clear in the ombrotrophic to weakly minerotrophic mire parts, where we recorded a long gradient from the wooded sloping mire margins to the mire expanse with its microtopographical differentiation of the surface, along which the floristically defined mire types occurred (Fig. 6). This may be attributed to subtle differences in morphological, anatomical and physiological adaptations between species to water table-driven site conditions (e.g. aeration, nutrition; HAYWARD & CLYMO 1982, MILLER 1982, WALLÉN 1987, RYDIN 1985, 1993). Notably, we cannot give a statement on year-round hydrological conditions because we did not measure WTD during winter and spring. This is especially important for the interpretation of WI since the degree of water table drawdown between the moist winter and spring season and the relatively drier summer and early autumn season and its variation among sites could not be detected (see SUCCOW & JOOSTEN 2001).



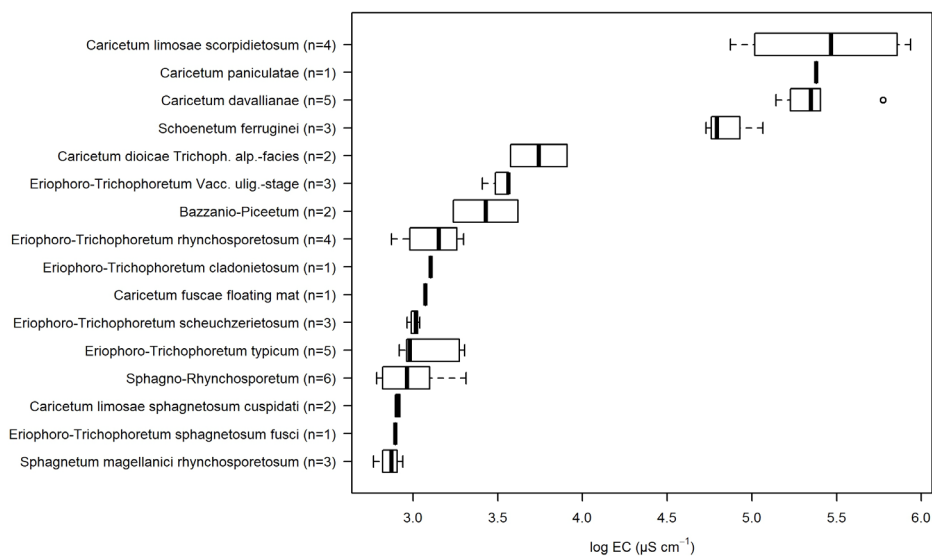
**Fig. 5.** Distribution of plant communities along the pH gradient.

**Abb. 5.** Verteilung der Pflanzengesellschaften entlang des pH-Gradienten.



**Fig. 6.** Distribution of plant communities along the water table gradient.

**Abb. 6.** Verteilung der Pflanzengesellschaften entlang des Wasserspiegel-Gradienten.



**Fig. 7.** Distribution of plant communities along the EC gradient.

**Abb. 7.** Verteilung der Pflanzengesellschaften entlang des Leitfähigkeits-Gradienten.

Given the fact that the reported moderate  $R^2$  values for Ellenberg N with the NMDS are probably still too high (see methods; ZELENÝ & SCHAFFERS 2012), differences in site fertility played only a minor role for floristic variation between sites. This supports findings of previous studies in which biomass production or nutrient contents have been measured directly and which detected only small or even no differences in fertility between bogs and fen types



(VITT & CHEE 1990, THORMANN & BAYLEY 1997, BRAGAZZA & GERDOL 2002, GOLOVATSKAYA & DYUKAREV 2009, GERDOL et al. 2010), because productivity is also limited in subneutral fens due to immobilized P (BOEYE et al. 1997, BOYER & WHEELER 1989, GERDOL et al. 2010). However, these patterns may result from a restricted range of mire sites under study and the inclusion of marshes, further tall sedge communities and wooded sites may change this picture (BRADBURY & GRACE 1983, RYDIN & JEGLUM 2006, GOLOVATSKAYA & DYUKAREV 2009). This is also suggested by the slight increase of Ellenberg N towards the tall sedge communities and Spruce stands in Fig. 4, which may be attributed to the temporarily better aeration and mineralization as well as the nutrient inflow at these marginal areas (BRAGAZZA 1996, FREEMAN et al. 1996, 1997). Furthermore, N content of peat in tall sedge communities is usually higher (SUCCOW & JOOSTEN 2001).

Our study was not explicitly designed to unravel changes in site conditions along the mire expanse–mire margin gradient. Moreover, given the asymmetric shape of the mires, we think that there would have been no clear trend relating to distance to the mire margins. However, tubes that were located in the margins of the bog parts of the mires (*Bazzanio-Piceetum* and the *Vaccinium uliginosum*-stage of the *Eriophoro-Trichophoretum*) showed a deeper water table and sometimes also slightly higher fluctuation of the water table than the other bog sites. Higher aeration of peat layers in the mire margins has been observed by other authors before (e.g. MALMER 1986, BRAGAZZA & GERDOL 1996, 1999a) and leads to slightly higher mineralization rates, which in turn are reflected in the higher EC at these sites (WILLIAMS & WHEATLEY 1988, FREEMAN et al. 1996, 1997).

Regarding the inventory of vegetation types, the results of this study are in line with previous phytosociological descriptions of montane mires in Central Europe and the European Alps (e.g. KAULE 1974, DIERBEN & DIERBEN 1984, GERDOL & TOMASELLI 1997, LEDERBOGEN 2003). However, this might be the first study that describes in detail the vegetational composition of the most common mire types in the German part of the Northern Limestone Alps, and therefore provides a basic reference for conservation and research in this area.

## Erweiterte deutsche Zusammenfassung

**Einführung** – Ökologische Untersuchungen, die sich mit Fragen der Vegetationsdifferenzierung entlang standörtlicher Gradienten in Mooren beschäftigen, liegen vor allem aus dem skandinavischen Raum, Nordamerika, Mitteleuropa, Osteuropa und dem südlichen Alpenraum vor (z. B. SJÖRS 1948, VITT et al. 1995, SUCCOW & JOOSTEN 2001, HÁJKOVÁ et al. 2006, BRAGAZZA & GERDOL 1999a, b). Dabei standen insbesondere die Einnischung von Pflanzenarten und Pflanzengemeinschaften entlang hydrochemischer Gradienten und unterschiedlicher Moorwasserstände, die relative Bedeutung einzelner Gradienten für die floristische Differenzierung, aber auch unterschiedliche Ansichten über die Grenzziehung zwischen verschiedenen Moortypen im Vordergrund. Vier Gradienten werden dabei als für die Vegetationsdifferenzierung wesentlich erachtet: der Säure-Basen-Gradient, der Wasserstands-Gradient, der komplexe Gradient vom Moorrand zum Moorzentrum, und der Fertilitätsgradient, dessen Unabhängigkeit von anderen Gradienten, insbesondere des erstgenannten, umstritten ist (WHEELER & PROCTOR 2000, ØKLAND et al. 2001, SJÖRS & GUNNARSSON 2002, HÁJEK et al. 2006). Demgegenüber ist nur sehr wenig über die Moore der Nördlichen Kalkalpen bekannt, was angesichts der Vielfalt an unterschiedlichen Moortypen überrascht (RINGLER 1981). Darüber hinaus birgt die rasante touristische und wirtschaftliche Erschließung des Alpenraums ein Gefährdungspotential für die dortigen Moore, was Kenntnisse der ökologischen Verhältnisse erfordert. Ziel dieser Arbeit ist es daher, eine detaillierte Beschreibung der Pflanzengesellschaften von Hochlagenmooren im deutschen Teil der Nördlichen Kalkalpen und ihrer Standortfaktoren zu geben sowie die für die floristische Differenzierung wesentlichen standörtlichen Gradienten zu identifizieren.

**Methoden** – Dazu wurden drei Hochlagenmoore in den Ammergauer Alpen untersucht (Abb. 1). Das Untersuchungsgebiet liegt auf 1100 m ü. NN und weist etwa 1750 mm Jahresniederschlag bei einer Jahresmitteltemperatur von 5 °C auf. Die Moore werden von glaziären und fluvioglaziären Sedimenten umgeben und unterlagert, die hauptsächlich aus Dolomit und Kalkstein bestehen. Zur vegetationskundlichen Beschreibung der Moore wurden 115 Aufnahmen angefertigt. Für gehölzfreie Bestände wurde eine Flächengröße von 1 m<sup>2</sup> gewählt, bei Gebüsch und Wäldern richtete sich die Flächengröße nach dem Minimalflächen-Prinzip. Die Aufnahmen wurden in Abhängigkeit von Anzahl und Deckung diagnostisch wichtiger Arten bestehenden Pflanzengesellschaften zugeordnet. An 46 Meßstellen wurden neben dem Zersetzungsgrad nach von Post (H) auch Pegelstand (WTD), pH-Wert und elektrische Leitfähigkeit (EC) des Moorwassers an sechs Tagen zwischen Anfang Juni und Anfang September 2011 gemessen. Aus den Pegelstanddaten wurde der Wechselfeuchte-Index (WI) nach SCHOLLE & SCHRAUTZER (1993) berechnet. Als Maß für die Fertilität des Standorts wurde aus jeder Vegetationsaufnahme die gewichtete mittlere Ellenberg-Stickstoffzahl kalkuliert. Um Muster in der floristischen Variation zwischen den Aufnahmen zu finden und um die vorgenommene soziologische Zuordnung zu untermauern wurde eine NMDS auf den Art-Datensatz angewendet. Zur Identifizierung der zugrundeliegenden wichtigen standörtlichen Gradienten wurden Umweltvektoren und Regressionsoberflächen an die NMDS angepasst.

**Ergebnisse** – Das Spektrum der aufgenommenen Pflanzengesellschaften und deren Standortverhältnisse kann den Tabellen 4–13 entnommen werden. Gesellschaften der Großseggen (*Magnocaricion elatae*) und Zwischenmoore (*Caricion lasiocarpae*) waren selten und auf die Laggbereiche der Moore beschränkt. Die wichtigsten Gesellschaften subneutraler und neutraler Niedermoorstandorte waren das *Caricetum davallianae* und das *Amblystegio stellati-Caricetum dioicae*, ferner das *Schoenetum ferruginei* und in Schlenken das *Caricetum limosae scorpidietosum* (Abb. 2). Saure, ombrotroph bis schwach minerotrophe Standorte wurden vorwiegend vom *Eriophoro-Trichophoretum cespitosi* bewachsen, bei größerem Abstand zum Moorwasserspiegel im Bereich der Randgehänge auch vom *Pino mugosphagnetum* und vom *Bazzanio-Piceetum*. In Schlenken der Hochmoorbereiche wuchsen das *Caricetum limosae sphagnetosum cuspidati* und das *Sphagno-Rhynchosporium albae*. Kleinseggenriede saurer Niedermoorstandorte (*Caricion fuscae*) waren aufgrund der karbonatreichen Gesteine im Untersuchungsgebiet äußerst selten. Deshalb ergab sich eine deutliche Trennung in Niedermoorstandorte mit pH  $\geq$  5.2 und EC  $\geq$  35  $\mu$ S cm<sup>-1</sup> und ombrotrophe bis schwach minerotrophe Hochmoorstandorte mit pH  $\leq$  5 und EC  $\leq$  30  $\mu$ S cm<sup>-1</sup> (Abb. 5 und 7). Die NMDS zeigte eine gute Übereinstimmung mit der vorgenommenen Klassifizierung der Bestände, auch wenn sich Überlappungen einzelner Assoziationen ergaben (Abb. 3). Die Anpassung der linearen Trends und Regressionsoberflächen ergab, dass der größte Teil der floristischen Variation entlang des Säure-Basen-Gradienten (ausgedrückt durch den pH-Wert) auftrat (Abb. 4). Eine nahezu orthogonale Achse hierzu stellte der Wasserstands-Gradient dar, der ebenfalls eine sehr starke Korrelation mit der NMDS-Konfiguration zeigte. Da sie mit dem pH-Wert stark korreliert ist, erwies sich auch die elektrische Leitfähigkeit als wichtiger Faktor. Unterschiede in der Fertilität der Standorte waren gering. Die höchste Fertilität hatten die Standorte von Großseggenengesellschaften sowie von Wäldern und Gebüsch der Moorränder. H und WI spielten nur eine untergeordnete Rolle für die floristische Differenzierung der Moorstandorte.

**Diskussion** – Trotz der generell guten Übereinstimmung der Ordinationsergebnisse mit der vorgenommenen Klassifizierung der Bestände konnten in der NMDS solche Pflanzengesellschaften, die durch die Dominanz einer Art gekennzeichnet sind (*Schoenetum*, *Pino-Sphagnetum*, Gebüschformen des *Bazzanio-Piceetum*), teilweise nicht klar von Gesellschaften mit ansonsten ähnlicher Artenzusammensetzung getrennt werden, was auf die starke Herabgewichtung hoher Deckungsgrade im Verlauf der NMDS zurückgeführt wird. Der Säure-Basen-Gradient wurde auch von anderen Autoren schon als der wichtigste standörtliche Gradient identifiziert, ist aber nur dann als solcher erkennbar, wenn ein breites Spektrum an unterschiedlich sauren bzw. basischen Moortypen untersucht wird. Ansonsten wäre der Großteil der floristischen Differenzierung auf unterschiedlich hohe Moorwasserstände zurückzuführen, die sich aufgrund der mikrotopographischen Feingliederung der Mooroberfläche einstellen (NORD-BAKKEN 1996a, b, BRAGAZZA & GERDOL 1999a, HÁJKOVÁ & HÁJEK 2004, BRAGAZZA et al. 2005).

Ein Fertilitätsgradient war in unserem Datensatz nur schwach ausgeprägt, was auf die P-Limitierung subneutraler und neutraler Moorstandorte zurückgeführt wird, die daher wie die Hochmoorstandorte wenig produktiv sind (BOYER & WHEELER 1989, BOEYE et al. 1997, THORMANN & BAYLEY 1997, GERDOL et al. 2010). Dass die Fertilität von Großseggen-Standorten und Wäldern und Gebüschern der Moorränder am höchsten war, wird mit der besseren Durchlüftung und Mineralisation sowie dem höheren Nährstoffeintrag in diesen randlichen Bereichen (BRAGAZZA 1996, FREEMAN et al. 1996, 1997) und den höheren N-Gehalten im Torf der Großseggenriede begründet. Die Studie war nicht darauf ausgerichtet den Gradienten vom Moorrand zum Moorzentrum zu untersuchen, da aufgrund der asymmetrischen Form der Moore keine klare Beziehung zwischen Vegetation und Distanz zum Moorrand zu erwarten war. Dennoch zeigten die randlich gelegenen Meßstellen im *Bazzanio-Piceetum* und im *Vaccinium uliginosum*-Stadium des *Eriophoro-Trichophoretum* etwas tiefere Wasserstände und eine stärkere Fluktuation des Moorwasserspiegels, was zu den etwas höheren Mineralisationsraten in diesen Bereichen führt, die sich wiederum in leicht höheren Leitfähigkeitswerten niederschlagen.

Hinsichtlich des Inventars an Pflanzengesellschaften stimmen die Ergebnisse dieser Arbeit mit vorausgegangenen pflanzensoziologischen Beschreibungen montaner Moore Mitteleuropas und der Alpen überein (z. B. KAULE 1974, DIERBEN & DIERBEN 1984, GERDOL & TOMASELLI 1997, LEDERBOGEN 2003). Dennoch handelt es sich bei der vorliegenden Arbeit wohl um die erste ausführliche Darstellung der Vegetationszusammensetzung der häufigsten Moortypen im deutschen Teil der Nördlichen Kalkalpen und deren Standortbedingungen. Sie stellt daher eine grundlegende Referenz für künftige Forschung und Naturschutzbestrebungen in diesem Gebiet dar.

## Acknowledgements

We thank Karl Offner for help with the determination of critical mosses, the Waldkörperschaft Buching-Trauchgau for the driving permission for the study area, and Emer Walker for improving the English in the manuscript. Michal Hájek, Florian Jansen, Johannes Kollmann and one anonymous reviewer contributed useful suggestions on earlier versions of the manuscript. Timo Conradi is sponsored by the Scholarship Programme of the German Federal Environmental Foundation (DBU).

## Supplements and Appendices

**Supplement 1.** Table 5. Relevés of the *Rhynchosporion albae* from the Ammergauer Alps.

**Beilage 1.** Tabelle 5. Aufnahmen des *Rhynchosporion albae* aus den Ammergauer Alpen.

**Supplement 2.** Table 10. Relevés of the *Caricetum davallianae campylietosum* from the Ammergauer Alps.

**Beilage 2.** Tabelle 10. Aufnahmen des *Caricetum davallianae campylietosum* aus den Ammergauer Alpen.

**Supplement 3.** Table 11. Relevés of the *Sphagnetum magellanici* and the *Eriophoro-Trichophoretum cespitosi* from the Ammergauer Alps.

**Beilage 3.** Tabelle 11. Aufnahmen des *Sphagnetum magellanici* und des *Eriophoro-Trichophoretum* aus den Ammergauer Alpen.

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**Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.**

**Appendix S1** R code, vegetation data and environmental data from mires of the Ammergauer Alps.

**Anhang S1.** R-Code, Vegetationsdaten und standörtliche Daten aus Mooren der Ammergauer Alpen.

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