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South Patagonian ombrotrophic bog vegetation reflects biogeochemical gradients at the landscape level

Kleinebecker, Till[1*]; Hölzel, Norbert[1,2] & Vogel, Andreas[1,3]

[1]*Institute of Landscape Ecology, University of Münster, Robert-Koch-Straße 26, 48149 Münster, Germany;*
[2]*E-mail nhoelzel@uni-muenster.de;* [3]*E-mail voghild@uni-muenster.de;*
[*]*Corresponding author; Fax +49 02518338352; E-mail tillhan@uni-muenster.de*

Abstract

Question: Which environmental variables affect the floristic composition of south Patagonian bog vegetation along a gradient of climate and biogeochemical changes with increasing distance from the Pacific ocean?

Location: Trans-Andean transect (53° S), southern Patagonia

Material and Methods: Floristic composition, peat characteristics (water level, decomposition, pH, total nitrogen, total carbon, ash content and plant available P, K, Na, Ca, Mg, Fe, Mn, Zn, and Al) and climatic constraints of ombrotrophic peatlands were measured at 82 plots along a gradient of increasing distance from the Pacific Ocean.

Results: Climatic constraints and biogeochemical peat characteristics significantly change with increasing distance from the Pacific. Peatland vegetation shifted from hyperoceanic blanket bogs dominated by cushion forming vascular plants to the west to *Sphagnum* bogs to the east. Climatic and biogeochemical variables explained a large proportion of the floristic variation along the first DCA axis. The second axis represented a water level gradient. When 'distance to the Pacific' was defined as a covariable in partial CCA, the proportion of variance explained declined for most other variables, especially in the case of annual precipitation and exchangeable base cations and related traits. The differences in biogeochemical characteristics related to peat were mainly attributed to the input of sea-borne cations.

Conclusions: While variation in vegetation composition along a longitudinal gradient crossing the southern Andes was attributed to climatic constraints as expected, vegetation composition was also strongly affected by the biogeochemical characteristics of peat. Sea spray was of high ecological importance to peat chemistry and, consequently, to floristic composition. Presumably, south Patagonian peat bogs represent a glimpse of pre-industrial environments, so that these peat bogs may act as reference systems with respect to atmospheric inputs in mire ecology research.

Keywords: Base cations; Blanket bog; CCA; Chile; Cushion bog; Ordination; Raised bog; Sea spray; *Sphagnum*.

Introduction

The world's natural vegetation is mainly affected by latitudinal, longitudinal and altitudinal gradients that are related to changes in climatic factors (Archibold 1995; Schulz 1995; Breckle 2002). In coastal situations, the longitudinal gradient is created by the temperature buffering influence of the sea and the changing precipitation regime with increasing distance to the ocean. These changing climatic constraints can have a strong impact on the distribution and floristic composition of species (e.g. Senterre et al. 2004; Fang & Lechowicz 2006; Franklin et al. 2006). Besides climatic conditions, the distance to the ocean also influences precipitation chemistry and enhances the supply of sea-borne base cations (Erisman et al. 1998; Vitousek 2002; Haragushi et al. 2003). Such trophic gradients have significant effects on plant growth (e.g. Sánchez-Blanco et al. 2003) and floristic composition (e.g. Vitt et al. 1990; Griffiths 2006).

Nutrient supply and mineral availability are well established as key factors affecting the ecology and the floristic composition of peatlands (e.g. Wheeler & Proctor 2000). Due to their disconnection from groundwater, ombrotrophic bogs receive all their nutrients from atmospheric sources. Thus, these ecosystems are particular sensitive to spatial changes in the chemical composition of precipitation that could originate from natural or anthropogenic processes (Vitt et al. 1990; Gunnarsson et al. 2002). Given this situation, the effect of sea-borne nutrients on floristic composition of ombrotrophic bog ecosystems should be clearly visible along longitudinal gradients near ocean environments. Such an impact has often been assumed (Damman 1995) but rarely confirmed by biogeochemical data.

In general, there is considerable spatial bias in the ecological knowledge of peatlands. In the northern hemisphere, the major ecological gradients affecting the floristic composition of mire vegetation are well known and have been summarized and discussed in several recent studies (e.g. Wheeler & Proctor 2000; Økland et al. 2001; Hájek et al. 2006). The bog-fen gradient (e.g. Wheeler & Proctor 2000), as well as the ecological consequences of anthropogenic nitrogen input and shifts in vegetation caused by climate change (e.g. Berendse et al. 2001; Gunnarsson & Flodin 2007), have been documented comprehensively. There are even a few studies that have explored the influence of sea-borne cations on the floristic composition of mires in relation to the distance to the ocean (e.g. Vitt et al. 1990).

In contrast, research on the peatlands of the southern hemisphere, especially those in southern Patagonia, has been neglected. Existing studies on south Patagonian peatland vegetation has usually focussed on syntaxonomical descriptions (e.g. Pisano 1983; Boelcke et al. 1985). Pisano (1983) interpreted the change in floristic composition of bog vegetation along a W-E transect in south Patagonia as a climatic gradient, mainly as a consequence of the precipitation regime. Also, Moore (1979) and Boelcke et al. (1985) pointed out that peatlands with an annual precipitation of more than 2000 mm are dominated by cushion forming vascular plants such as *Astelia pumila* and *Donatia fascicularis*. In contrast, *Sphagnum*-dominated raised bogs occur in regions with an annnual precipitation between 600 mm and 1500 mm (Pisano 1983). In a transition zone, both types intermingle in the south Patagonian peatlands (Boelcke et al. 1985).

Investigations into broad-scale vegetation-environment relationships that include biogeochemical measurements and lead to a better ecological understanding of vegetation patterns at a landscape level (e.g. Vitt et al. 1990; Virtanen et al. 2006) do not exist for the southern hemisphere. One study of the southern hemisphere presented peat chemical data and focussed on a local scale description of ecological characteristics of a single mire complex (Ruthsatz & Villagran 1991). The south Patagonian region provides particularly suitable conditions for ecological research in mire ecosystems across longitudinal gradients. Due to the strong westerly winds bringing unpolluted air masses, the low human population density and the lack of intense agriculture, the atmospheric nitrogen input in southern Patagonia is marginal (Godoy et al. 2001). Thus, southern Patagonia provides a unique opportunity to study the ecology of ombrotrophic peatlands under pristine conditions with almost no anthropogenic input. Such studies could provide a reference for the trophic status of corresponding northern-hemisphere peatlands under pre-industrial conditions (e.g. Wassen et al. 2005).

Here, we present the first comprehensive study that combines vegetation data with climatic constraints and biogeochemical peat characteristics along the entire trans-Andean climatic gradient. In particular, we will address the following questions:

1. Are climatic constraints the major determinants affecting south Patagonian peatland vegetation?
2. How important are biogeochemical peat characteristics, and is there a detectable effect of sea spray on peatland vegetation?
3. Do south Patagonian peat bogs show biogeochemical constraints that could provide clues about the pre-industrial conditions of peatlands in other regions including the northern hemisphere?

Material and Methods

Study area

The steep climatic gradient created by the southern Andes probably is the strongest climatic divide worldwide and its orographic effects can be observed more clearly there than anywhere else on earth (Miller 1976). This climate gradient is most significantly reflected by the precipitation regime (Endlicher & Santana 1988). The hyperoceanic western Chilean channel region has up to 10 000 mm annual precipitation, whereas on the eastern side of the Andes, precipitation decreases to less than 500 mm towards the Patagonian steppe (Schneider et al. 2003). Although mean annual temperatures hardly change along that gradient (ca. 6 °C), the inter-annual amplitude of temperature increases significantly towards the more continental parts of the gradient (Pisano 1977). This temperature difference is best expressed by regular frost events in winter and higher summer temperatures in the east, as well as the absence of frost periods and cool summer temperatures in the hyperoceanic west (Tuhkanen 1992).

This steep climatic gradient is reflected in the vegetation types across these zones (Boelcke et al. 1985). From west to east, one can observe a clear zonation pattern from coastal blanket bog to cool temperate evergreen rainforest, deciduous forest and dry Patagonian steppe. Along this longitudinal gradient, ombrotrophic peatland vegetation also changes in its floristic composition. With increasing distance from the Pacific Ocean, hyperoceanic blanket bogs, which were built by cushion-forming vascular plants such as *Donatia fascicularis* and *Astelia pumila* are gradually replaced by *Sphagnum magellanicum* dominated bogs that exist exclusively under more continental climatic conditions (Kleinebecker et al. 2007).

Sampling of ombrotrophic peatland vegetation took place along a trans-Andean transect of ca. 100 km west of the Patagonian steppe zone in southern Chile. Most of the investigated sites are located NW of Punta Arenas, the capital of the XIIth Region (Fig. 1). The most western study site was located on Isla Tamar in the Magellan Strait

(52°54' S, 73°48' W). The most eastern peatlands were situated near Estancia Kerber in the Río Rubens valley (52°04' S, 72°2' W) and north of the Estancia Skyring near the Río Pérez (52°28' S, 71°54' W) (Fig. 1). All investigated sites were located below 300 m a.s.l.

The entire study area is situated within the geological unit of the Andean cordillera that can be divided from west to east into three units (Pisano 1977) including the coastal, central and marginal cordillera. The coastal cordillera occupies the western parts of the study area and is mainly comprised of acid igneous rocks, such as andesites, diorites and granites. The central Cordillera consists principally of strongly metamorphosed rocks, such as crystalline schists, which are penetrated by intrusions of granites and granodiorites. The marginal cordillera is situated on the east side of the Andes bordering the Magellanes sedimentary basin further east (Palmer & Dalziel 1973) and this cordillera is made up of sedimentary rocks such as sandstones, claystones and conglomerates. In general, one can conclude that the bedrock of the entire study area is uniformly acidic and base-poor resulting in substrate conditions which are very similar in nutrients.

Sampling and biogeochemical analysis

A total of 82 relevés were made in floristically and structurally homogenous stands in predominantly ombrotrophic peatland complexes. Sampling took place during March and April 2004 and 2005. Vegetation was sampled in 11 geographic regions with the number of plots per region ranging from three to 17, depending on accessibility and logistic necessities during field work (Fig. 1). The plot size was 1 m^2. Cover-abundance data was recorded following the Braun-Blanquet approach (Westhoff & van der Maarel 1973; Braun-Blanquet 1964). Because of difficulties in determination and differentiation in the field of some cryptogams, uncertain species were named at the level of genus or, in the case of some liverworts, species were merged into one group named ‘other liverworts’.

Ground water level was measured by digging a hole and measuring the distance of the water level to the surface of the ground. We used an ordinal scale ranging from 0 = ground water at the soil surface to 7 = groundwater > 40 cm below the soil surface (see Kleinebecker et al. 2007). While water table can be variable and display large seasonal differences (Wheeler & Proctor 2000), continental Patagonian *Sphagnum* bogs show a surprisingly low variation of water table depth (Baumann 2006). Thus, the water table data of this investigation may be utilized for an approximate description of the edaphic moisture regime. The degree of decomposition of the peat was estimated to a depth of 5-10 cm below the surface using the ten stage scale of von Post (Anon. 2005). Annual precipitation, mean annual temperature and mean temperature of the coldest and the warmest months were interpolated from available data (Pisano 1977; Tuhkanen 1992; Schneider et al. 2003; Schneider & Kilian unpubl. data). The distance to the Pacific Ocean of the sampled sites was estimated using a graphically derived ordinal scale of nine stages, which differentiates distances to the Pacific Ocean using equal divisions between the sites closest and farthest from the Pacific Ocean (Kleinebecker et al. 2007). The influence of the Atlantic Ocean was considered to be marginal and was not included in the ordination due to the strong and constant westerly winds creating a steep west to east climatic gradient.

For each relevé, volumetric mixed surface samples of peat were taken at a depth of 5-10 cm. Roots were eliminated as precisely as possible in the field. Samples were dried at 50 °C and screened through a sieve with

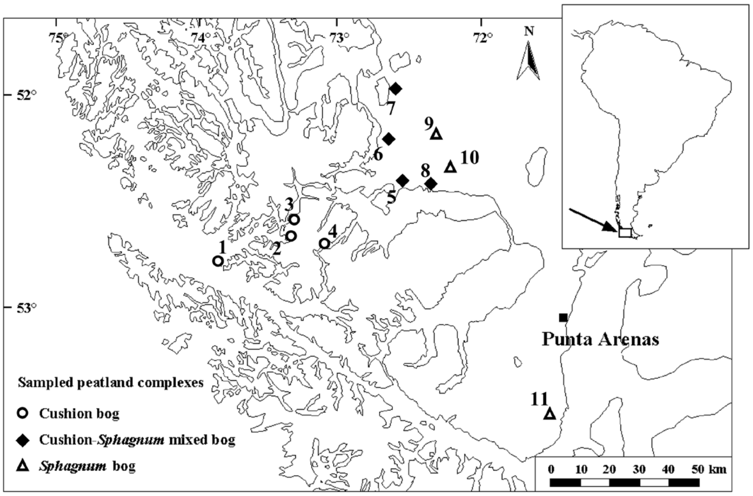

Fig. 1. Locations of peatland complexes sampled in the study. Numbers indicate sampling regions: 1 = Isla Tamar ($N = 3$), 2 = Lago Muy Profundo ($N = 3$), 3 = Muños Gamero ($N = 7$), 4 = Bahía Bahamondes ($N = 17$), 5 = Río Azocar ($N = 11$), 6 = Río Blanco ($N = 5$), 7 = Lago Aníbal Pinto ($N = 7$), 8 = Bahía Williams ($N = 10$), 9 = Río Rubens ($N = 9$), 10 = Río Pérez ($N = 5$), and, 11 = San Juan ($N = 4$).

2 mm mesh wire. Total contents of C and N (element autoanalyzer, CARLO ERBER NA 1500), the ash-content (ashing overnight in a muffle furnace at 550 °C), CAL-soluble P (Schüller 1969, photometrical measurement with 578 nm, PERKIN ELMER) and NH_4Cl exchangeable fractions of K, Na, Ca, Mg, Fe, Mn, Zn and Al (Meiwes et al. 1984, determination with an AAS, PERKIN ELMER) were measured in the laboratory.

Data analysis

For numerical analysis, Braun-Blanquet cover-abundance values were transformed into the 1-9 ordinal scale of van der Maarel (1979). For ordination, only species present on at least three plots were used. Liverworts and lichens that could not be determined at species level were not included. Major gradients were explored by detrended correspondence analysis (DCA, Hill & Gauch 1980), a method of indirect gradient analysis (Jongman et al. 1995). Running the DCA with detrending by 26 segments revealed a gradient length on the first axis of 4.599 standard deviation units and on the second axis of 2.814. All relevés were allocated to three major vegetation types including the hyperoceanic cushion plant type ($n = 34$) dominated by cushion-forming vascular plants, the *Sphagnum magellanicum* type ($n = 36$) at the east side of the Andes and the transitional cushion-*Sphagnum* mixed type ($n = 12$) (see Kleinebecker et al. 2007).

We compared means of the three major vegetation types using the parametric Tukey HSD test for unequal sample size for the normally distributed environmental variables with homogeneous variances. Non-normal and ordinal-scaled data were analysed using the Kruskal-Wallis H-test with pairwise comparisons analysed using the Mann-Whitney *U*-tests. Probability values from multiple pairwise comparisons were adjusted using Bonferroni corrections (Sokal & Rohlf 1981).

Spearman rank correlations between the environmental variables and the axis scores of DCA ordination were calculated. Environmental variables showing a high correlation to DCA axes were extracted and reapplied for the following direct gradient analysis (Ejrnæs 2000). For a further reduction of the number of explanatory variables, Ca, Mg, Na and K were merged to one group (base cations) by building up the sum of the respective contents. To estimate the relative importance of the measured environmental variables, we applied a Canonical Correspondence Analysis (CCA), which gave a gradient length of 3.837 standard deviation units for the first axis and 2.559 for the second. We performed a decomposition of variance by running a series of partial CCAs to isolate and specify the relative importance of the variable 'distance to the Pacific Ocean' on species composition in relation to other environmental variables. For all statistical calculations, metric environmental variables were log-transformed. DCA was performed using the PCORD 5.0 software package (McCune & Mefford 2006), CCA using CANOCO 4.5 (ter Braak & Šmilauer 2002). ANOVA and Spearman rank correlation were carried out using SPSS 11.0 (Anon. 2002).

Results

Vegetation gradients and biogeochemistry

The first axis in the DCA ordination resulted in a distinct separation of vegetation types along a gradient of increasing distance to the Pacific Ocean (Fig. 2). With an increasing distance of our sites to the Pacific Ocean, hyperoceanic blanket bogs built up by cushion building vascular plants such as *Donatia fascicularis* and *Astelia pumila* were gradually replaced by *Sphagnum magellanicum* dominated bogs, which existed exclusively under more continental climatic conditions at the east side of the Andes. Within a transition zone, the cushion-*Sphagnum* mixed types occurred as the species intermingled, sometimes in different proportions. These major vegetation types showed significant differences in climatic constraints as well as in biogeochemical peat characteristics (Table 1).

The sample scores of Axis 1 of the DCA analysis were also strongly correlated with the measured peat characteristics (degree of peat decomposition, ash content, total N, pH, CAL soluble P and plant available Na, Ca and Mg) as well as with climatic variables (annual precipitation and temperature of the coldest month), which increased with proximity to the Pacific Ocean, respectively (Table 2). The opposite was true for the C:N ratio, plant-available Mn and the temperature of the warmest month, which showed a significant decrease with increasing proximity to the Pacific Ocean. The DCA Axis 2 exhibited a clear separation of samples along a water level gradient that could be found at both sides of gradient along the first axis. No, or only weak, correlations were calculated for the mean annual temperature, the elevation above sea level and for the NH_4Cl soluble contents of K, Fe, Zn and Al (Table 2).

Decomposition of shared variance

The constraining variables used in CCA explained 39.5% of the variance in the floristic composition of the investigated mire vegetation (Table 2). Excluding the factor distance to the Pacific Ocean, all other environmental variables explained 29.0% of the total inertia. Taken as the only constraining variable in CCA, the distance to the Pacific Ocean explained 10.5% of the total inertia,

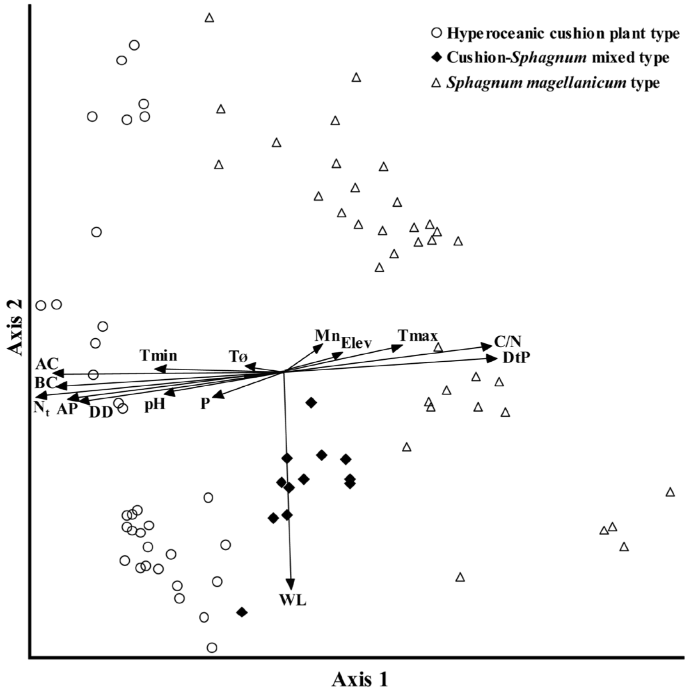

Fig. 2. Biplot of DCA ordination of 82 samples and selected environmental variables of south Patagonian peatlands. Environmental variables: DtP = distance to the Pacific ocean, DD = degree of decomposition, WL = water level, AC = Ash content [mg.l^{-1}], N_t = total N [mg.l^{-1}], C/N = C:N ratio, pH = pH (CaCl$_2$), P = CAL soluble P [mg.l^{-1}], BC = sum of NH$_4$Cl soluble base cations (Ca, Mg, Na, K) [cmol$_c$.l^{-1}], Mn = NH$_4$Cl soluble Mn [cmol$_c$.l^{-1}], TØ = mean annual temperature, Tmax = mean temperature of the warmest month, Tmin = mean temperature of the coldest month, AP = annual precipitation, Elev = elevation above sea level. Vectors point in the direction of increasing values for the respective variables, with longer vectors indicating stronger correlations between vectors and axes.

which was similar to other environmental factors such as annual precipitation, degree of decomposition, ash content, total N, C:N-ratio and NH$_4$Cl soluble base cations (Table 3). Slightly lower percentages of the total variance were explained by the water level and temperature of the coldest month, while the pH, plant available Mn and the temperature of the warmest month explained at least 5% of the variance of our data set. Minor explanatory values were calculated for plant available P and elevation. After adjustment for the distance to the Pacific Ocean, the explained variance dropped most drastically in the cases of annual precipitation, degree of decomposition,

Table 1. Mean and SE of environmental variables in the three major types of south Patagonian bog vegetation. Different letters indicate significant differences ($P < 0.05$) after parametric Tukey-test (a, b, c) or non-parametric Mann-Whitney U-test (A, B, C; Bonferroni corrected: correction of the significance level due to multiple testing). * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	Hyperoceanic cushion plant type (N = 34)		Cushion-*Sphagnum* mixed type (N = 12)		*Sphagnum magellanicum* type (N = 36)		
	Mean	Min / Max	Mean	Min / Max	Mean	Min / Max	P
Degree of decomposition$^{\#}$	6 ± 0.23^{A}	4 / 9	5 ± 0.30^{B}	4 / 7	2 ± 0.22^{C}	1 / 5	***
Water level$^{\#}$	4 ± 0.28	0 / 6	4 ± 0.08	4 / 5	2.5 ± 0.39	0 / 6	-
Elevation [m a.s.l.]	74 ± 6.85^{A}	15 / 170	56 ± 8.64^{A}	15 / 130	122 ± 13.11^{A}	10 / 280	*
Annual precipitation [1000 mm]	5.3 ± 0.22^{A}	2.5 / 7.0	1.6 ± 0.17^{B}	1.0 / 2.5	1.2 ± 0.11^{B}	0.6 / 2.5	***
Mean annual T [°C]	5.8 ± 0.09^{A}	4.5 / 6.5	6.2 ± 0.09^{A}	5.5 / 6.5	5.5 ± 0.14^{A}	4.5 / 6.5	*
Mean T of coldest month [°C]	2.4 ± 0.17^{A}	1.0 / 5.5	2.0 ± 0.21^{A}	0.0 / 3.0	0.5 ± 0.24^{B}	-1.5 / 3.0	***
Mean T of warmest month [°C]	9.3 ± 0.10^{A}	8.0 / 10.5	10.8 ± 0.08^{B}	10.5 / 11.0	10.5 ± 0.08^{B}	9.5 / 11.5	***
PH (CaCl$_2$)	3.4 ± 0.05^{a}	2.9 / 4.4	3.0 ± 0.05^{b}	2.7 / 3.3	3.0 ± 0.02^{b}	2.7 / 3.3	***
Total N [mg.l^{-1}]	1.94 ± 0.15^{A}	0.58 / 4.33	1.03 ± 0.07^{B}	0.76 / 1.66	0.88 ± 0.07^{C}	0.54 / 1.52	***
C:N	32 ± 2.07^{a}	15 / 61	50 ± 2.92^{b}	31 / 68	140 ± 8.82^{c}	29 / 242	***
Ash content [mg.l^{-1}]	5.12 ± 0.57^{A}	1.30 / 15.06	2.53 ± 0.21^{B}	1.50 / 3.60	1.40 ± 0.09^{C}	0.65 / 3.23	***
CAL soluble P [mg.l^{-1}]	7.83 ± 0.67^{A}	1.95 / 19.72	12.83 ± 0.68^{B}	8.98 / 17.66	3.90 ± 0.57^{C}	1.03 / 13.67	***
NH$_4$Cl soluble K [cmol$_c$.l^{-1}]	1.37 ± 0.08^{a}	0.49 / 2.43	2.08 ± 0.28^{b}	0.90 / 4.61	1.07 ± 0.10^{c}	0.32 / 2.77	***
NH$_4$Cl soluble Na [cmol$_c$.l^{-1}]	3.86 ± 0.41^{A}	0.64 / 9.17	1.83 ± 0.19^{B}	1.27 / 3.72	1.30 ± 0.10^{C}	0.31 / 2.90	***
NH$_4$Cl soluble Ca [cmol$_c$.l^{-1}]	13.49 ± 1.06^{a}	6.51 / 34.81	8.42 ± 0.47^{b}	5.72 / 10.84	4.97 ± 0.37^{c}	0.74 / 10.20	***
NH$_4$Cl soluble Mg [cmol$_c$.l^{-1}]	14.06 ± 1.15^{a}	2.57 / 31.52	10.25 ± 0.75^{b}	4.17 / 14.27	5.55 ± 0.45^{c}	2.01 / 13.32	***
Base Cations (sum of Ca, Mg, Na, K)	32.78 ± 1.90^{a}	10.75 / 62.28	22.58 ± 1.18^{b}	12.63 / 26.49	12.90 ± 0.80^{c}	3.87 / 24.76	***
NH$_4$Cl soluble Fe [cmol$_c$.l^{-1}]	0.28 ± 0.07	0.00 / 1.58	0.67 ± 0.19	0.03 / 2.01	0.47 ± 0.21	0.00 / 5.57	-
NH$_4$Cl soluble Mn [cmol$_c$.l^{-1}]	0.07 ± 0.02^{a}	0.01 / 0.51	0.45 ± 0.11^{b}	0.11 / 1.24	0.29 ± 0.05^{b}	0.01 / 1.56	***
NH$_4$Cl soluble Zn [cmol$_c$.l^{-1}]	0.01 ± 0.00	0.00 / 0.05	0.02 ± 0.00	0.00 / 0.04	0.02 ± 0.00	0.00 / 0.04	-
NH$_4$Cl soluble Al [cmol$_c$.l^{-1}]	1.01 ± 0.18^{ab}	0.09 / 4.41	1.48 ± 0.35^{a}	0.13 / 3.69	0.88 ± 0.26^{b}	0.01 / 6.12	*

$^{\#}$ For ordinally scaled variables, the median is given.

Table 2. Spearman rank correlations between Axes 1, 2 and 3 from the DCA analysis, and the measured environmental variables. Significant correlation coefficients are given as: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. See Table 1 for units of variables.

Environmental variables	Axis 1		Axis 2		Axis 3	
Distance to Pacific Ocean	**0.848**	***	0.280	*	-0.226	*
Degree of decomposition	**-0.789**	***	-0.357	***	0.179	
Water level	0.172		**-0.789**	***	0.106	
Elevation	0.300	**	0.112		-0.011	
Annual precipitation	**-0.844**	***	-0.262	*	0.250	*
Mean annual temperature	-0.213		0.001		0.019	
Mean temperature of coldest month	**-0.627**	***	-0.089		0.117	
Mean temperature of warmest month	**0.628**	***	0.289	**	-0.303	**
Ash content	**-0.810**	***	-0.135		0.104	
Total N	**-0.872**	***	-0.274	*	0.265	*
C:N	**0.824**	***	0.312	**	-0.324	**
pH ($CaCl_2$)	**-0.652**	***	-0.274	*	0.265	*
CAL soluble P	-0.406	***	-0.290	**	0.172	
NH_4Cl soluble K	-0.251	*	-0.106		-0.152	
NH_4Cl soluble Na	**-0.656**	***	-0.337	**	0.002	
NH_4Cl soluble Ca	**-0.806**	***	-0.273	*	0.172	
NH_4Cl soluble Mg	**-0.659**	***	-0.290	**	0.221	*
NH_4Cl soluble Fe	0.036		-0.087		-0.205	
NH_4Cl soluble Mn	0.390	***	0.221	*	-0.294	**
NH_4Cl soluble Zn	-0.059		0.034		-0.157	
NH_4Cl soluble Al	-0.187		-0.087		-0.185	
Base Cations (sum of Ca, Mg, Na, K)	**-0.790**	***	-0.347	**	0.188	

ash content, total N, C:N-ratio and base cations and became insignificant in case of pH-value (Table 3). After adjustment for all other environmental variables, the explanatory value of the variable distance to the Pacific Ocean declined to 1.0% and became non-significant.

Tables 2 and 3 indicate a high degree of shared variance between the distance to the Pacific Ocean and all of the biogeochemical and climatic variables mentioned above. The water level was the only environmental variable that did not show a noteworthy proportion of shared variance when using the distance to the Pacific Ocean as a covariable. This means that the water level had a significant effect on the floristic composition of the investigated bog complexes irrespective of their position along the trans-Andean transect.

Discussion

Importance of climatic constraints

The striking differences in floristic composition of south Patagonian bog vegetation from west to east has been attributed to climate in past studies (Pisano 1983; Boelcke et al. 1985; Blanco & de la Balze 2004), but climate alone is not sufficient to explain these differences. In our study, biogeochemical variables that were related to the distance to the Pacific Ocean explained a high proportion of the variance. These results concur with Nicholson et al. (1996), who found that biogeochemical variables such as pH and surface water chemistry explained more of the floristic variation in North American peatlands than climatic variables. Also, Gignac et al. (1991) emphasized the importance of biogeochemical factors on species composition along a gradient of increasing distance to the Pacific Ocean in western Canada. Thus, in addition to the hygric and thermic component of the gradient, the shift in biogeochemical properties along the gradient should be considered, because these also affect the vegetation of these peatlands.

Climatic factors directly affect plant growth and biogeochemical peat characteristics by controlling processes such as mineralization and decomposition rates (Aerts 2006), so climatic factors should not be neglected while considering floristic composition of peatlands. It must also be noted that the importance of precipitation that is considered to be the controlling factor of the floristic composition of south Patagonian peatland vegetation (e.g. Pisano 1983) may be overestimated. Although the explanatory value of the annual precipitation was high in our study, the ground water level clearly separated our vegetation samples on both sides of the longitudinal gradient. This ground water level difference means that both edaphically wet and relatively dry sites occurred under hyper-humid Pacific as well as under less humid and more continental climatic conditions. Consequently, even in the hyperoceanic western parts of the gradient, water level conditions should be suitable for *Sphagnum magellanicum*, which is known to be a hummock species with a preference for drier site conditions (Hájková & Hájek 2004). However, this species dominates the vegetation only in the eastern bog complexes, which means that the precipitation regime alone does not provide a sufficient explanation for the dominance of cushion-

Table 3. Results of various CCA analyses isolating the effect of the variable ‘distance to Pacific’ on floristic composition including covariable, Eigenvalue (sum of all canonical eigenvalues – measure for explanatory power of the variables (total inertia: 3.826)), % = percentage of explained variance, *F* (*F*-ratio statistics for the test on the trace), *P* = corresponding probability value obtained by the Monte-Carlo-permutation test (499 permutations). * variables with strong colinearity (degree of decomposition, C:N ratio, mean temperature of warmest month; variance inflation factor > 10) were excluded. See Table 1 for the units of variables.

Explanatory variables	Covariable	Eigenvalue	%	*F*	*P*
Distance to Pacific	-	0.402	10.5	9.400	0.002
	All variables*	0.039	1.0	1.173	0.218
All variables*	-	1.511	39.5	3.752	0.002
	Distance to Pacific	1.109	29.0	3.004	0.002
Degree of decomposition	-	0.388	10.1	9.019	0.002
	Distance to Pacific	0.142	3.7	3.428	0.002
Water level	-	0.349	9.1	8.031	0.002
	Distance to Pacific	0.351	9.2	9.017	0.002
Ash content	-	0.387	10.1	8.992	0.002
	Distance to Pacific	0.121	3.2	2.896	0.002
Total N	-	0.469	12.3	11.167	0.002
	Distance to Pacific	0.156	4.1	3.759	0.002
C:N ratio	-	0.433	11.3	10.205	0.002
	Distance to Pacific	0.134	3.5	3.219	0.002
pH	-	0.271	7.1	6.086	0.002
	Distance to Pacific	0.041	1.1	0.966	0.486
P	-	0.176	4.6	3.858	0.002
	Distance to Pacific	0.146	3.7	3.380	0.002
Base cations	-	0.394	10.3	9.196	0.002
	Distance to Pacific	0.162	4.2	3.918	0.002
Mn	-	0.242	6.3	5.397	0.002
	Distance to Pacific	0.128	3.3	3.078	0.002
Elevation	-	0.142	3.8	3.073	0.002
	Distance to Pacific	0.094	2.5	2.172	0.004
Annual precipitation	-	0.451	11.8	10.687	0.002
	Distance to Pacific	0.099	2.6	2.357	0.004
Mean temperature of coldest month	-	0.334	8.7	7.648	0.002
	Distance to Pacific	0.135	3.5	3.247	0.002
Mean temperature of warmest month	-	0.266	7.0	5.977	0.002
	Distance to Pacific	0.085	2.2	2.016	0.018

building vascular plants and the lack of *S. magellanicum* in the west.

The mean annual temperature does not show significant differences in southern Patagonia (Tuhkanen 1992). Consequently, mean annual temperature explained a low proportion of the variance in our data set. The interannual temperature amplitude significantly increases with increasing distance to the Pacific Ocean (Pisano 1977). Distinct frost periods in winter along with warmer and drier periods during the summer season are important factors affecting the floristic composition in the peatlands of the northern hemisphere (Dierßen 1982; Sjörs 1983). However, our results suggested that variables related to temperature are not the key-factors, because other factors explained a significantly higher proportion of the floristic variability.

Biogeochemical peat characteristics, sea spray

Base cations available to plants decreased in the peat from oceanic to more sheltered sites at the east side of the Andean range in our study. Higher concentrations of these base cations in the peat of oceanic mires are most likely attributable to mineral input via sea spray. This shift in base cations across the gradient concurs with the findings by the analysis of surface water and precipitation chemistry of western Canadian mires (Malmer et al. 1992). They found significantly higher concentrations for Na, Ca and Mg in surface water in exposed localities than in sheltered ones. Precipitation showed higher concentrations of Na in oceanic regions whereas the amounts of the other base cations were higher in continental areas due to dry and wet deposition of dust. Concerning the high amount of annual precipitation on the Pacific side of Canada, the input of sea-borne cations was a major source even for Ca, Mg and K that are normally of terrestrial origin.

Along a gradient of increasing distance to the ocean in western Canada, Vitt et al. (1990) demonstrated that the gradient was highly correlated with surface water chemistry indicating the effect of sea spray. Van Groenendael et al. (1982) drew similar conclusions for western European peatland lakes. For the southern hemisphere, Damman (1995) pointed out that differences in precipitation chemistry caused by the increased input of base cations in proximity to the ocean had a significant impact on the floristic composition of Tasmanian peatland vegetation. Due to the lack of information on peat and surface water chemistry in our study area, the variation in floristic composition on a regional scale was formerly almost exclusively interpreted as a consequence of the steep climatic gradient created by the south Patagonian Andes (e.g. Pisano 1983; Blanco & de la Balze 2004). Our findings strongly suggest an important role of sea spray in influencing the nutritional status of peatland vegetation when considering the shift in floristic composition of peatlands across the Andes.

However, even after recognizing the effect of sea spray on peatland vegetation with the distance to the Pacific Ocean, the content of plant available base cations still explained a minor part of the floristic variation of our samples. This might indicate that base cations may be impacted by underlying bedrock in the Pacific region, a situation that is typical of many blanket bogs (Dierßen 1982). On the other hand, atmospheric inputs can vary within wide limits (Wheeler & Proctor 2000), so that the linear relationship of decreasing mineral input via sea spray with increasing distance to the ocean at the landscape level can be overruled by a certain variation in atmospheric deposition at the local scale.

Nitrogen availability is a growth-limiting factor in many peatland ecosystems (Bridgeham et al. 1996), and nitrogen is supposed to be the most important limiting factor in low deposition sites (Aerts et al. 1992). Our study sites are all supposed to receive low anthropogenic N deposition due to the strong westerly winds and the lack of intensive agriculture (Godoy et al. 2001). Nevertheless, we measured large differences in the total N content and the C:N ratio that were obviously not caused by atmospheric inputs. Bayley & Thormann (2005) reported increasing mineralization and decomposition rates along a bog - fen gradient. Under oceanic conditions our study sites had a better mineral supply due to the input of base cations via sea spray. Thus, mineralization and decomposition are presumably enhanced by the higher availability of base cations, which results in a better litter quality and higher total N contents and lower C:N ratios of the more oceanic sites. In general, hummock *Sphagnum* species are more resistant to decomposition than vascular plants in peatlands (Szumigalski & Bayley 1996). We found that the degree of decomposition and the total N content were significantly higher in the oceanic peatlands dominated by vascular plants. The higher decomposition rates expressed by the higher degree of decomposition and the higher total N contents as well as the lower C:N ratio of the more oceanic bogs indicated a stronger micro-biological activity, which could mobilize the high N stocks in the upper peat layer.

Plant available P showed a weak but significant decrease with increasing distance to the ocean. A possible explanation for this decrease could be that peat samples originating from closer to the Pacific Ocean have higher N contents, which induces a higher mineralization of P. Such a secondary effect of higher P mineralization is assumed by Malmer & Wallén (2005) for Swedish mires. In general, the plant available P content measured in our peat samples was relatively low and explained only a minor part of the floristic variation in our data set. Thus, phosphorous seems to be of minor importance for the floristic and ecological differentiation of ombrotrophic south Patagonian peatlands.

Although the explanatory value of Mn was also relatively low, it was the only cation that was increasingly available for plants in the eastern sites. The dissolubility of Mn increases with decreasing pH and Mn remains stable even in strongly acidic organic soils (Lavelle & Spain 2001). We found higher Mn contents in the more acid eastern *Sphagnum*-dominated peatlands, and there was less Mn in the extremely precipitation-rich hyperoceanic peatlands on the western side of the gradient.

South Patagonian bogs represent pre-industrial trophic conditions

The decomposition of *Sphagnum* is stimulated by N deposition, which also affects litter N concentration and release (Limpens & Berendse 2003). In Europe, heavy atmospheric nitrogen inputs caused by emissions from agriculture have been measured, which often reach critical loads for ombrotrophic peatland ecosystems (Bragazza et al. 2004). In contrast, the input of atmospheric nitrogen into south Patagonian ecosystems is extremely low (Godoy et al. 2001). In our study, we measured extremely variable C:N ratios reaching values up to 250 (Table 1) in the eastern *Sphagnum* bogs not influenced by sea spray. C:N ratios reported from Malmer & Wallén (1993) reaching up to 180 in extreme cases were the only comparable values. The normal value of C:N ratio for an ombrotrophic boreal bog in Canada is ca. 80 (Bayley & Thormann 2005). The extremely N-poor conditions of the south Patagonian *Sphagnum* bogs documented in this study presented a unique opportunity to study peatlands in conditions not affected by atmospheric deposition. Ecological relationships such as trophic effects caused by sea spray could be studied without anthropogenic influence, so that these peatlands act as excellent reference systems for mire ecology research.

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