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GRADIENTS OF CONTINENTALITY AND MOISTURE IN SOUTH PATAGONIAN OMBROTROPHIC PEATLAND VEGETATION

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Abstract: This study presents the analysis of 381 phytosociological relevés describing predominantly ombrotrophic South Patagonian lowland peatland vegetation along a gradient of increasing continentality. Numerical methods such as cluster analysis and detrended correspondence analysis (DCA) were carried out to explore the data set. Cluster analysis resulted in nine vegetation types that were also distinctly separated in DCA ordination. The major floristic coenocline along the first DCA axis reflected a gradient of continentality ranging from pacific blanket bogs dominated by cushion plants to *Sphagnum*-dominated continental raised bogs. Increasing continentality along the first axis was parallel with decreasing peat decomposition and increasing peat depth and acidity. In contrast, floristic variation along the second DCA axis represented a water level gradient.

The typical sequence of vegetation types along the hollow-hummock moisture gradient that is well established for north hemispherical peatlands could also be observed in *Sphagnum*-dominated South Patagonian raised bogs with a surprising similarity in floristic and structural features. Concerning the gradient of continentality significant differences in comparison with the northern hemisphere could be established. Most obvious was the dominance of cushion building plants (e.g. *Astelia pumila*, *Donatia fascicularis*) in South Patagonian oceanic peatlands, whereas this life form is totally absent from the northern hemisphere. Similar to the continental *Sphagnum* bogs the cushion plant vegetation of hyperoceanic peatlands exhibited a clear separation along the moisture gradient.

Keywords: Blanket bog, Climatic gradient, Cluster analysis, Cushion bog, DCA, Mire, Raised bog

INTRODUCTION

During the past decade, peatland ecosystems have become a major subject of ecological research because of their carbon storing nature and their importance in global carbon cycling (e.g. TURUNEN & TOLONEN 1996, VITT et al. 2000, KELLER et al. 2004). The vegetation and ecology of the north hemispherical boreal peatlands, where most of the global peat resources are located (LAPPALAINEN 1996), have been studied intensively since the beginning of vegetation science. The major ecological gradients affecting the floristic composition of north-west European mire vegetation have been discussed and summarized in several recent studies (e.g. WHEELER & PROCTOR 2000, ØKLAND et al. 2001, HÁJEK et al. 2006). Even a deeper knowledge of nutrient status and cycling (e.g. MALMER 1986) and restoration of peatlands is well established in this part of the world (e.g. ROCHEFORT & LODE 2006). In contrast, south hemispherical peatlands, especially those in southern Patagonia, have been neglected so far by research. Comprehensive ecological studies in these pristine and largely undisturbed peatlands are urgently needed because they could act as reference systems of

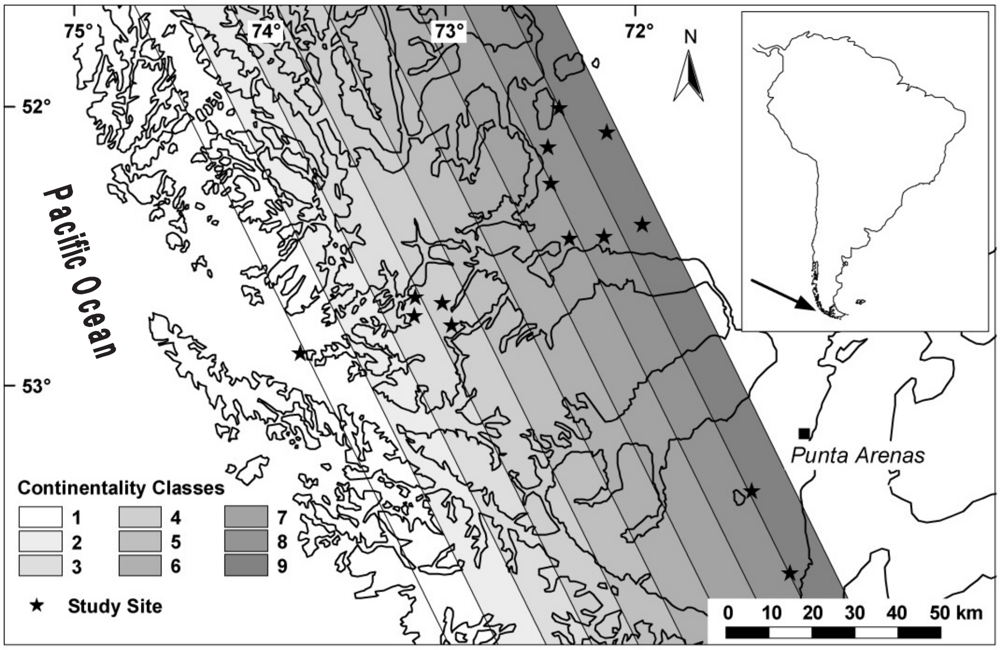

Fig. 1. Locations of studied peatland complexes of southernmost Patagonia along the trans-andine climatic gradient. Continentality classes were determined graphically as equal division between the most pacific and the most continental sites.

pre-industrial conditions. Such work could contribute to a better understanding of unspoiled natural processes in peatlands and may even provide highly relevant information for mire conservation and restoration in the northern hemisphere. Basic knowledge on major floristic and ecological gradients in these so far poorly studied systems is of crucial importance as a starting point for more detailed research.

Existing studies on South Patagonian peatland vegetation usually had a relatively narrow spatial and syntaxonomical focus (DOLLENZ 1980, 1982, 1986, PISANO 1971, 1972, 1973, 1983a) or were based on a relatively small number of vegetation records (ROIG et al. 1985). None of these studies include a sufficient consideration of cryptogams. The overviews of MOORE (1979), PISANO (1983b) and BLANCO & DE LA BALZE (2004) lack any vegetation sample and are probably based on the scarce literature or subjective observations in the field. Comprehensive studies based on sufficient data and covering larger areas are still missing. Due to their inaccessibility, high logistical effort for research and the unpleasant climatic conditions for researchers, in particular the peatlands of highly oceanic western parts of the region have been poorly investigated so far.

Southern Patagonia provides a unique opportunity to study the floristic variation in peatland vegetation along a very steep climatic gradient that ranges within a distance of less than 100 km from hyperoceanic peatlands of the South Patagonian Channels to continental peat bogs at the east side of the Andes. Along this very steep trans-andine climatic gradient,

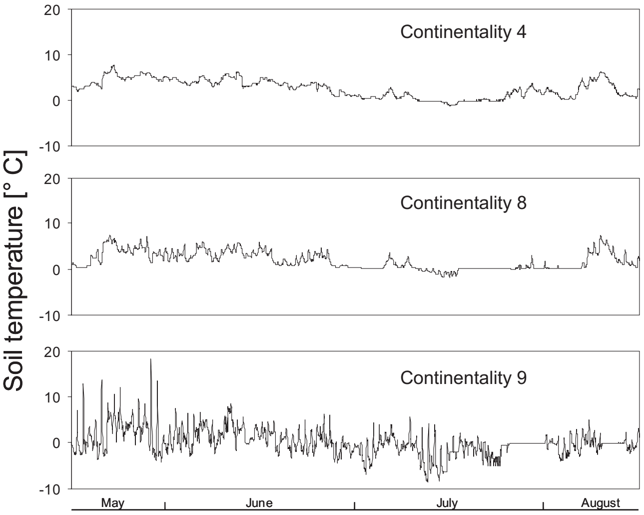

Fig. 2. Soil temperature in three peatlands along the gradient of continentality. Temperature was measured by dataloggers (ONS-TBI32-20+50) 2 cm below the surface between 17 May 2004 and 16 August 2004. Continentality 4: oceanic cushion bog at Bahía Bahamondes (52°48′ S, 72°57′ W), Continentality 8: mixed *Sphagnum*-cushion plant peatland at Bahía Williams (52°31′ S, 72°08′ W), Continentality 9: continental *Sphagnum* bog near Estancia Kerber (52°04′ S, 72°02′ W), see also Fig. 1.

vegetation changes distinctly from cushion bogs in the west dominated by *Astelia pumila* and *Donatia fascicularis* to *Sphagnum*-dominated continental raised bogs towards the east (ROIG et al. 1985). In this paper, we present the first comprehensive study based on a large data set covering the entire gradient of continentality. Using multivariate statistical methods we will explore major patterns and gradients of floristic variation in the vegetation of ombrotrophic South Patagonian peatlands.

MATERIALS AND METHODS

Study area

The study area is situated in southernmost Chile. Most of the investigated sites are located NW of Punta Arenas, the capital of the XIIth Region (Fig. 1). The South Patagonian Andes create a steep climatic gradient, which is most significantly reflected by the precipitation regime. The hyperoceanic western parts have up to 10,000 mm annual precipitation, whereas at the east side of the Andes precipitation decreases to less than 500 mm towards the Patagonian Steppe (GLASER 2001, SCHNEIDER et al. 2003). Although mean annual temperatures rarely change along the gradient (annual mean ~6 °C, PISANO 1977), the inter-annual and daily amplitudes increase significantly towards the continental parts (Fig. 2). This is best expressed by regular frost periods in winter and higher summer temperatures in the continental parts as well as the absence of frost periods and cooler summer temperatures under hyperoceanic conditions in the west (BURGOS 1985). In terms of the low variability of the annual temperature, the western parts of southern Patagonia show more pronounced oceanic conditions than any other area of the northern hemisphere (TUHKANEN 1992).

This steep climatic gradient is well reflected in the zonal vegetation types (BOELCKE et al. 1985). From east to west, one can observe a zonation from dry Patagonian steppe, deciduous forest, cool temperate evergreen rainforest to coastal blanket bogs. The latter are often misleadingly called “Magellanic Tundra” (PISANO 1983b). Sampling of ombrotrophic peatland vegetation took place along this trans-andine transect of about 100 km (Fig. 1) west of the Patagonian steppe zone. Due to low precipitation in the steppe zone itself, only groundwater-fed topogenous fens can exist (ROIVAINEN 1954) that were not included in this study.

All investigated peatland complexes were situated below 300 m above sea level. The most oceanic study site was located on the Isla Tamar in the Magellan Strait (52° 54´ S, 73° 48´ W). The most continental peatlands were situated near Estancia Kerber (52° 04´ S, 72° 02´ W) and north of the Estancia Skyring (52° 28´ S, 71° 54´ W) (Fig. 1).

Sampling of vegetation and site conditions

A total of 381 relevés were recorded in floristically and structurally homogenous stands of predominantly ombrotrophic peatland complexes. Vegetation was sampled in 14 geographic regions (Fig. 1) partially containing a couple of peatland complexes. The plot size was 1 m^2. For each relevé, cover abundance data for all vascular plants and the most important cryptogams were recorded according to the Braun-Blanquet approach (BRAUN-BLANQUET 1964, WESTHOFF & VAN DER MAAREL 1973). The nomenclature of plants refers to the following sources: vascular plants (MOORE 1983), mosses (HE 1998), liverworts (FULFORD 1963, 1966, 1976, ENGEL 1978, HÄSSEL de MENÉNDEZ & SOLARI 1985), and lichens (FEUERER 2006). Because of difficulties in determination and the incompleteness and other deficits of local floras some cryptogams, especially liverworts, were merged to groups and named at the level of genus or in one group named “other liverworts”.

Supplementary ecological information such as water level and peat depth were determined for each sample using ordinal scales (Table 1). Water level measurements were carried out at a single point in time within a time span of two months. The degree of decomposition of the peat was estimated at a depth of 5–10 cm using the von Post´s humification scale (AG Boden 2005). Soil acidity was analyzed for 82 plots by measuring the pH value ($CaCl_2$) in a peat depth of 5–10 cm.

In southern South America the climatic gradient does not run definitely meridionally, but turns to W-E direction at the southernmost tip of the continent. In the study area a turning of about 30° was estimated. Attempts to classify climatic gradients in southern Patagonia are mostly unsatisfactory and generally suffer from the scarcity and low spatial resolution of available meteorological data. PISANO (1977) interpolated a climatic map of southern Patagonia according to the Köppen climatic classification model. He described four climatic zones with partially misleading names from the steppe climate (BSk) in the east to the isothermal tundra (Etik’c) in the west. Especially in the western part, where the climatic gradient is very steep, the interpolation is based on an extremely scarce data set of climatic stations. TUHKANEN (1992) created a thermal continentality map of southern Patagonia, but his interpolation had the same problems: a lack of data in the western region.

Table 1. Ordinal scales to estimate water level and peat depth.

Scale	Water level	Peat depth (cm)
0	40 cm below surface	< 10
1	30–40 cm below surface, peat relatively dry	> 10–20
2	30–40 cm below surface, peat relatively wet	> 20–30
3	20–30 cm below surface	> 30–40
4	10–20 cm below surface	> 40–50
5	< 10 cm below surface	> 50–60
6	at surface	> 60–70
7	-	> 70–80
8	-	> 80–90
9	-	> 90–100
10	-	> 100

Given this situation, we used a simple graphically derived nine-stage ordinal scale to describe the degree of continentality, consciously neglecting fine scale effects. Each relevé was allocated according to its position along the continentality gradient (Fig. 1). Some general information about the distribution of our samples along the continentality gradient is given in Table 2.

Data analysis

For numerical analysis, Braun-Blanquet cover-abundance values were transformed into a 1–9 ordinal scale by VAN DER MAAREL (1979). We classified the entire data set by cluster analysis using relative Euclidean distance and Ward's group linkage method (JONGMAN et al. 1995). We used the JUICE 6.3 program (TICHÝ 2002) and the phi coefficient of association as a measure of fidelity (CHYTRÝ et al. 2002) to evaluate the quality of diagnostic species for the clusters calculated before. In these calculations, the frequency of each species and each cluster was compared with the frequency of the same species in the rest of the data set, which was treated as a single undivided group. Because the unequal numbers of relevés included in individual clusters resulted in higher Φ values for larger clusters, each cluster was virtually equalized to the same proportion of the entire data set (TICHÝ & CHYTRÝ 2006). The threshold Φ value for a species to be considered as diagnostic was set subjectively at 0.25 after testing lower and higher threshold values.

Major gradients were explored by detrended correspondence analysis (DCA, HILL & GAUCH 1980), a method of indirect gradient analysis (JONGMAN et al. 1995). For DCA calculation, only species present in at least eight plots were used. Not specified taxa of liverworts grouped e.g. by genus were not included in the calculation. Running the DCA with detrending by 26 segments revealed a gradient length of the first axis of 5.324 SD-units and of the second axis of 3.451 SD-units. This indicated a strong unimodal response and thus the appropriateness of DCA (TER BRAAK & ŠMILAUER 1998). Environmental variables including continentality were correlated with the axis scores of DCA ordination using the Spearman rank correlation. Cluster analysis and ordination were performed using the PCORD 5.0 software package (MCCUNE & MEFFORD 2006). All other statistical calculations were carried out with SPSS 11.0.

Table 2. General characteristics of sampling.

	Number of peatland complexes	Number of relevés	Presence in continentality classes
Sphagnum-dominated samples	15	171	(7) 8, 9
Sphagnum-cushion mixed samples	5	64	7, 8
Cushion plant-dominated samples	7	146	1, 3, 4 (7)

RESULTS

Gradient analysis

The first axis in DCA ordination (Fig. 3) displayed a distinct separation of samples along a gradient of increasing continentality, ranging from hyperoceanic cushion plant blanket bogs to continental *Sphagnum* bogs. The sample scores of DCA axis 1 were also strongly correlated with the degree of peat decomposition and peat depth that increased and decreased towards the Pacific, respectively (Table 3). The second axis exhibited a clear separation of samples along a water level gradient that could be found at both sides of the continentality gradient along the first axis. Along these major gradients we observed a significant change in vegetation properties. Species richness per plot was strongly correlated with the first DCA axis and increased with decreasing distance to the Pacific Ocean (Table 3). Cover values of mosses showed the opposite trend. Cover values of dwarf-shrubs traced the water level gradient well and increased towards drier site conditions. Cover values of cushion plants increased with decreasing distance to the ocean and towards wetter site conditions (Table 3).

Classification and ecological characterization

The cluster analysis resulted in nine major vegetation types (Table 4) that were also clearly split in ordination space (Fig. 3). The first cut level separated the pacific cushion bogs from more continental bogs characterized by *Sphagnum magellanicum*. In line with the results of DCA ordination, the second cut level differentiated mainly along a moisture gradient. In detail, cluster analysis resulted in the following types:

Cluster 1: *Sphagnum cuspidatum* hollows

This species-poor community was dominated by *Sphagnum cuspidatum* and occurred exclusively in continental *Sphagnum* and mixed *Sphagnum*-cushion bogs. Constant species were *Carex magellanica* and *Tetroncium magellanicum* (Table 4). The water level was at the surface and the peat was scarcely decomposed. As in all investigated peatland complexes dominated by *Sphagnum* peat depth always exceeded one meter (Fig. 4).

Cluster 2: Wet *Sphagnum magellanicum* carpet

This community could be found in wet parts of continental peat bogs with water levels mainly close to the surface, often surrounding hollows. The dense intensively red carpet of *Sphagnum magellanicum* allowed only a few other plants with relatively low cover to grow (Table 4). Merely graminoids contributed a nameable portion of the vegetation cover. The degree of peat decomposition was very low (Fig. 4).

Table 3. Spearman rank correlations between DCA axis 1–3 and continentality, degree of decomposition, water level, peat depth and vegetation properties. High correlation coefficients (> 0.5) are given in bold; * – P < 0.05, ** – P < 0.01, *** – P < 0.001, n.s. = not significant.

	Axis 1	Axis 2	Axis 3
Continentality	**0.879*****	0.087 n.s.	-0.411***
Degree of decomposition	**-0.855*****	-0.115*	**0.547*****
Water level	0.042 n.s.	**-0.813*****	-0.011 n.s.
Peat depth	**0.639*****	-0.153**	-0.166**
Species richness	**-0.833*****	0.297***	0.312***
Cover mosses	**0.686*****	0.024 n.s.	**-0.644*****
Cover lichens	-0.047 n.s.	0.151**	**0.526*****
Cover liverworts	-0.465***	0.474***	0.130*
Cover shrubs	**-0.604*****	0.303***	0.063 n.s.
Cover dwarf-shrubs	0.089 n.s.	**0.517*****	-0.056 n.s.
Cover herbs	**-0.684*****	0.008 n.s.	0.124*
Cover graminoids	-0.444***	0.070 n.s.	-0.005 n.s.
Cover cushion plants	**-0.724*****	**-0.520*****	**0.513*****

Cluster 3: Dry *Sphagnum magellanicum* carpet

This community occurred where the water level dropped to 20–30 cm below ground. Frequent species of the wet communities disappeared and dwarf-shrubs prevailed (Table 3 and 4). In particular, *Empetrum rubrum* became more dominant, growing above a dense but quite pale *Sphagnum magellanicum* carpet with minute liverworts frequently occurring between the capitulae (Table 4 – see Appendix). The degree of decomposition was slightly higher than in the previous types (Fig. 4).

Cluster 4: Hummocks of *Sphagnum magellanicum*

Hummocks showed decreasing dominance and vitality of *Sphagnum magellanicum*, which was even absent at some plots. *Empetrum rubrum* became the dominant species, and also *Marsippospermum grandiflorum* was an important constituent. A number of cryptogams frequently grew within the carpet of the dwarf-shrubs (Table 4). The water level was usually below 40 cm and the degree of peat decomposition was slightly higher than in the previous types. Soil pH values in *Sphagnum* bogs (Cluster 1–4) were slightly lower than in their oceanic counterparts (Fig. 4).

Cluster 5: *Sphagnum magellanicum* cushion plant mixed type

With decreasing continentality, we found cushion building vascular plants typical of the oceanic peatlands progressively more intermingled with *Sphagnum magellanicum*. The dwarf-shrub conifer *Lepidothamnus fonkii* and a number of species either predominantly occurring in *Sphagnum*-dominated bogs or in mires dominated by cushion plants exhibited high constancies (Table 4). The water level was about 10 cm below the surface and the degree of decomposition was remarkably higher than in pure *Sphagnum* stands. Soil acidity was similar to pure *Sphagnum* stands (Fig. 4).

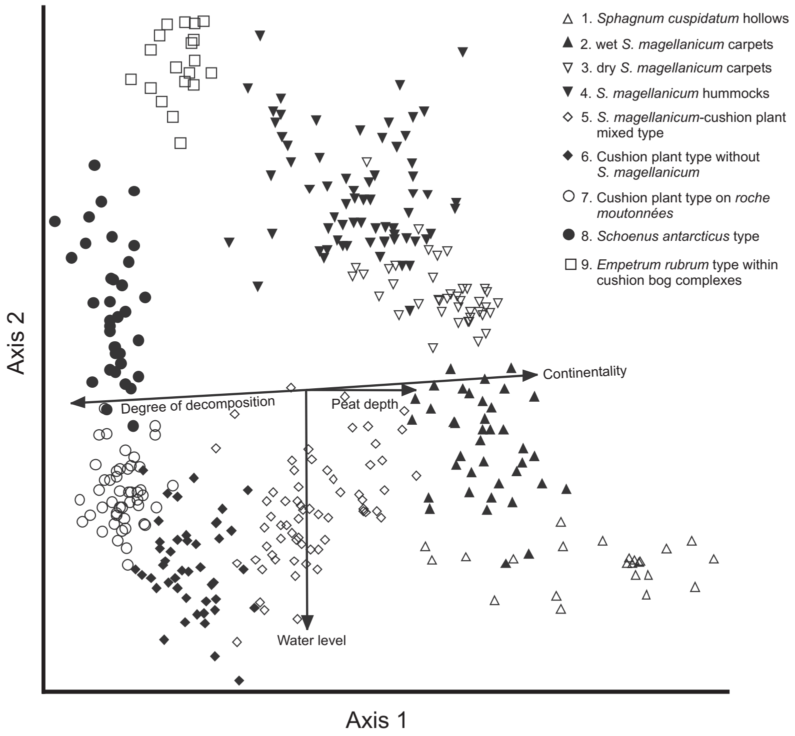

Fig. 3. Biplot of DCA ordination of 381 samples of South Patagonian peatlands. Differentiation of the nine vegetation types resulted from cluster analysis (Table 4). Vectors indicate correlation of DCA axis with the displayed environmental factors (vector length indicates the strength of correlation, see Table 3).

Cluster 6: Cushion plant type without *Sphagnum magellanicum*

In pacific peatland complexes *Sphagnum magellanicum* was totally absent and vegetation was characterized by the dominance of cushion building vascular plants such as *Donatia fascicularis* and *Astelia pumila* dominating with changing cover (Table 4). The cushion plant type occurred at flat sites on fluvio-glacial planes or larger smooth areas within *roche moutonnées*. In general, water level was close to the surface. Peat depth normally exceeded one meter and degree of decomposition was high. Soil acidity was slightly higher than in *Sphagnum*-dominated communities (Fig. 4).

Cluster 7: Cushion plant type on *roche moutonnées*

This community occurred on slopes and little plains within the glacially eroded landscape of the South Patagonian Channels. In addition to the dominance of cushion plants, vegetation was characterized by the constant occurrence of species typical for cluster 8 (Table 4). Despite the better drainage, the water level was relatively high, but lower than in the latter type. The degree of decomposition was high and peat depth rarely exceeded one meter (Fig. 4). The *roche moutonnées* of the South Chilean Channels were typically dominated by this and the following vegetation type giving the landscape a blanket bog character. Vegetation might have a soligenous influence caused by permanent water flow. This made it difficult to separate clearly ombrotrophic systems from those that might have minerotrophic influence. This may also be indicated by slightly higher pH values (Fig. 4). Tree growth was restricted to well drained and strongly inclined slopes.

Cluster 8: *Schoenus antarcticus* type

Gramineous species constituted the aspect of the *Schoenus antarcticus* type. A number of species also occurring in the previous community showed higher constancies and cover values here (Table 4). Besides the well-developed grass layer and the less dominant cushion plants a number of liverworts were characteristic of this community. In general, this vegetation type occurred under better drainage conditions within the *roche moutonnées* landscape or at clearly inclinated positions of more or less plane cushion bog complexes. Peat depth was more or less equal to cluster 7 and the degree of decomposition was slightly lower (Fig. 4).

Cluster 9: *Empetrum rubrum* type within cushion bog complexes

Within western cushion plant peatland complexes relatively dry sites were characterized by the *Empetrum rubrum* type. Additionally *Marsippospermum grandiflorum* often had a remarkable cover (Table 4). Although the structure was similar to hummocks of *Sphagnum* bogs this pacific community differed floristically through the absence of *Sphagnum* and a number of lichens as well as by a higher proportion of liverworts and shrubs (Table 4). Compared to the *Sphagnum* hummocks peat was slightly more decomposed. Peat depth normally exceeded one meter, but could be lower (Fig. 4).

DISCUSSION

The floristic variation in the vegetation of Patagonian peatlands correlated with two major environmental gradients: continentality and soil water level.

Continentality gradient

Most of the floristic variability was explained by continentality. With an increasing distance of our plots from the Pacific Ocean hyperoceanic cushion plant bogs were gradually replaced by *Sphagnum* bogs that existed exclusively under more continental climatic conditions. Within a transition zone both types intermingled.

Our samples did not show a perfectly even distribution along the measured gradient of continentality. This bias was caused by the inaccessibility of the respective areas and the logistical restrictions during field work. However, since the pure *Sphagnum* stands were only found in continentality class 8 and 9, the mixed type in the classes 7 and 8, and pure cushion bogs in the classes 1, 3 and 4 we suppose we covered the entire gradient sufficiently (Table 2).

PISANO (1983b) interpreted this continentality gradient mainly as a consequence of the strong change in precipitation regime. Also MOORE (1979) and ROIG et al. (1985) pointed out that peatlands with 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 having a yearly precipitation between 600 and 1500 mm (PISANO 1983b). According to the precipitation regime the *Sphagnum*-cushion

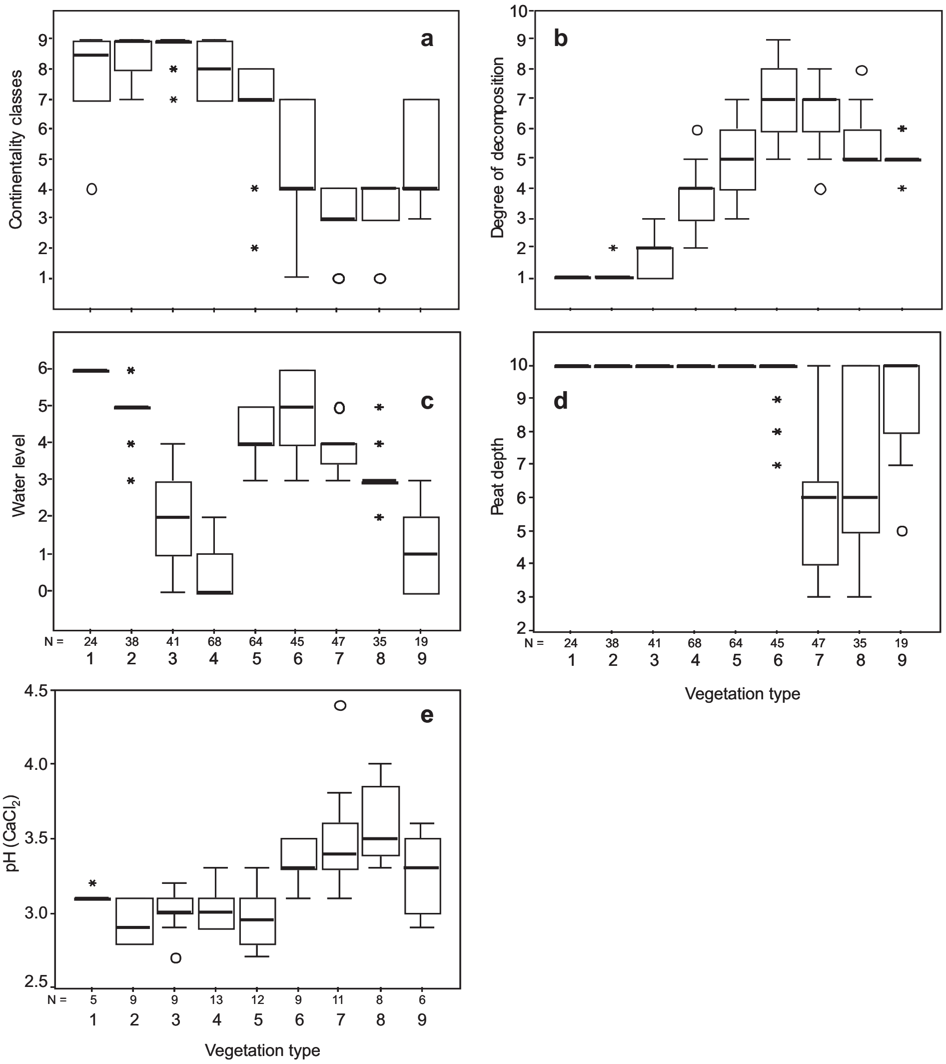

Fig. 4. Continentality (a – see Fig. 1), degree of decomposition (b – von Post's scale, AG BODEN 2005), water level (c – see Table 1), peat depth (d – see Table 1) and pH (e – only a subset of samples per cluster was analyzed) of South Patagonian peatland vegetation types (Table 4). Line within the box: median, the box is defined by the first and third quartile and contains at least 50% of all values. The whiskers are lines that extend from the box to the highest and lowest values, excluding outliers and extreme cases. Outliers (circles) are 1.5 – 3 box length outside the box, extreme cases (stars) more than 3 box length outside the box.

plant mixed type is supposed to be somewhere in between (ROIG et al. 1985). Considering European mires, *Sphagnum magellanicum* is regarded as a hummock *Sphagnum* species with an ecological optimum of water level about 20 cm below the surface (DIERSSEN & DIERSSEN 1984). In general, the hyperoceanic climatic conditions of the South Patagonian Channels lead to a higher water level in the peatlands. However, also relatively dry sites exist, exhibiting more or less optimal water level conditions for *S. magellanicum* growth. Thus, precipitation regime alone does not provide a sufficient explanation for the lack of *S. magellanicum* in the west.

Other important consequences of the degree of continentality such as distinct frost periods in winter or the duration of snow cover, which also play an important role along continentality gradients in the north hemispherical peatlands (DIERSSEN 1982, SJÖRS 1983), were neglected so far. GERDOL (1995) showed the dependence of the growth rate of *S. magellanicum* on different temperature and light intensity. The combination of low temperature and low light intensity reduced growth and may even lead to dormancy of *Sphagnum* species. Exactly this combination of environmental conditions is realized in the hyperoceanic parts of southern Patagonia, where the frequent cloudiness lowers the direct solar radiation and the proximity to the ocean results in a constantly cool climate.

GIGNAC et al. (1991) emphasize the influence of several environmental factors on species composition along a gradient of increasing continentality. One important gradient caused by the distance to the ocean is the mineral input by sea spray. MALMER et al. (1992) presented distinct west-east concentration gradients for most elements in plants and the surface water of western Canadian mires. In general, competition for mineral nutrients has an important influence on the floristic composition of peatland vegetation. VAN GROENENDAEL et al. (1982) emphasize the significant effect of sea spray on floristic composition of western European peatlands via the input of mineral nutrients. Also for the southern hemisphere DAMMAN (1995a) showed that differences in precipitation chemistry had a significant impact on the floristic composition of Tasmanian peatland vegetation, in particular via the increased input of base cations in proximity to the ocean. *Sphagnum* species catch inputs of the wet deposition very quickly with the whole plant surface area (DIERSSEN & DIERSSEN 2001). This is a strong competitive advantage in comparison with vascular plants under low deposition conditions. Ionic concentration in peat varies with the season and the climatic conditions. Fluctuation of ionic concentrations in oceanic peatlands is low, which indicates a well buffered system (PROCTOR 1994). As a result of higher and constant inputs the strong ion-catching ability of *Sphagnum* becomes less important in oceanic regions. This might reduce its strength in competition with oceanic cushion plants and could be another factor for the lack of *Sphagnum magellanicum* in western Patagonia. In contrast, VITT et al. (1990) described a higher diversity of *Sphagnum* species in western British Columbian peatlands compared to continental bogs. However, there are two differences compared to the situation in southern Patagonia: First the annual precipitation is remarkably lower in British Columbia, and second, there are only three *Sphagnum* species in the South Patagonian flora, among them only *S. fimbriatum* preferring minerotrophic conditions. Besides these floristic differences, VITT et al. (1990) could also demonstrate a significant change in peatland vegetation along a continentality gradient that was highly correlated with surface water chemistry indicating (at least partially) the effect of sea spray.

By the accumulation of peat, mire plants create their own environmental conditions. Along the gradient of continentality the degree of decomposition increased significantly towards the oceanic peatlands. The controlling factor in this situation is most likely the resistance to decomposition processes of the peat creating plants (DIERSSEN & DIERSSEN 2001, BRAGAZZA et al. 2006). *Sphagnum*, especially the hummock species, show a high resistance to decomposition processes (JOHNSON & DAMMAN 1991). Under oceanic conditions decomposition is presumably significantly enhanced by the input of base cations via sea spray and the resulting higher quality of litter indicated by slightly higher pH values (Fig. 4). The higher decomposition rates in this situation are supposed to have a significant impact on the degree of nutrient cycling and trophic conditions.

Water level gradient

Floristic variation along the second DCA axis was highly correlated with the measured water level. Along the whole continentality gradient corresponding with the first DCA axis one could observe a distinct floristic separation between relatively dry and wet sites. Due to the high logistical effort, our water level measurements were carried out at a single point in time. It has to be considered that the water table is variable and can show large seasonal differences (WHEELER & PROCTOR 2000). In the study area, precipitation rates do not show significant seasonal differences (SCHNEIDER et al. 2003). In line with this finding, BAUMANN (2006) described a surprisingly low variation of the water table in a *Sphagnum*-dominated raised bog in Tierra del Fuego, although he measured time spans with low and high precipitation. Thus, since our sampling was done during a relatively narrow time span of less than two months effects of seasonal differences are expected to be low and the water table data should give a sufficiently sound description of the moisture gradient.

Vegetation types exhibited a relatively clear grouping along the moisture gradient even in the most western parts. PISANO (1983b) and MOORE (1979) described the *Empetrum rubrum* type (Cluster 9 in Table 4) as a relatively dry community within western cushion bog complexes occurring under slightly better drainage conditions because of the underlying substrate. The cushion plant type (Cluster 6 in Table 4) showed the wettest site conditions on poorly drained plane or scarcely inclinated surfaces (DOLLENZ 1986). The abundance and dominance of graminoid plants increased under better drainage conditions (DOLLENZ 1982, PISANO 1983b). The vegetation types of Cluster 7 and 8 (Table 4) predominantly occurred on inclinated slopes and showed both, drier site conditions because of better drainage and a high proportion of graminoids in the vegetation.

A floristic separation along a moisture gradient of Patagonian *Sphagnum magellanicum* raised bogs has already been described by other authors, e.g. PISANO (1983b). TENEB & DOLLENZ (2004) and BAUMANN (2006) emphasized the importance of microtopography for the hydrology of Patagonian *Sphagnum* bogs. Our study showed a differentiation into four major vegetation types (Cluster 1 to 4 in Table 4) following the hollow-hummock moisture gradient that is also well established for *Sphagnum*-dominated bogs of the northern hemisphere (COUWENBERG & JOOSTEN 2005).

All older publications dealing with South Patagonian bogs described *Sphagnum fimbriatum* as the most important constituent of the hollows (PISANO 1983b, ROIG et al. 1985). Surprisingly, we found hollows of continental South Patagonian bogs to be generally dominated by *Sphagnum cuspidatum* whereas *S. fimbriatum* could only be found at the margins of ombrotrophic continental raised bogs under clear minerotrophic conditions. Our findings are supported by MOEN (2005), who described similar patterns of distribution.

The wet *S. magellanicum* carpets (Cluster 2 in Table 4) were intermediate in terms of moisture and floristic composition, situated between the hollows and dry *S. magellanicum* carpets (Cluster 3 in Table 4) dominated by dwarf-shrubs (SCHWAAR 1976). The driest site conditions were observed in *S. magellanicum* hummocks (Cluster 4 in Table 4) showing a distinct floristic composition. The *S. magellanicum*-cushion plant mixed type (Cluster 5 in Table 4) is separated as an own type of relatively high water table at more pacific sites in the transition zone to hyperoceanic cushion bogs (ROIG et al. 1985). Floristically this type was characterized by elements of both, the western cushion bogs and the continental *Sphagnum* bogs with only the conifer dwarf-shrub *Lepidothamnus fonkii* showing a clear preference for this community.

Comparison with north-hemispherical mires

In Europe the gradient of continentality and its effect on peatlands and their floristic composition is well known and described comprehensively (DIERSSEN & DIERSSEN 2001, JESCHKE et al. 2001). In southern Patagonia the distance from the oceanic peatlands to the continental *Sphagnum* bogs is very short. Within less than 100 km bog vegetation changes from hyperoceanic blanket bogs to *Sphagnum*-dominated raised bogs near the limit of the occurrence of ombrotrophic peatlands towards the Patagonian Steppe (ROIG et al. 1985). In Central Europe the gradient of continentality is much longer and smoother. A barrier such as the Andes in southern Patagonia creating a steep climatic gradient with a strong rain shadow effect is lacking. Western North America and Fennoscandia also show a steep gradient in precipitation, but, in contrast to South Patagonia the annual range of temperatures even in oceanic regions is quite large (BANNER et al. 1988, DAMMAN 1995b).

In the western parts of Europe the boundary between clearly ombrotrophic and minerotrophic peatlands becomes indistinct (DIERSSEN 1982) resulting in a typical mosaic of blanket bog and moist heath vegetation (RODWELL 1991). Similar observations were made by BANNER et al. (1988) and WELLS (1996) for Canadian oceanic wetlands. Atmospherical inputs can vary within wide limits along the gradient of continentality that overlap the range of telluric inputs into poor fens, so that there is no universal distinction between the water or peat chemistry signatures of ombrotrophic bogs and minerotrophic poor fens (WHEELER & PROCTOR 2000). DAMMAN (1995a) emphasized the floristic affinities of *Sphagnum*-dominated bogs and poor fens, which is in line with multivariate floristic analyses of oceanic peatland vegetation of the northern hemisphere that did not identify bog vs. fen as the primary split (DANIELS 1978, GIGNAC et al. 1991). As indicated by a higher deviation of pH values in South Patagonian oceanic blanket bogs a clear separation of minerotrophic and ombrotrophic parts is presumably also not realized.

European oceanic blanket bog vegetation is characterized by dwarf-shrubs and some hemicryptophytes such as *Schoenus nigricans*, *Narthecium ossifragum* or *Molinia caerulea* usually indicating minerotrophic conditions in more continental regions (DIERSSEN 1982, DAMMAN 1995a). SJÖRS (1983) also described this phenomenon for southern Alaska pointing out similarities and differences to Fennoscandian bogs. South Patagonian blanket bogs exhibited the same tendency with some species such as *Schoenus antarcticus* or *Festuca purpurascens* considered indicative of telluric water. Especially vegetation of inclinated *roche moutonnées* areas do have soligenous influence, but this influence might be buffered by the generally base-poor bedrock (PISANO 1977) and the immense and continuous precipitation.

SCHWAAR (1976, 1981) and MOEN (2005) pointed out the structural (hollows and hummocks) and even floristic similarity between continental South Patagonian and European *Sphagnum* bogs (e.g. OBERDORFER 1992). Closely related taxa such as *Empetrum rubrum* in the southern and *E. nigrum* in the northern hemisphere are constituents of *Sphagnum*-dominated peatlands. Partly the same species such as *Sphagnum magellanicum* itself, *Carex magellanica* or lichens of the genus *Cladonia* occur in raised bogs of both hemispheres.

In contrast to the *Sphagnum* bogs the oceanic peatlands of both hemispheres differ significantly. South-hemispherical oceanic peatlands are characterized by cushion building plants (PISANO 1983b, GIBSON & KIRKPATRICK 1985), which are totally absent in the northern hemisphere. The taxa of cushion building plants such as *Astelia*, *Donatia* or *Oreobulus* show a south-hemispherical distribution due to their gondwanic origin (DAWSON 1963), but even convergent forms are lacking in Eurasia and North America.

European oceanic bogs are treeless. With increasing distance to the ocean a higher importance of trees, up to forested peat bogs in continental areas, can be observed (DIERSSEN & DIERSSEN 2001, JESCHKE et al. 2001). In oceanic mires of southern Alaska the high abundance of trees is a feature that differentiates them from the atlantic European peatlands (SJÖRS 1983), whereas in Canadian atlantic blanket bogs – similar to the situation in western Europe – trees are nearly lacking (WELLS 1996). In southern Patagonia trees do not expand into central parts of continental raised bogs. If tree species (e.g. *Nothofagus antarctica*) occur, they do not grow higher than 1 m. In pacific cushion bog complexes trees such as *Nothofagus betuloides* or *Pilgerodendron uviferum* grow exclusively on well-drained sites (PISANO 1983b) even though seedlings may be abundant.

Human impact over a long time on nearly all oceanic peatlands make it difficult to describe the natural vegetation of the Western Europe blanket bog complexes (DIERSSEN 1982). Many of the blanket bog complexes are even of an anthropogenic origin. They expanded through grazing and burning at the expense of woodland (DIERSSEN 1996). In South Patagonia direct human impact is nearly absent in the western parts. In the continental parts peat harvesting has been developed in the last decade (CASPERS 2002), but has not yet destroyed all natural peat bog ecosystems like in Central Europe (SUCCOW 2001). In Great Britain, Central Europe and southern Fennoscandia heavy atmospherical input of nutrients caused by emissions from industry and agriculture have been measured that often reach critical loads for ombrotrophic peatland ecosystems. Significant changes in ecological processes such as decomposition and mineralization (BRAGAZZA et al. 2004, 2006) accompany the anthropogenic enhancement of nutrient supply. In contrast, the input in southern Patagonian ecosystems is marginal (GODOY et al. 2001), which gives the unique opportunity to study peatlands under unspoiled pre-industrial conditions. More ecological data on South Patagonian peatland ecosystems could provide useful facts in the discussion of the major gradients affecting species composition in mire ecosystems (WHEELER & PROCTOR 2000, ØKLAND et al. 2001, HÁJEK et al. 2006).

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Table 4. Synoptic table summarizing results of cluster analysis of South Patagonian peatland vegetation. Species values are percentage frequencies. Species with a fidelity of $\Phi > 0.25$ are considered as diagnostic. They are indicated by asterisks. * = $\Phi > 0.25$; ** = $\Phi > 0.35$ (Φ was calculated for groups with equal numbers of relevés). Species with a frequency < 10% in all clusters are omitted. Superscripts indicate the range of the cover-abundance values (1–9 ordinal scale by VAN DER MAAREL (1979)). Classification of life forms: M: moss, LW: liverwort, Li: lichen, HH: herbal hemicryptophyte, GH: graminoid hemicryptophyte, CP: cushion plant, cushion forming hemicryptophyte, F: fern, D-S: dwarf-shrub, S: shrub (shrubby tree).

Species	Classification of life forms	Cluster 1 *Sphagnum cuspidatum* hollows	Cluster 2 Wet *Sphagnum magellanicum* type	Cluster 3 Dry *Sphagnum magellanicum* type	Cluster 4 *Sphagnum magellanicum* hummocks	Cluster 5 *Sphagnum*-cushion plant mixed type	Cluster 6 Cushion plant type	Cluster 7 Cushion plant type on roche moutonnées	Cluster 8 *Schoenus antarcticus*-type	Cluster 9 *Empetrum* type within cushion bog complexes
Sphagnum cuspidatum	M	$**100^{6-9}$	5^{2}	.	.	.	29^{2-5}	.	.	.
Tetroncium magellanicum	GH	$*92^{2-7}$	$*97^{2-7}$	12^{1-2}	13^{1-6}	88^{2-5}	87^{2-5}	34^{2-5}	54^{2-4}	16^{3}
Carex magellanica	GH	$**71^{2-7}$	$**82^{2-6}$	2^{2}	12^{2-3}	23^{2-5}	.	.	.	.
Sphagnum magellanicum	M	50^{2-7}	$**100^{6-9}$	$**100^{8-9}$	56^{2-8}	$*92^{2-8}$	.	.	.	.
Neolepidozia oligophylla	LW	.	$**89^{2-4}$	$**98^{2-4}$	16^{2-4}	34^{2-4}	2^{2}	.	.	.
Pernettya pumila	D-S	4^{2}	$*42^{2-4}$	$**54^{1-4}$	12^{2-4}	3^{2}	.	26^{2-4}	3^{3}	.
Microisophylla saddlensis	LW	.	8^{2-4}	$**80^{2-5}$	34^{2-5}	20^{2-5}	2^{2}	.	3^{3}	5^{2}
Juncus scheuchzerioides	GH	.	8^{2-3}	$*27^{2-4}$	6^{2-3}	3^{2}	2^{2}	.	.	.
Drapetes muscosa	HH	.	3^{2}	$**20^{2-4}$	1^{2}	.	.	.	.	.
Empetrum rubrum	D-S	4^{2}	47^{2-6}	$**100^{2-7}$	$**99^{2-9}$	33^{1-5}	.	.	3^{7-7}	$*84^{2-7}$
Marsippospermum grandiflorum	GH	.	3^{2}	41^{1-7}	$*72^{1-9}$	.	16^{1-5}	49^{1-3}	46^{2-6}	$**100^{5-7}$
Riccardia prehensilis	LW	.	.	.	$**40^{2-5}$	.	22	.	9^{2-3}	$**42^{2-5}$
Cladonia rangiferina	Li	.	3^{2}	12^{2-3}	$**57^{2-7}$	33^{1-5}	20^{2-5}	.	3^{1}	.
Cladonia borealis	Li	.	5^{2-3}	5^{2-3}	$**40^{2-5}$	6^{2-3}	.	.	.	.
Ochrolechia frigida	Li	.	.	12^{2-3}	$**32^{2-7}$	11^{1-3}	2^{3}	.	.	.
Lepidozia fuegiensis	LW	.	3^{2}	24^{2-3}	$*32^{2-4}$	12^{2-4}	4^{2-3}	.	.	.
Cladonia cornuta	Li	.	5^{1-2}	2^{2}	$**22^{2-6}$	.	.	.	.	.
Bunodophoron sp.	Li	.	.	.	$**24^{2-5}$	6^{1-3}	.	.	.	.
Avenella caespitosa	GH	.	3^{2}	2^{3}	$*16^{2-5}$	.	.	.	.	.
Campylopus clavatus	M	.	.	2^{2}	$*15^{2-5}$	3^{2}	.	.	3^{5}	.
Dicranoloma billardieri	M	.	.	2^{3}	$*13^{2-5}$	2^{2}	.	.	.	.
Cladonia arbuscula subsp. *squarrosa*	Li	.	8^{1-2}	24^{2-5}	$**57^{2-7}$	$*55^{1-6}$	18^{2-3}	.	.	.
Microisophylla setiformis	LW	.	3^{2}	.	$**56^{2-6}$	$**62^{2-6}$	13^{2-5}	.	.	.
Cladonia arbuscula subsp. *mitis*	Li	.	5^{2}	12^{2-3}	$*51^{2-7}$	$*50^{1-5}$	24^{1-3}	2^{2}	23^{2-3}	16^{2}
Lepidothamnus fonkii	D-S	.	3^{1}	.	29^{2-9}	$**86^{1-9}$	.	.	.	.
Drosera uniflora	HH	.	24^{2-3}	.	1^{2}	$**84^{2-4}$	$*60^{2-4}$	49^{2-3}	14^{2-3}	.
Carpha alpina	GH	33^{2-6}	16^{2-3}	.	10^{2-6}	$*91^{1-6}$	$*100^{2-7}$	$*83^{2-6}$	49^{2-7}	21^{2-3}
Oreobulus obtusangulus	CP	.	8^{2}	.	3^{3-5}	$**83^{2-8}$	$*71^{2-6}$	$**85^{2-5}$	54^{2-5}	.
Donatia fascicularis	CP	.	.	.	.	67^{2-9}	$**98^{2-9}$	$**98^{3-8}$	$*83^{2-7}$	.
Astelia pumila	CP	.	.	.	.	53^{2-8}	$**96^{2-9}$	$**100^{3-8}$	$**89^{2-7}$	5^{6}
other LWs	LW	8^{3-5}	5^{3-5}	2^{5}	10^{2-6}	3^{2-3}	$**89^{2-6}$	53^{2-5}	$**83^{2-6}$	21^{2-5}
Gaimardia australis	CP	.	.	.	.	25^{2-5}	$**84^{1-6}$	$**91^{2-6}$	$**77^{2-5}$	.
Racomitrium lanuginosum	M	.	.	.	.	12^{2-5}	$*69^{2-8}$	64^{2-6}	$**86^{2-6}$	53^{2-6}
Taipenia magellanica	GH	.	.	.	.	.	$**67^{1-4}$	$**87^{2-4}$	$*60^{1-4}$	.
Pallavicinia pisicolor	LW	.	.	.	.	.	$**40^{2-6}$	.	.	.
Riccardia pallidevirens	LW	.	8^{3-4}	5^{2-3}	3^{2-3}	2^{3}	$**33^{2-5}$	.	.	.
Riccardia georgiensis	LW	.	.	.	.	.	$**20^{2-5}$	.	.	.
Caltha dioneifolia	HH (CP)	4^{3}	5^{3}	17^{1-3}	1^{2}	16^{2-5}	$*71^{2-5}$	$**94^{2-5}$	60^{2-5}	.

Thamnolia vermicularis	Li	.	.	.	.	.	4^{2-3}	**81^{2-4}	34^{2-3}	.
Adelanthus lindenbergianus	LW	.	.	49^{2-4}	49^{2-7}	22^{2-5}	4^{2}	*64^{2-5}	34^{2-5}	.
Perezia magellanica	HH	.	.	.	.	.	2^{2}	**30^{2-3}	17^{2-3}	.
Bolax caespitosa	CP	.	.	.	.	.	.	**30^{2-5}	6^{2-3}	.
Azorella lycopodioides	CP	.	.	.	.	.	.	**28^{2-3}	.	.
Schoenus antarctica	GH	.	.	.	.	2^{2}	27^{1-6}	**100^{2-6}	**100^{5-8}	5^{2}
Lepidozia chordulifera	LW	.	3^{4}	2^{2}	62^{2-6}	9^{2-4}	4^{2-4}	*79^{1-4}	*80^{2-5}	**84^{1-4}
Acaena pumila	HH	.	.	10^{2}	9^{2-4}	5^{2}	49^{2-4}	*72^{2-3}	**94^{2-5}	16^{2}
Philesia magellanica	S (D-S)	.	.	.	4^{2-5}	.	4^{2}	**53^{2-4}	*46^{2-4}	21^{2}
Festuca purpurascens	GH	.	.	.	.	.	4^{1-3}	*47^{1-5}	**69^{2-6}	16^{3}
Myrteola nummularia	D-S	.	21^{2-3}	29^{1-4}	40^{2-5}	64^{2-4}	91^{2-5}	89^{2-5}	*97^{2-5}	89^{2-6}
Carex microglochin	GH	.	8^{3-4}	12^{2-4}	6^{2-4}	.	11^{2-3}	32^{2-4}	**54^{2-3}	5^{4}
Luzuriaga radicans	HH	.	.	2^{2}	12^{2-3}	.	.	6^{1-2}	**37^{1-3}	21^{2-3}
Gleichenia quadripatita	F	.	.	.	.	.	.	4^{2}	**23^{2-5}	.
Garckstroemia magellanica	LW	.	.	.	28^{2-7}	5^{1-2}	.	19^{2-4}	**94^{2-6}	**100^{2-6}
Pilgerodendron uviferum	S	.	.	.	12^{2-6}	8^{1-3}	20^{1-5}	23^{1-3}	**91^{1-7}	*58^{1-5}
Apometzgeria frontipilis	LW	.	.	.	.	.	2^{2}	9^{2-3}	**80^{1-4}	**68^{1-5}
Jamesionella colorata	LW	.	.	.	31^{2-7}	2^{2}	7^{2}	13^{2-4}	**66^{2-5}	**74^{2-6}
Leptoscyphus expansus	LW	.	.	17^{2}	35^{2-6}	14^{2-3}	2^{5}	.	**63^{1-4}	*58^{2-4}
Tribeles australis	D-S	.	.	.	1^{2}	.	13^{1-2}	2^{2}	**63^{1-5}	**58^{2-6}
Blechnum penna-marina	F	.	.	2^{2}	15^{2-4}	.	.	4^{1-2}	**57^{1-3}	**68^{2-4}
Plagiochila hirta	LW	.	.	.	.	.	.	6^{2}	**51^{2-4}	**63^{2-4}
Hypochoeris palustris	HH	.	.	2^{2}	13^{2-4}	22	4^{1-2}	4^{2-3}	**51^{1-5}	*42^{2-4}
Lepicolea ochroleuca	LW	.	.	.	.	3^{3-5}	.	.	*43^{2-3}	**79^{2-6}
Riccardia sp.	LW	.	5^{3}	20^{2-4}	60^{2-5}	61^{2-5}	78^{2-7}	74^{2-5}	77^{2-6}	*100^{2-4}
Riccardia fuegiensis	LW	.	.	.	.	.	.	.	11^{2-6}	**100^{2-6}
Blephnaridophyllum densifolium	LW	.	5^{2}	.	37^{2-5}	20^{2-5}	33^{2-6}	26^{2-5}	49^{2-6}	*63^{2-5}
Berberis ilicifolia	S	.	.	.	4^{2-3}	.	.	11^{1-2}	29^{1-2}	**53^{1-3}
Chiliotrichum diffusum	S	.	.	17^{1-3}	18^{1-3}	.	.	6^{1}	11^{1-2}	**42^{1-2}
Pernettya mucronata	S	.	.	2^{2}	4^{1-2}	.	.	.	6^{1-2}	**32^{1-2}
Desfontainia spinosa	S	.	.	.	.	.	.	.	62	**26^{2-3}
Uncinia tenuis	GH	.	.	.	42	.	.	.	6^{2-3}	*21^{2-3}
Macrachaenium gracile	HH	.	.	.	12	.	.	.	.	**21^{2}
Lebethantus myrsinitis	D-S	.	.	.	.	.	.	.	6^{2-3}	*16^{4-5}
Dicranoloma robustum	M	25^{2-6}	11^{2-4}	29^{2-5}	72^{2-8}	75^{2-7}	91^{2-6}	98^{2-6}	86^{2-6}	95^{3-7}
Nothofagus betuloides	S	4^{1}	21^{2-3}	46^{1-4}	41^{1-6}	77^{1-5}	78^{1-3}	60^{1-3}	86^{2-3}	53^{2-3}
Caltha appendiculata	HH	8^{3}	18^{2-4}	17^{2-3}	19^{1-5}	38^{1-4}	40^{2}	36^{2-4}	49^{2-3}	47^{2-3}
Nothofagus antarctica	S	4^{2}	8^{2}	37^{1-3}	12^{2-5}	8^{2-5}	49^{1-3}	45^{2-5}	43^{1-3}	26^{1-2}
Gaultheria antarctica	D-S	.	63^{2-5}	85^{2-4}	81^{2-5}	95^{2-5}	91^{2-6}	91^{2-5}	94^{2-5}	89^{2-5}
Nanodea muscosa	HH	.	24^{1-4}	29^{2-4}	19^{1-3}	9^{2-3}	20^{1-3}	6^{2}	.	.
Pseudocephalozia quadriloba	LW	.	16^{2-4}	7^{2}	.	19^{2-4}	2^{4}	.	.	.
Polytrichum strictum	M	.	3^{2}	2^{2}	10^{3-6}	.	.	.	.	.
Hymenophyllum secundum	F	.	.	2^{2}	16^{2-4}	.	.	.	17^{2-3}	26^{2-3}
Schizeilema ranunculoides	HH	.	.	10^{1-3}	4^{2-3}	.	.	.	.	.
Gunnera lobata	HH	.	.	.	7^{2-4}	3^{2}	51^{2-4}	43^{2-5}	46^{1-4}	47^{2-3}
Cladonia subsubulata	Li	.	.	.	6^{2-3}	6^{2-5}	.	.	.	11^{2-3}
Heteroscyphus integrifolius	LW	.	.	.	.	.	16^{1-2}	2^{5}	9^{2-3}	5^{3}