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Magellanic Wetlands: More than Moor

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Abstract Magellanic wetlands in the Patagonian steppe are unique habitats from the point of view of conservation and agriculture. Little is known about their environmental characteristics and plant communities. Our aim was to describe vegetation variability to improve current classifications and reveal environmental factors correlated with vegetation variability in the meadow wetlands (*vegas*) of southern Chilean Patagonia and Chilean Tierra del Fuego. Five vegetation types resulted from TWINSPAN classification and subsequent interpretation, based on which four new associations were delimited: Magellanic acidic marshes – the *Scirpo cernui-Calthetum sagittatae*, Magellanic alkaline wet grasslands – the *Samolo spathulatae-Azorelletum trifurcatae*, Magellanic tall sedge marshes – the *Carici maclovianae-Agrostietum stoloniferae*, and Magellanic pastures – the *Hordeo lechleri-Trifolietum repentis*. The fifth vegetation type, saline wetlands, is the rarest and so far the least known community. Magellanic wetland vegetation forms a gradient from short saline marshes to tall graminoid-dominated communities. They reflect a major soil gradient of pH and organic matter content, along with the content of major elements (N, P, K, Fe, Al). Other important factors are ground water regime and grazing intensity.

Keywords Acidity gradient · Classification · Patagonia · Soil chemistry · Tierra del Fuego · Wetland vegetation

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Plant nomenclature Moore (1983) except for grasses; Clayton et al. (2002, 2006) for grasses

Introduction

The harsh nature of the southernmost region of the Americas, Southern Patagonia, has fascinated scientists since Charles Darwin's famous voyage in 1833–1834 (Darwin 1989). The conspicuous natural variability of Patagonia is largely due to climate. Over a 200–300 kilometer distance, there is a steep precipitation gradient from the Pacific coast receiving over 3,000 mm of rain per year to the eastern steppes receiving only about 200 mm of rain per year. Four main habitat types can be distinguished in Southern Patagonia (Moore 1983). Magellanic moorland and evergreen forest are confined to the wet oceanic west, while deciduous forest and Patagonian steppe are distributed in the continental east. The forest-steppe transition is controlled by soil moisture conditions while the relatively recent grazing impact has led to deforestation and to an expansion of the steppe area (Wille and Schaebitz 2009; Markgraf and Huber 2010).

Vegetation in four main habitat types was studied with varying intensity and focus. Both forest habitats were studied relatively intensively resulting in reasonably good knowledge of their composition and ecology (e.g., Hertel et al. 2008; Fajardo and González 2009). The two major non-forest habitat types constitute contrasting environments. Magellanic moorlands are described as a pristine wetland ecosystem (Pisano 1972; Kleinebecker et al. 2007, 2008, 2010) without a parallel in the Northern Hemisphere (Tuhkanen 1992). By contrast, Patagonian steppe is extensively grazed dry grassland with crucial economic importance for the region. The steppes were rather intensively studied focusing on species composition (Pisano 1977; Collantes et al. 1999), production (Paruelo et al. 2000; Strauch et al. 2006), and disturbance dynamics following sheep and cattle grazing (León et al. 1998; Posse et al. 2000).

There is a less studied habitat type embedded in the steppe − Magellanic wetlands, locally called *vegas* or *mallines* (Collantes and Faggi 1999; Clausen et al. 2006; see also Gandullo and Faggi 2005). Ecologically, these are oligo- to mesotrophic mires, which provide a high productivity biomass resource (e.g., SAG 2004) for grazing animals (Golluscio et al. 1998). Because sheep and cattle breeding is the principal agricultural activity in the region (Pisano 1985), *vegas* are of great economic importance (e.g., Covacevich and Ruz 1996; Paruelo et al. 2000; Brinson and Malvárez 2002; SAG 2004). Agriculture exerts intensive pressure on this habitat making it a location not only of economic but also of conservation interest. The wetlands provide habitats for birds like sheldgees and penguins (Blanco and de la Balze 2004; Kerr and McAdam 2008) and mammals like guanacos (Banks et al. 2003). Buono et al. (2010) recently studied ecosystem productivity. Soil properties were described by Sáez (1994) who characterized surface horizons, and recently by Filipová et al. (2010) who analyzed 47 soil profiles in detail.

Nonetheless, knowledge of the compositional diversity and ecology of the Magellanic wetlands is far from sufficient. Pisano (1971, 1972, 1973, 1977) pioneered vegetation research in southern Patagonia by describing vegetation types accompanied by lists of species. However, these analyses comprised a wide range of communities and did not include information on ecological characteristics, such as soil properties. A study by Roig et al. (1985) was based on sampling along a cross-Patagonian transect, not explicitly focusing on wetlands; nevertheless it was the first modern vegetation survey of Southern Patagonia. Collantes et al. (2009) published the first study of the Southern Patagonian steppic wetlands comparing vegetation patterns with soil properties. It was spatially limited to the Argentinean northern part of the Tierra del Fuego island. Patterns in vegetation and their relation to environmental factors in the extensive Chilean southern Fuego-Patagonia remained an unexplored topic.

In the light of scarcity of information, field data collection and a subsequent revision of the classification system of Magellanic wetlands is a worthwhile task. In addition, information on the main ecological vegetation drivers needs to be examined. According to observations from oceanic (Wheeler and Proctor 2000) and continental Europe (Hájková et al. 2004) as well as from North America (Nekola 2004), three main ecological gradients affect broad vegetation composition patterns in mesotrophic and oligotrophic mires. These are soil reaction, site productivity (mainly via available nitrogen and phosphorus), and water table level. Water regime and organic matter content can also be important.

In this study the aim was to analyze vegetation patterns of the Magellanic wetlands – an important representative of southern temperate mires. In particular, we aim to *i*) classify the vegetation to the level of vegetation types reflecting species composition, *ii*) revise the existing classification systems, *iii*) establish differences in environmental properties between the vegetation types, and *iv*) identify environmental variables explaining most of the vegetation variability.

Material and Methods

Study Area

This study was conducted in the southern part of Chilean Patagonia including the Chilean section Tierra del Fuego (48°36′–56°30′ S and 66°25′–75°40′ W). It was delimited as the area of agricultural use in the XIIth Region of Magellan and the Chilean Antarctic (administrative subdivision of Chile) (Fig. 1).

The study area is climatically very variable. Following the Köppen–Geiger's classification map by Peel et al. (2007), the climatic zones comprise temperate without a dry season (Cfb, Cfc), cold arid steppe (BSk), cold arid desert (BWk) and polar tundra (ET). The annual thermal amplitude is relatively low. By contrast, average yearly precipitation varies in the steppe zone from 932 mm (1,000 mm according to Schneider et al. 2003) in the west to 233 mm in the east (Pérez et al. 2006), with even lower values of 150 mm in the northeast (Collantes and Faggi 1999). About one-third of the precipitation is confined to the vegetation season from November to March (Tuhkanen 1992). Although there is no conspicuous dry season, a hydric deficit occurs in the Patagonian steppe from September to April due to strong western winds (Collantes and Faggi 1999). Ground-water-saturated wetlands thus represent contrasting spots in the matrix of dry steppes (Fig. 2a).

Geomorphology and geology are determined by glacial activity in the Quaternary. The main substrates are coarse-grained and base-poor glacial and fluvioglacial

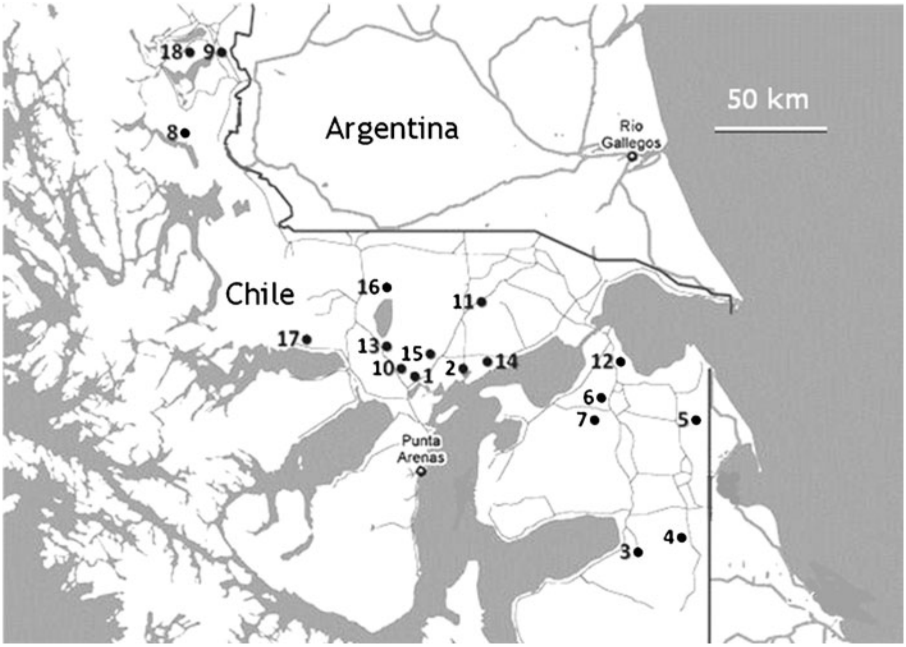


Fig. 1 Map of the southern Fuego-Patagonia showing locations of farms with studied Magellanic wetland sites. 1 – Kampenaike, 2 – Oazy Harbour, 3 – Tres Hermanos, 4 – El Álamo, 5 – San Isidro, 6 – Quinta Esperanza, 7 – Miriana, 8 – Puerto Consuelo, 9 – Shotel Aike, 10 – El Calafate, 11 – Vega Vieja, 12 – Estancia Springhill, 13 – Domaike, 14 – Los Coipos, 15 – Estancia Josefina, 16 – Laguna Blanca, 17 – Las Coles, 18 – Cerro Castillo

sediments (Pisano 1977). Fine-grained carbonates-rich Tertiary and Quaternary sediments cover relatively small areas and include lacustrine and slope sediments (Codignotto and Malumián 1981). Soils are usually poorly developed but in wetlands organic sediments can reach depths of several meters. Two main soil groups in Magellanic wetlands are fluvisols and histosols (Filipová et al. 2010).

Study Sites

Study sites were visited and sampled from November 2004 to April 2005. They were located using satellite images focusing on areas with soils saturated by water, the *vegas*. Our objective was to cover the maximum variability of *vegas*. Due to lack of relevant information, this was only possible with a field survey of potential sites, using vegetation-science and pedological approaches (see Filipová et al. 2010). At each site, an undisturbed plot in the central part was sought. One soil pit and one adjacent vegetation plot were used for sampling and recording soil and vegetation. The elevation and geographic position of each site were recorded using GPS. All study sites were situated below 200 m above sea level. During the first phase of fieldwork, we concentrated on the *vegas* of the experimental station of the Institute for Agricultural Research (INIA) in Kampenaike, 60 km north of the city of Punta Arenas. Twenty-four sites were sampled in Kampenaike. Following this, an extensive search was performed in *vegas* of cattle farms throughout the study region. Twenty-

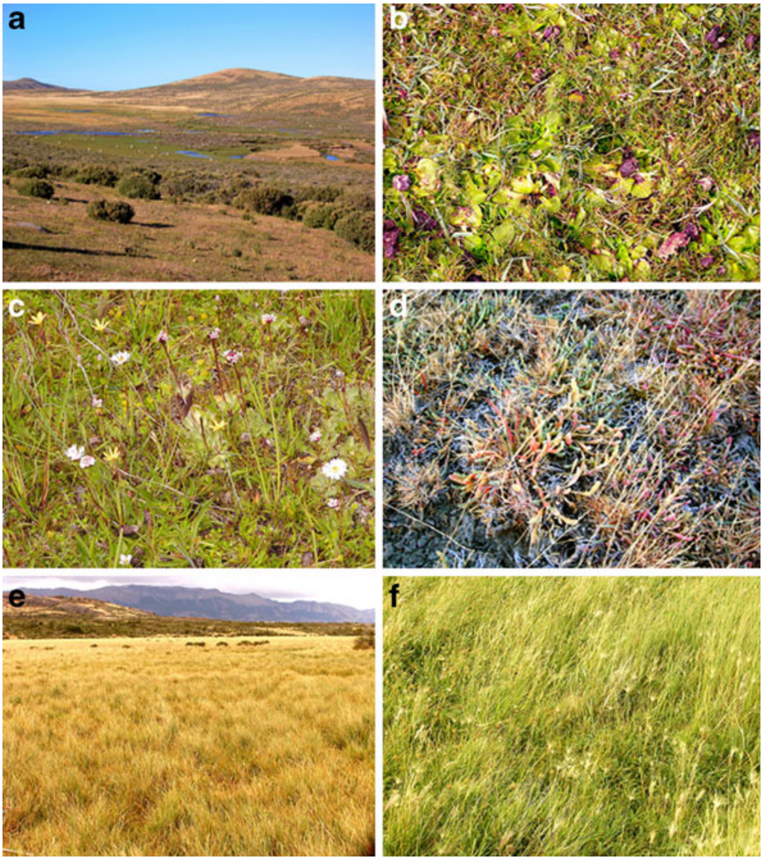


Fig. 2 Vegetation of Magellanic wetlands. **a** In the steppic landscape of Chilean Patagonia, wetlands are important pasturing sites; Farm Tres Hermanos. **b** Short-grazed acidic marsh, *Scirpo cernui-Calthetum sagittatae*; Farm Quinta Esperanza, Tierra del Fuego. **c** Species-rich alkaline wetland, *Samolo spathulatae-Azorelletum trifurcatae*; type site. **d** *Salicornia*-dominated saline wetland; Laguna Blanca. **e** Extensively grazed tall sedge marsh, *Carici maclovianae-Agrostietum stoloniferae*; type site. **f** Grasses-dominated pasture, *Hordeo lechleri-Trifolietum repentis*; type site. Photos were taken by L. Filipová, except for **a** and **d**, by R. Hédl

three sites representing wetlands were added to the Kampenaike set resulting in 47 sampled sites in total (Fig. 1, Appendix 1).

Data Sampling

At each site, soil and vegetation were sampled. First a soil pit was dug at a place with representative topography. We dug to a maximum depth of 1 m. Soil profiles were described and classified according to the guidelines of the World Reference Base WRB (IUSS 2006). Water-table depth was determined as a single measurement in the soil pit. Soil samples for laboratory analyses were taken from homogeneous parts of the topsoil horizons (0–20 cm). Samples were air-dried and passed through a 2-mm sieve. Fine earth samples were analyzed in the soil laboratory of INIA in Chillán. The following parameters were determined: pH in H_2O, pH in $CaCl_2$, organic matter content (weight % of dry soil), C:N ratio, electric conductivity (EC, in dS/m), effective cation exchange capacity (CEC, in mmol/g), available N (NO_3^-+NH_4^+, in mg/kg), exchangeable P (PO_4^{3-}, in mg/kg), four main base cations (Ca^{2+}, Mg^{2+}, Na^+, all in cmol/kg; and K^+, in mg/kg), exchangeable Al (in cmol/kg), S (SO_4^{2-}, in mg/kg), B (in mg/kg), and micronutrients (Cu, Zn, Mn, Fe, all in mg/kg). For the laboratory methods of the analyses, see Filipová et al. (2010). Environmental data are in Table **S1** in Electronic Supplementary Material.

Subsequently, vegetation was recorded using plots selected in floristically and structurally homogenous representative parts. A square plot of 25 m^2 was placed as close as possible to the soil pit. A list of all vascular plant species was recorded. Projective cover of the species was assessed using the modified 9-degree Braun-Blanquet scale (van der Maarel 1979). Total cover of vascular plants and mosses was visually estimated in percentages. Species that could not be determined in the field were sampled and vouchered for later determination.

Data Analysis

A species data matrix of 47 sites containing 77 species of vascular plants was prepared (Table **S2** in Electronic Supplementary Material). Species projective cover was transformed from the 9-degree ordinal scale used in the field to percentages representing medians of the degree ranges. In multivariate analyses, the percentage cover values were log-transformed (cf. Jongman et al. 1995). The other data matrix contained environmental parameters, i.e., topsoil (0–20 cm) chemical variables and water table level. To test for normality of the environmental variables distribution, Shapiro-Wilks W test and visual examination (histograms and boxplots) were applied in Statistica, version 10 (StatSoft, Inc. 2011). We found that all variables except for base cations (Ca, Mg and CEC) were not normally distributed. Therefore, all values were log-transformed prior to the numerical analyses.

Four data analyses were performed:

1) Vegetation classification was carried out using TWINSPAN; we used JUICE, version 7 (Tichý 2002) to perform the TWINSPAN analyses. Two variants and four settings of TWINSPAN were applied. *i*) Two classifications with the modified TWINSPAN according to Roleček et al. (2009) differed in the dissimilarity measure (Jaccard or Sørensen) and setting of pseudospecies cutlevels (0-5-25 and 0-2-5-15-50, respectively). Maximal dissimilarity was the default option 0.787 and division was into six groups in both modified TWINSPAN classifications. *ii*) Two regular TWINSPAN classifications (Hill 1979) differed only in the number of pseudospecies cutlevels. These were three (0-5-25) or five (0-2-5-15-50), the maximum number of divisions was four in both cases. The four classifications in the form of species-plot tables were further examined. The resulting classification was established subjectively so that the clusters formed floristically and ecologically homogeneous units. The classification pattern was visualized through a non-metric multidimensional scaling (NMDS) scatterplot. The NMDS analysis was performed in R using *vegan* library (Oksanen et al. 2011), with 2 dimensions, 400 random starts, and using Bray-Curtis distance measure.

2) Vegetation types were compared with previous classifications published by Pisano (1977), Roig et al. (1985) and Collantes et al. (2009). Standardized phytosociological nomenclature of syntaxa according to Weber et al. (2000) was applied. Syntaxa at the level of vegetation type/association were characterized using diagnostic species. These were defined with thresholds of percentage frequency in a vegetation type the following way: 1. Species with frequency ≥33 % in an association while having frequency <33 % in the other four associations. 2. A second frequency threshold was set to 66 %, applied the same way and given a priority if occurred jointly with the 33 % threshold. 3. Species with frequency ≥15 % while having 0 % everywhere else. 4. Negatively diagnostic species with frequency ≤25 % in one or two associations while having >25 % elsewhere.
3) To evaluate differences in environmental conditions between the vegetation types established in the classification procedure, a Kruskal-Wallis test was performed. Twenty-one variables were examined; these included the 19 soil parameters, total vegetation cover and water-table depth. Differences between the vegetation types regarding the most important environmental variables were visualized using distribution plots. Statistica version 10 (StatSoft, Inc. 2011) was used to perform both tasks.
4) To reveal the main gradient in vegetation composition, Detrended Correspondence Analysis (DCA) was calculated. Scores of 47 sites in the first DCA axis were subsequently correlated with corresponding values of the entire set of 21 environmental variables. Spearman rank correlations were applied in Statistica version 10 (Statsoft, Inc. 2011). Canonical Correspondence Analysis (CCA) then helped to refine the understanding of the observed patterns using a selection of environmental variables. Parametric correlations between all environmental variables were then calculated. Correlations with $r>0.60$ and significance $P<0.05$ were further examined to avoid multicollinearity by pairs of strongly correlated variables. The following environmental variables were excluded from CCA: organic matter content, pH ($CaCl_2$), K, Mg, Na, cation exchange capacity (CEC), Zn, Fe, Cu, Mn, B, S, electric conductivity (EC), C:N ratio, and total vegetation coverage. These variables were mostly correlated with pH in H_2O and/or base cations content (represented by Ca), which we considered important and retained them for further analyses. As a result, only soil reaction (pH in H_2O), content of N, P, Ca, Al and water-table level (WT) were included in CCA. The statistical significance of each variable was tested using Monte Carlo permutation tests under full model with 499 permutations. Ordination analyses of vegetation and environmental variable patterns were performed in Canoco for Windows, version 4.5 (ter Braak and Šmilauer 2002).

Results

Vegetation Classification

Five vegetation types were recognized in the TWINSPAN classifications and the subsequent analyses. All four classification variants resulted in mutually compatible clusters. They are briefly characterized below as Vegetation types I to V, with photographs of typical stands (Fig. 2). Table 1 shows the diagnostic species for each

Table 1 Synoptic table showing percentage frequency of diagnostic and selected frequently occurring species in Types I to V. Diagnostic species are framed, for explanation on definition of diagnostic species see Methods. Species with frequency ≥33 % are in bold

Herb species	Type I	Type II	Type III	Type IV	Type V
Caltha sagittata	**44**	9	0	0	8
Scirpus cernuus	**44**	9	0	0	8
Gunnera magellanica	**33**	0	0	0	8
Erigeron leptopetalus	11	**45**	0	13	0
Samolus spathulatus	0	**45**	0	0	0
Eriachaenium magellanicum	22	**45**	17	0	0
Azorella trifurcata	11	**91**	**33**	0	8
Sisyrinchium patagonicum	0	27	0	0	0
Agrostis inconspicua	0	18	0	0	0
Plantago litorea	0	18	**50**	0	0
Deschampsia patula	0	9	**50**	0	0
Puccinelia magellanica	0	27	**50**	0	0
Plantago maritima	0	0	17	0	0
Salicornia ambigua	0	0	17	0	0
Carex macloviana	11	9	0	**50**	15
Alopecurus magellanicus	11	0	0	**38**	23
Calamagrostis stricta	0	0	0	**38**	8
Agrostis stolonifera	0	0	0	**88**	**38**
Hordeum lechleri	0	0	0	**38**	**77**
Trifolium repens	22	0	0	0	**62**
Taraxacum officinale agg.	**44**	**55**	17	13	**100**
Bromus araucana	0	0	0	0	15
Myosotis arvensis	0	0	0	0	15
Euphrasia antarctica	**33**	**45**	0	0	15
Cotula scariosa	**100**	**91**	0	0	**46**
Carex gayana	**78**	**82**	0	**50**	23
Juncus scheuchzerioides	**89**	**100**	**33**	25	**46**
Pratia repens	**78**	**73**	**33**	**38**	15
Koeleria mendocinensis	22	27	0	0	0
Colobanthus quitensis	22	**64**	**33**	25	0
Holcus lanatus	0	0	0	25	15
Colobanthus subulatus	**67**	**64**	**67**	0	15
Festuca gracilima	**44**	**36**	**50**	0	23
Deschampsia antarctica	**44**	**55**	**33**	25	0
Hordeum pubiflorum	**78**	**55**	**67**	13	8
Acaena magellanica	**67**	**36**	0	**63**	**85**
Poa pratensis	**56**	**45**	17	**50**	**54**

Type. The TWINSPAN classification was well recovered in the NMDS diagram (Fig. 3). Three clearly separated groups were the saline wetlands (Type III), low-grown marshes and grasslands (Types I and II), and tall-grown sedge and grass communities (Types IV and V). All vegetation types were in some manner distinguished in previous surveys. The vegetation types received standardized phytosociological names at the level of associations, with the exception of Type III comprising several ecologically similar communities. Four new associations were established in our analysis. Type relevés of the four described associations are in Table 2. Our communities can be classified as follows:

Class: *Hordeetea pubiflori* Roig et al. 1985
 Order: *Hordeetalia pubiflori* Roig et al. 1985
  Alliance: *Poo-Hordeion pubiflori* Roig et al. 1985
   Association: *Scirpo cernui-Calthetum sagittatae* ass. nova
   Association: *Samolo spathulatae-Azorelletum trifurcatae* ass. nova

Class: *Hordeetea lechleri* Roig et al. 1985
 Order: *Hordeetalia lechleri* Roig et al. 1985
  Alliance: *Hordeion lechleri* Roig et al. 1985
   Association: *Carici maclovianae-Agrostietum stoloniferae* ass. nova
   Association: *Hordeo lechleri-Trifolietum repentis* ass. nova

The classification of the *Scirpo cernui-Calthetum sagittatae* and the *Samolo spathulatae-Azorelletum trifurcatae* into the *Poo-Hordeion pubiflori* is only tentative. The *Hordeo lechleri-Trifolietum repentis* represents a transition between the classes of *Hordeetea lechleri* and *Molinio-Arrhenatheretea*.

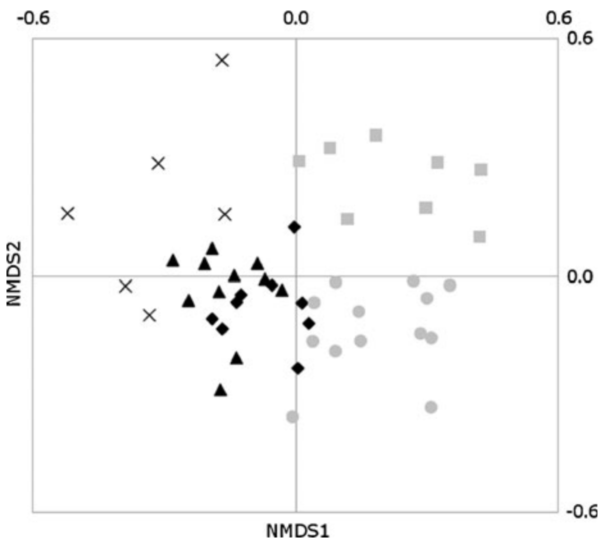


Fig. 3 NMDS diagram of the study sites, first two ordination axes. Vegetation types revealed by TWINSPAN are I Magellanic acidic marshes (black diamonds), II Magellanic alkaline wet grasslands (black triangles), III Salt wetlands (crosses), IV Magellanic tall sedge marshes (grey squares) V and Magellanic pastures (grey circles)

Table 2 Holotype relevés of four newly described associations. 7-degree Braun-Blanquet scale is used for species abundance-dominance values. Supplementary information to relevés: Association name: **1.** *Scirpo cernui-Calthetum sagittatae*, **2.** *Samolo spathulatae-Azorelletum trifurcatae*, **3.** *Carici maclovianae-Agrostietum stoloniferae*, **4.** *Hordeo lechleri-Trifolietum repentis*. Date (dd-mm-yyyy): **1.** 01-03-2005, **2.** 04-01-2005, **3.** 07-03-2005, **4.** 28-02-2005. UTM coordinates: **1.** 19F048471-4073821, **2.** 19F0372025-4159996, **3.** 18F0664685-4282915, **4.** 19F0481983-4075614. Farm (Fig. **1**): **1.** Tres Hermanos, **2.** Kampenaike Los Sauces, **3.** Puerto Consuelo, **4.** Tres Hermanos. Altitude (m a.s.l.): **1.** 60, **2.** 13, **3.** 37, **4.** 0. Slope (degrees): **1.** 0, **2.** 5, **3.** 0, **4.** 0. Water table depth (cm): **1.** >130, **2.** >120, **3.** >120, **4.** >130. Geomorphology: **1.** Plain, hilly terrain, **2.** Gentle slope, hilly, **3.** Plain, glacial valley, **4.** Plain, river estuary. E1 coverage (%): **1.** 90, **2.** 85, **3.** 85, **4.** 80. E0 coverage (%): **1.** 10, **2.** 2, **3.** 1, **4.** 0. Plot size (m^2): **1.** 25, **2.** 25, **3.** 25, **4.** 25

Relevé Nr.	1	2	3	4
Acaena magellanica	1	+	1	3
Acaena pinnatifida	.	.	1	.
Agrostis inconspicua	.	+	.	.
Agrostis stolonifera	.	.	3	.
Alopecurus magellanicus	.	.	1	1
Azorella trifurcata	.	3	.	.
Calamagrostis stricta	.	.	2	2
Caltha sagittata	2	.	.	.
Carex gayana	3	+	.	.
Carex macloviana	.	.	2	2
Colobanthus quitensis	+	+	.	.
Cotula scariosa	3	1	.	.
Deschampsia antarctica	1	.	.	.
Erigeron leptopetalus	.	2	.	.
Euphrasia antarctica	.	1	.	.
Festuca gracilima	.	.	.	.
Galium antarcticum	.	.	r	1
Gentianella magellanica	.	1	.	.
Gentiana prostrata	.	+	.	.
Geranium sessiliflorum	.	.	.	.
Gunnera magellanica	.	.	.	.
Hierochloe pusilla	.	+	.	.
Holcus lanatus	.	.	+	.
Hordeum lechleri	2	.	.	2
Hordeum pubiflorum	.	+	1	.
Juncus scheuchzerioides	.	1	.	.
Koeleria mendocinensis	.	.	.	.
Luzula alopecurus	.	+	.	.
Plantago tenella	.	+	.	.
Poa pratensis	+	.	.	1
Poa trivialis	.	+	.	.
Pratia repens	1	.	.	.
Primula magellanica	.	+	.	.
Ranunculus peduncularis	.	1	+	.
Samolus spathulatus	.	2	.	.

Table 2 (continued)

Relevé Nr.	1	2	3	4
Scirpus cernuus	2	.	.	1
Sisyrinchium patagonicum	.	1	.	.
Taraxacum officinale agg.	.	.	.	1
Trifolium repens	.	.	.	2
Trisetum spicatum	.	1	.	.

Vegetation type I – Magellanic acidic marshes

Scirpo cernui-Calthetum sagittatae Filipová, Hédl et Dančák ass. nova hoc loco; nomenclatural type: Table 2, relevé 1; Farm Tres Hermanos, Province of Tierra del Fuego, Chile (holotypus). Fig. 2b.

Diagnostic species: *Caltha sagittata*, *Scirpus cernuus*, *Gunnera magellanica*

This is a relatively species-rich (11 species per plot on average) community occurring predominantly on slightly acidic (mean topsoil pH-H_2O is 6.6), relatively nutrient-rich organic soils (mean organic matter content is 49.7 %, N=53.2 mg/kg, P=28.5 mg/kg), classified predominantly as histosols and histic fluvisols. In addition to the diagnostic species (see above), this community is characterized by the frequent occurrence of *Cotula scariosa*, *Carex gayana*, *Juncus scheuchzerioides*, *Pratia repens*, *Koeleria mendocinensis* and several species common to other Magellanic wetland types (e.g., *Colobanthus subulatus*, *Hordeum pubiflorum*, *Acaena magellanica*). Vegetation cover is generally high (80 % on average). A condition crucial for the development of this vegetation type is probably good water saturation throughout the whole year. The stands of this community were often encountered in riverine wetlands on organic soils, in the proximity of water courses or on organic soil flats.

This vegetation type is compositionally and ecologically similar to a community described as the *Calthetum sagittatae* Roig et al. 1985, which is largely dominated by *Calamagrostis stricta*, yet we do not consider it identical with the *Scirpo cernui-Calthetum sagittatae*.

Vegetation type II – Magellanic alkaline wet grasslands

Samolo spathulatae-Azorelletum trifurcatae Filipová, Hédl et Dančák ass. nova hoc loco; nomenclatural type: Table 2, relevé 2; Farm Kampenaike – Los Sauces, Province of Magallanes, Chile (holotypus). Fig. 2c.

Diagnostic species: *Erigeron leptopetalus*, *Samolus spathulatus*, *Eriachaenium magellanicum*, *Azorella trifurcata*, *Sisyrinchium patagonicum*, *Agrostis inconspicua*

This is a species-rich (14 species on average) community of low-grown grassland growing predominantly on slightly alkaline to alkaline (mean topsoil pH-H_2O is 7.64), relatively organic- and nutrient-poor soils (mean organic matter content is 24.0 %, N=26.0 mg/kg, P=19.1 mg/kg). The soils were classified predominantly as fluvisols and occur mainly on mineral soil flats or on lacustrine fringes. This vegetation is characterized by the high frequency of *Azorella trifurcata*, *Cotula* *scariosa*, *Carex gayana*, *Juncus scheuchzerioides*, *Pratia repens*, *Colobanthus quitensis* and *C. subulatus*. Other species confined to this association are *Sisyrinchium patagonicum* and *Agrostis inconspicua*. Vegetation cover is very variable, ranging from 40 % to 95 %, with an average of 74 %. This type of grassland, as well as most stands of the *Scirpo cernui*-*Calthetum sagittatae*, is markedly preferred by sheep and cattle due to the frequent occurrence of highly palatable plant species. Signs of moderate to severe overgrazing could often be observed.

Azorella-dominated wetlands were recognized in all previous vegetation surveys. They represent a common type of poor alkaline wetlands.

Vegetation type III – Saline wetlands

Diagnostic species: *Plantago litorea*, *Deschampsia patula*, *Puccinelia magellanica*, *Plantago maritima*, *Salicornia ambigua*. Fig. 2d.

Species-poor (six species on average) short grassland developed on alkaline (mean pH-H_2O=8.26) mineral-rich (K and Na reaching twice or three times the values measured in other vegetation types), organic poor clayey fluvisols and salty soils (mean topsoil organic matter content is 6.8 %, N=16.7 mg/kg, P=6.9 mg/kg). Soil types are solonchak and solonetz of generally lacustrine origin. Grasses dominate this vegetation, yet the total plant cover is low (ca. 40 % on average). This vegetation type includes stands with typical halophytic plant species (*Plantago litorea*, *Salicornia ambigua*) on salty plains but also grasslands with *Puccinellia magellanica* and *Deschampsia patula* occurring typically on fringes of vernal pools and also in a mosaic with floristically and ecologically related Magellanic alkaline wet grasslands (*Samolo spathulatae-Azorelletum trifurcatae*). The saline wetlands may experience a period of flooding during the spring season.

This vegetation comprises several ecologically and floristically related types and cannot be defined as a single association but rather as a broad community.

Vegetation type IV – Magellanic tall sedge marshes

Carici maclovianae-Agrostietum stoloniferae Filipová, Hédl et Dančák ass. nova hoc loco; nomenclatural type: Table 2, relevé 3; Farm Puerto Consuelo, Province of Última Esperanza, Chile (holotypus). Fig. 2e.

Diagnostic species: *Carex macloviana*, *Alopecurus magellanicus*, *Calamagrostis stricta*, *Agrostis stolonifera*

The *Carici maclovianae-Agrostietum stoloniferae* is a tall and relatively species-poor (ca. eight species per plot on average) grassland associated with moderately acidic (mean pH-H_2O=6.21), organic matter and nutrient-rich soils (topsoil mean organic matter content is 63.1 %, *N*=101.7 mg/kg, *P*=24.6 mg/kg). The soils were classified as histosols or histic fluvisols and occur on flat terrains (mineral or organic flats) or on slope springs. Vegetation is dominated by tall sedges such as *Carex macloviana* and grasses such as *Agrostis stolonifera, Calamagrostis stricta* and *Alopecurus magellanicus.* Vegetation cover is generally high (84 % on average).

Magellanic tall sedge marshes were described only in some of the previous studies (e.g., Collantes et al. 2009) and in any case rather coarsely, although they are a conspicuous and frequent vegetation type of the Fuego-Patagonian wetlands.

Vegetation type V – Magellanic pastures

Hordeo lechleri-Trifolietum repentis Filipová, Hédl et Dančák ass. nova hoc loco; nomenclatural type: Table 2, relevé 4; Farm Tres Hermanos, Province of Tierra del Fuego, Chile (holotypus). Fig. 2f.

Diagnostic species: *Hordeum lechleri*, *Trifolium repens*, *Taraxacum officinale* agg., *Bromus araucana*, *Myosotis arvensis*

This medium to tall grassland vegetation occurs mainly on acidic (mean topsoil pH-H_2O is 5.95), moderately to well-drained histosols. Soils are relatively organic-rich (organic matter content is 57.1 %) and contain intermediate amounts of nutrients (N=45.0 mg/kg, P=11.4 mg/kg). Under low water saturation, deep cracks (occasionally more than one meter) develop in dried and hardened organic layers. Vegetation cover and species richness are relatively high (83 % on average and ca. 10 species/plot, respectively). This association is poorly defined by species; most of the flora is common with at least one other vegetation type. It is characterized by a high proportion of alien plant species introduced to intensive pastures. Vegetation is dominated by grasses, such as *Agrostis stolonifera, Holcus lanatus* and *Hordeum lechleri* and dicotyledons, with dominating *Trifolium repens* and *Taraxacum officinale* agg. The community is affected by occurrence of alien weeds, such as *Descurainia sophia* or *Capsella bursa-pastoris*.

The Magellanic pastures were not encountered in the previous vegetation surveys except for their affinity to grazed grasslands in general. A reason for their exclusion from the surveys of Magellanic vegetation can be anthropic influence. However, both floristically and ecologically they clearly belong to Magellanic wetlands.

Vegetation-Environment Relationships

Relating environmental and vegetation characteristics between the vegetation types, significant differences in soil acidity (both pH-H_2O and pH-$CaCl_2$), content of organic matter, content of N, P, K, Al and Fe, and in total vegetation coverage were revealed (Table 3). Distributions of ten environmental variables important for the distinction between the five vegetation types are shown in Fig. 4. The pattern of two main environmental gradients, i.e., soil acidity and overall nutrient conditions expressed as N:P ratio, are summarized in Fig. 5. Pattern of sites in this environmental diagram corresponds to the pattern based on vegetation composition, as in Fig. 3.

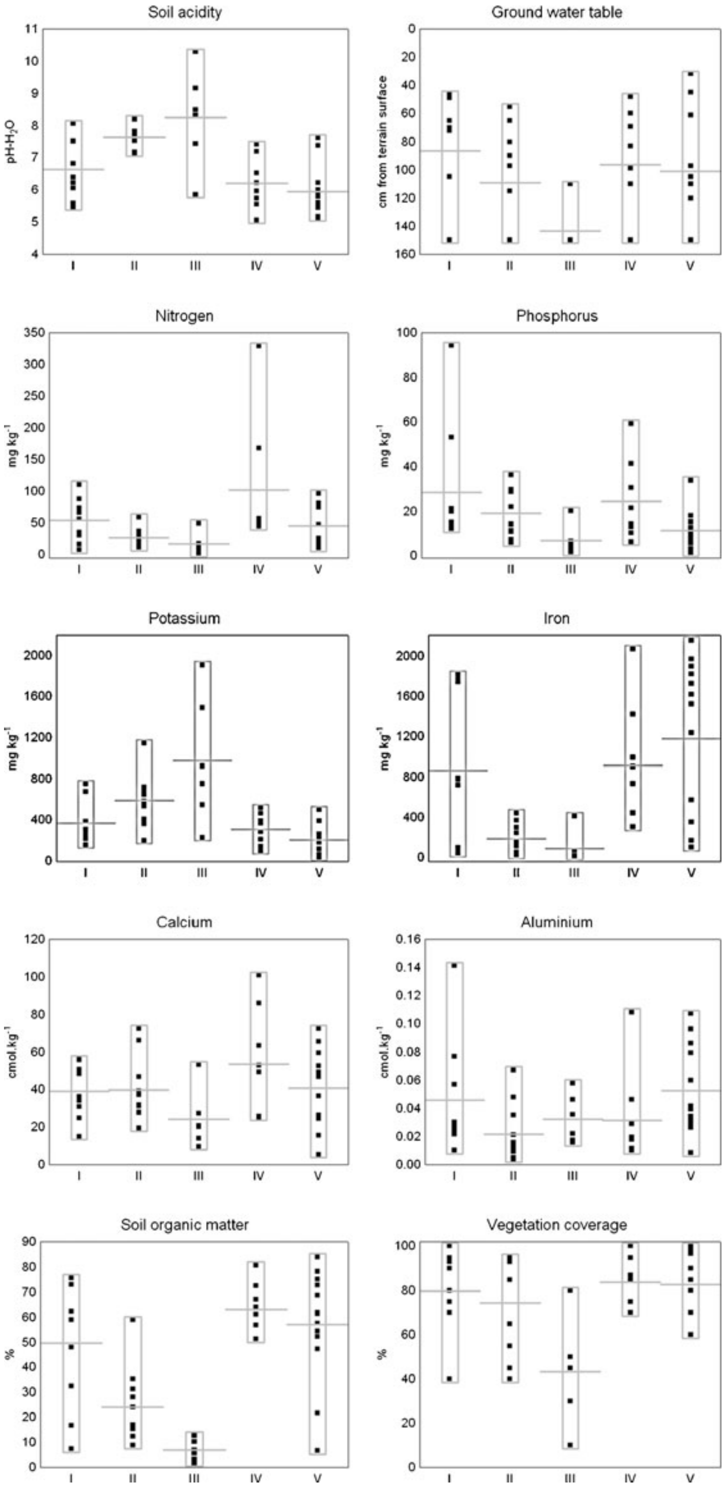
About a half (11) of the 21 environmental variables was statistically significantly correlated ($P<0.05$) with the main vegetation compositional gradient extracted by DCA (Table 3). It was linked to most of the environmental variables with significantly different values between the five vegetation types (Table 3). The most significant correlations ($P<0.001$) found were with pH-H_2O, organic matter content, contents of K and Fe and total vegetation coverage. Weaker significant correlation ($P<0.01$) was revealed for content of N and correlations with $P<0.05$ for contents of Na, Zn, Mn and electric conductivity. The most conspicuous feature is a negative correlation of pH with organic matter content and N. This mirrors two contrasting habitats, i.e., calcareous base rich inorganic sediments (pedologically fluvisols) and acidic organic peaty sediments (histosols).

Table 3 Characteristics of five vegetation types with means and standard deviations of the group values. Results of testing for differences using Kruskal-Wallis test are shown, statistically significant values are in bold (P<0.05). The last column shows correlation coefficients of the correlations between environmental variables and the plot scores at the first DCA axis. Significant correlations provide the axis' ecological interpretation; they are printed in bold and marked with asterisks: * – P<0.05, ** – P<0.01, *** – P<0.001. Abbreviations and units of the variables are: pH-H_2O, pH-$CaCl_2$ – soil acidity in water or $CaCl_2$ solution, OM-organic matter (% of soil dry weight), N, P, K (mg/kg), Ca, Mg, Na, exchangeable Al (cmol/kg), CEC – cation exchange capacity (mmol/g), Zn, Fe, Cu, Mn, B, S (mg/kg), EC – electric conductivity (dS/m), vegetation coverage (% of horizontal projection), WT – water table (cm from terrain surface)

	Type I n=9	Type II n=11	Type III n=6	Type IV n=8	Type V n=13	K-W test P-value	DCA 1st axis
pH-H_2O	6.6±0.9	7.6±0.4	8.7±1.5	6.2±0.8	6.0±0.8	**0.0001**	**0.665*** **
pH-$CaCl_2$	6.3±1.0	7.4±0.4	7.9±1.5	6.0±0.9	5.6±0.9	**0.0001**	**0.677*** **
OM	49.7±25.5	24.0±14.	6.8±4.1	63.1±10.2	57.1±22.1	**0.0001**	**−0.592*** **
N	53.2±34.3	26.0±13.4	16.7±16.7	101.7±100.4	45.0±31.4	**0.0067**	**−0.444** **
P	28.5±27.8	19.1±10.5	6.9±6.7	24.6±18.2	11.4±8.3	**0.0107**	−0.172
K	366.3±208.7	588.8±241.6	975.8±622.2	308.9±151.9	201.4±129.2	**0.0002**	**0.622*** **
Ca	39.2±14.5	39.9±16.4	24.2±15.5	53.6±28.7	40.7±20.2	0.1997	−0.252
Mg	12.3±4.1	11.5±6.0	6.8±3.0	11.6±5.4	9.0±3.5	0.1115	−0.026
Na	9.0±8.1	11.3±9.0	12.4±9.9	6.5±4.4	4.7±4.2	0.136	**0.314***
Al	0.1±0.0	0.0	0.0	0.0	0.1±0.0	**0.0415**	−0.150
CEC	61.5±23.2	64.2±20.7	45.9±18.5	72.5±37.7	55.0±25.1	0.492	−0.052
Zn	8.3±6.0	5.9±4.7	2.7±4.6	8.8±9.2	8.9±8.6	0.0901	**−0.297***
Fe	867.8±744.9	185.3±139.1	89.7±161.0	914.3±590.7	1176.9±783.8	**0.0003**	**−0.634*** **
Cu	2.0±1.3	2.2±1.3	3.1±0.9	3.3±2.5	2.3±2.3	0.4663	0.014
Mn	38.3±30.8	52.3±54.8	19.6±16.3	58.4±36.2	85.0±94.3	0.1541	**−0.356***
B	2.2±1.5	4.5±4.5	3.7±1.6	3.4±1.9	3.0±1.7	0.5147	0.052
S	185.2±170.9	132.4±84.3	95.4±41.0	231.9±144.7	188.5±152.3	0.3403	−0.242
EC	1.2±1.3	1.7±1.5	1.7±1.2	1.4±1.3	0.7±0.5	0.1685	**0.290***
C:N	13.9±3.1	15.0±4.7	28.9±30.5	12.8±2.0	14.5±3.1	0.2985	0.286
coverage	79.8±18.2	74.4±21.1	43.3±23.2	84.0±10.3	82.7±13.1	**0.0302**	**−0.466*** **
WT	86.6±39.7	109.0±36.2	143.3±16.3	96.1±38.8	100.9±45.1	0.098	0.168

The first two CCA axes explain 9.7 % (four axes 14.1 %) of the variance of species data and 56.1 % of the variance of species-environment relation. CCA biplot (Fig. 6) shows patterns of species constrained by the six environmental variables alongside with the classified vegetation types. Interestingly, the topsoil base cations (Ca) and pH (in H_2O) were not correlated (see also Table 3) each representing an independent factor significantly affecting vegetation variability.

Fig. 4 Differentiation of vegetation types I to V (x-axis) regarding the main environmental parameters: topsoil acidity (pH in H_2O), soil productivity (as contents of N, P) and water table level (in vegetation season), as well as some other important parameters revealed with statistical analyses (topsoil organic matter content – OM, contents of K, Fe, Ca, Al in soil, and vegetation coverage). Distributions (black squares with envelopes) and mean values (horizontal lines) are shown ▶


Soil acidity
pH-H2O
Ground water table
cm from terrain surface
Nitrogen
mg kg-1
Phosphorus
mg kg-1
Potassium
mg kg-1
Iron
mg kg-1
Calcium
cmol.kg-1
Aluminium
cmol.kg-1
Soil organic matter
%
Vegetation coverage
%
I
II
III
IV
V

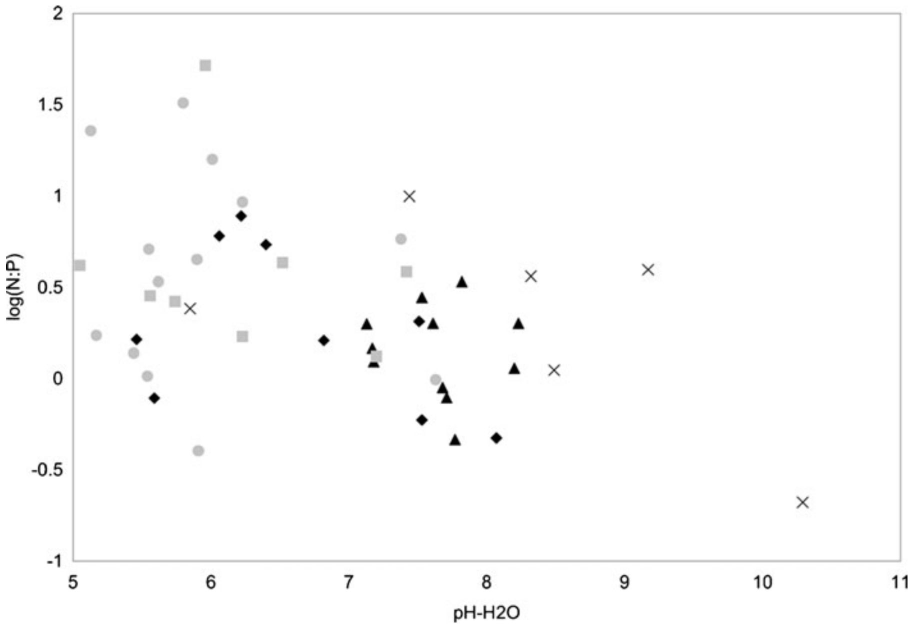


Fig. 5 Distribution of plots of five vegetation types along two environmental gradients: soil acidity (x-axis) and soil nutrient conditions represented with N:P ratio (y-axis; logarithmic scale). For reading of symbols of five vegetation types see Fig. 3

In summary, the most important environmental gradient driving compositional patterns in vegetation is the transition from alkaline lacustrine sediments to acidic peaty soils. Vegetation is only weakly and statistically insignificantly correlated with the water-table level. The five vegetation types are more or less distinctly separated along this gradient. There is a gradient of soil acidity reflected in a sequence from

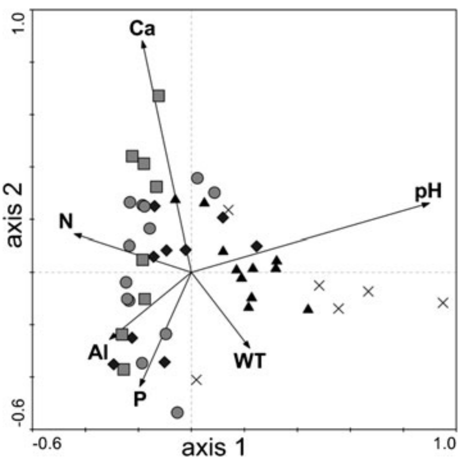


Fig. 6 CCA ordination diagram showing plots classified to five vegetation types and environmental variables. pH – soil reaction (pH-H_2O), Ca – calcium, N – available nitrogen, Al – exchangeable aluminium, P – exchangeable phosphorus, WT – ground-water table level. For reading of symbols of five vegetation types see Fig. 3

alkaline (vegetation Types III and II) through neutrophilous (Type I) to acidophilous communities (Types IV and V). An inverse, but less clearly pronounced, sequence of vegetation types follows the content of organic matter and soil characteristics related to this (content of N, P).

Discussion

Classification of Magellanic Wetlands

The vegetation of Magellanic wetlands was studied by only a few authors. The vegetation units and their abiotic characteristics were previously described by Pisano in his works from the 1970s, followed by Roig et al. (1985) and Collantes et al. (2009). The overview of results of these studies and of the present one, are presented in Table **4**. In a revision of the higher syntaxa of the vegetation of South America, Galán de Mera and Vicente Orellana (2006) confirmed Roig et al.'s (1985) view of this vegetation, with the exception of inclusion of the *Hordeetea lechleri* into the *Hordeetea pubiflori*, thus forming a single class of pastured wetlands.

Pisano (1971, 1973 and 1977) described a number of vegetation units in Fuego/ Patagonia. He concluded that most dominant or ecologically distinct species were common in many vegetation types and that it was often difficult to assign diagnostic species to the vegetation units he described. A community of *Gunnera magellanica-Deschampsia antarctica* was classified within the herbaceous hydromorphic vegetation of the humid Brunswick Peninsula (Pisano 1973). It could comprise most of *vegas* of the steppe except the saline and tall sedge types. Other communities of wet meadows described by Pisano (1977) showed some affinities to vegetation types resulting from our formalized classification. Two floristic similar communities, Type I Magellanic acidic marshes (*Scirpo cernui-Calthetum sagittatae*) and Type II Magellanic alkaline wet grasslands (*Samolo spathulatae-Azorelletum trifurcatae*), can be related to the *Gunneretum magellanicae*. Several species occurring frequently in both associations named above (*Euphrasia antarctica*, *Cotula scariosa*, *Carex gayana*, *Juncus scheuchzerioides*, *Pratia repens* and *Koeleria mendocinensis*) make them distinct from saline and tall-sedge communities. Alkaline wet grasslands also show some similarities with the hydrophytic phase of the *Festucetum gracillimae* (Pisano 1977). The broadly defined Type III Saline wetlands show resemblance to the *Eriachaenietum*, and some stands also to the *Salicornietum ambiguae* and to the *Deschampsietum antarcticae*. Vegetation corresponding to the Magellanic tall-sedge marshes (Type IV) and the Magellanic pastures (Type V) was not described by Pisano.

Roig et al. (1985) based their study of Patagonian vegetation on a landscape transect located about 150 km north of our study area. It comprised a broad range of communities including wetlands; environmental characteristics were not recorded. This study covered vegetation of periodic lakes corresponding to our Type III Saline wetlands, but without proper syntaxonomical treatment. The described vegetation units included a *Hordeetea pubiflori* Roig et al. 1985 comprising vegetation types of periodically flooded pastures and meadows, unclassified to associations in this study. Some vegetation appears to be similar to our Type II Magellanic alkaline wet

Table 4 Properties of the five vegetation types of the Magellanic wetlands compiled from [1]Pisano 1977, [2]Roig et al. 1985, [3]Collantes et al. 2009, and [4]this study and Filipová et al. 2010 (soil typology)

Veg. type	I	II	III	IV	V
Name	*Gunneretum magellanicae*[1], continental marshes *Carico-Calthetea*[2], acidic *Caltha* marshes[3], *Scirpo cernui-Calthetum sagittatae*[4]	*Gunneretum magellanicae*[1], *Hordeetea pubiflori*[2], *Azorella* wet grasslands, eutrophic[3], *Samolo spathulatae-Azorelletum trifurcatae*[4]	*Eriachaenietum*[1], Saline wetlands[3, 4]	Tall sedge marshes[3], *Carici maclovianae-Agrostietum stoloniferae*[4]	*Hordeetea lechleri*[2], *Hordeo lechleri-Trifolietum repentis*[4]
Soil	accumulation of peat[1], histic gleysols, sapric histosols, mixed lithology[3], histosols, fluvisols and gleysols, slightly acidic and nutrient-rich[4]	accumulation of peat[1, 2], compacted soils[2], mollic gleysol[3], fluvisols[3, 4], gleysols [4], low organic matter content, mineral-rich[4]	rich in Cl^- and carbonates[1], solonchaks[3], mineral-rich fluvisols, solon chak, solonetz, regosol[4]	histic gleysols, mixed lithology[3], histosols[3,4]	soils developed on eolic arenic deposits[2], histosols[4]
Soil acidity / pH (water)	acidic[1], 6.0[3], 6.6 (mean)[4]	acidic[1], 6.9[3], 7.6 (mean)[4]	8.2[3], 8.7 (mean)[4]	5.1[3], 6.2 (mean)[4]	6.0 (mean)[4]
Geomorphology	gentle slopes in an undulating landscape[1], riversides[2, 3, 4], small depressions[3]	gentle slopes in an undulating landscape[1, 2], depressions and floodplains[2, 3], flats and lacustrine fringes[2, 4]	depressions[1], lacustrine fringes[1, 4], at playas, lakes and swales[3]	riverine[3], flats (with deposits)[3, 4], slopes[4]	river plains[2], lacustrine fringes[2], flats (with deposits)[4]
Ground water regime	periodically frequently inundated[1], water table at 10–20 cm[2], water table at 20–50 cm[3], high water saturation, water table at >40 cm[4]	periodically and frequently inundated[1], rarely inundated, water table at >70 cm[3], no or rare inundation, water table at >55 cm[4]	periodical flooding[1], may experience periodical flooding[4]	water-saturated, water table at 0–20 cm[3], water table at >50 cm[4]	water-saturated[2], water table at >30 cm[4]
Dominant plant taxa	*Gunnera magellanica*[1], grasses[1], sedges[1, 2, 3, 4], rushes, dicots[1, 4], *Caltha sagittata* [2, 3, 4]	*Gunnera magellanica*[1], dicots[1, 4], sedges[1, 2, 3], grasses[1, 2, 4], other monocots[4], *Acaena*[3], *Azorella*[3, 4]	grasses[1, 3, 4], *Salicornia* and *Suaeda* [1, 3, 4]	sedges[3, 4], grasses[3, 4], *Agrostis stolonifera*[4]	sedges[2], grasses[2, 4], rushes[2, 4], introduced species (grasses, *Trifolium repens*, *Taraxacum officinale* agg.)[2, 4]

Table 4 (continued)

Veg. type	I	II	III	IV	V
Vegetation diversity	relatively high[1, 3], high[2, 4]	relatively high[1], high[2, 3, 4]	low[1, 3, 4]	relatively high[3], relatively low[4]	medium[2, 4]
Vegetation cover	high[1, 2, 3, 4]	high[2], relatively high[3], relatively low[4]	low[1, 3, 4]	high[3, 4]	high[2], relatively high[4]
Vegetation physiognomy	short[1, 2, 3, 4], dense[2], tufted[1]	tufted[1], short[1, 3, 4]	short[1, 3, 4]	tall[3, 4]	medium to tall[2, 4]

grasslands (*Samolo spathulatae-Azorelletum trifurcatae*). The *Calthetea* Roig et al. 1985 included the *Calthetum sagittatae*, somewhat resembling our Type I Magellanic acidic marshes. However, this association is not identical with the *Scirpo cernui-Calthetum sagittatae* due to different species composition and especially due to the high frequency of species of the *Hordeetea pubiflori* (e.g., *Hordeum pubiflorum*, *Euphrasia antarctica*, *Carex gayana*). The vegetation dominated with *Caltha sagittata*, studied in mountains of northern Patagonia by Gandullo and Faggi (2005) and classified in *Calthion sagittatae* Roig et al. 1985 is different from our vegetation types. Therefore, we decided to assign the two described associations to the *Hordeetea pubiflori* Roig et al. 1985.

Roig et al. (1985) studied pastures of *Holcus lanatus,* describing them as the association *Holco-Acaenetum ovalifoliae* (*Molinio-Arrhenatheretea*). These are physiognomically and to a certain extent ecologically similar to the Type IV Magellanic tall-sedge marshes (*Carici maclovianae-Agrostietum stoloniferae*). However, there are considerable differences in species composition, thus we decided to describe a new association to accommodate our vegetation type. Similarly, the Type V Magellanic pastures (*Hordeo lechleri-Trifolietum repentis*) somewhat resembles Roig's et al. (1985) meadows of the *Molinio-Arrhenatheretea*. At the same time, this vegetation type shows ecological and floristic affinities to Chilean pastures of the *Dactylo-Festucetum gracilimae* (order *Gamochaeto-Festucetalia*, class *Festucetea gracillimae*, both described by Roig et al. 1985). They were sampled in humid parts of the transect in the Chilean province of Última Esperanza. *Hordeum lechleri* dominates vegetation of the Types IV and V and pastures of the *Hordeetea lechleri* Roig et al. 1985, which lead us to provisional assigning *Carici maclovianae-Agrostietum stoloniferae* and *Hordeo lechleri-Trifolietum repentis* to this class. However, some differences in species composition could be observed, which may be due to regional differences in plant species composition; in addition, the vegetation of *Hordeion lechleri* typically occurs on arenic deposits of eolic origin with water table level situated at the soil surface (Roig et al. 1985). Finally, assuming temporal changes in vegetation, 20 more years of sheep grazing and invasion of alien species may have contributed to the differences observed between the vegetation sampled in the 1980s and in the 2000s.

Collantes et al. (2009) published a recent survey of Magellanic wetlands in the Argentinean part of Tierra del Fuego. Vegetation of wet grasslands dominated by *Azorella trifurcata* conforms to our Type II Magellanic alkaline wet grasslands (*Samolo spathulatae-Azorelletum trifurcatae*). However, except for the general similarity, there are differences in species composition. Type I Magellanic acidic marshes (*Scirpo cernui-Calthetum sagittatae*) do not differ much in species composition between Tierra del Fuego (sampled by Collantes et al. 2009) and continental Patagonia (this study). Only in the latter, steppic elements (e.g., *Lathyrus magellanicus*, *Geranium sessiliflorum*, *Empetrum rubrum*) can sometimes be encountered. Our saline wetlands (Type III) represent depleted forms of the Fuegian saltwater communities reported by Collantes et al. (2009). The depletion can be ascribed to the humid climate of the central part of the Fuego-Patagonia where saline soils are rare. In Argentinean (Collantes et al. 2009) and Chilean (this study) territories the communities of tall-sedge marshes are similar in species composition as well as environmental conditions. They correspond to our Type IV Magellanic tall sedge marshes

(*Carici maclovianae-Agrostietum stoloniferae*). Nevertheless, *Agrostis stolonifera* appears as a dominant species in the Chilean tall sedge marshes, whereas it is was not reported for the Argentinean ones. Moreover, Type V Magellanic pastures (*Hordeo lechleri-Trifolietum repentis*) had no parallel in the study by Collantes et al. (2009). These are extensive pastures with species composition influenced either by sowing of forage grasses, or by natural spreading of alien plants such as *Descurainia sophia* and *Capsella bursa-pastoris*.

Main Ecological Drivers

The pH/calcium gradient, the fertility gradient and the water regime are the key factors that influence vegetation composition in the wetlands of the Northern Hemisphere (Wheeler and Proctor 2000; Tahvanainen et al. 2002; Hájek et al. 2006). Analogous factors are responsible for variability in wetlands and moorlands in the southern temperate and cold zones (Kleinebecker et al. 2007, 2008; Kerr and McAdam 2008; Collantes et al. 2009). Confirming the existing knowledge, our findings indicated that the Magellanic wetlands mainly reflected a broad soil pH range on the transition from alkaline lacustrine sediments to acidic peaty soils. Significant differences were also found in the content of nutrients (nitrogen and phosphorus). The water regime was the least significant of the three major variables, which was probably the consequence of lack of information about this complex factor. Climate, site geomorphology and human impact can all have profound effect on the water regime.

However, neither water regime nor geomorphology alone is usually able to determine the occurrence of a certain vegetation type (Allen-Diaz 1991; Wheeler and Proctor 2000; Kerr and McAdam 2008; Collantes et al. 2009). Former studies detected the influence of climatic variability on the vegetation of Magellanic moors (Kleinebecker et al. 2007, 2008) and Fuegian wetlands (Collantes et al. 2009). In the former, there was a strong correlation between the steep continentality gradient and vegetation variability. In the latter the influence of precipitation on soil chemistry was reported, however no direct climatic patterns correlated with vegetation in this study. Our study concurs the findings much similar to those of Collantes et al. (2009) to a large extent. The reasons are likely threefold. Study sites do not cover significant parts of the climatic gradient, namely oceanic wetlands are poorly represented; climatic parameters available were not those influencing vegetation patterns; or climate does not play a major role in the steppic wetlands, as they represent azonal vegetation driven mainly by soil parameters, as shown in this study.

Human Impact

Grazing intensity was detected as a significant factor shaping the Patagonian steppe vegetation (e.g., Milchunas et al. 1989; Cingolani et al. 1998; Posse et al. 2000). A significant impact of sheep and cattle grazing and trampling was observed in the wetlands as well (Golluscio et al. 1998; SAG 2004; Kerr and McAdam 2008). Although the magnitude of changes in floristic composition produced by grazing was found to decrease with increasing soil moisture (Adler et al. 2005), it is still an important factor in some wetland vegetation types. In the Falkland Islands, the variation in vegetation of wetland meadows was caused mainly by disturbance by livestock, penguins and sheldgees (Kerr and McAdam 2008). It was hypothesized that the effects of grazing, manuring and trampling of sheep were the primary cause of vegetation change from the dominant vegetation of *Cortaderia*/*Empetrum* (Kerr and McAdam 2008).

The first TWINSPAN division in our classification separated heavily grazed short grasslands (Types I, II) and lightly- to non-grazed tall grasslands (Types IV and V). The confinement of *Azorella trifurcata*, a species indicating strong grazing, and of other rosette-forming species (*Samolus spathulatus*, *Eriachaenium magellanicum*, *Primula magellanica*) to Types I–II (III), together with livestock-preferred grass (*Deschampsia antarctica*) indicated regular grazing. There is also a conspicuous difference in the occurrence of *Azorella trifurcata* and other rosette species in the studies of Pisano (1973, 1977) and recent studies (Collantes et al. 2009, this study). Nowadays such species flourish, probably due to decades of excessive sheep grazing that is well-reflected especially in *vegas*.

The other group (Types IV and V) includes types characterized by the prevalence or almost exclusive presence of tall grasses, such as *Agrostis stolonifera*, *Bromus araucanus, Deschampsia cespitosa*, *Calamagrostis stricta* or *Trisetum spicatum* and sedges, such as *Carex aematorrhyncha*. The Type V seems to occupy sites with moderately to severely drained organic soils that can exhibit elevated amounts of available nitrogen and enhance the growth of nutrient-demanding species (e.g. *Agrostis stolonifera*). Interestingly, drainage in many sites causes the formation of deep cracks in peaty soils so it inhibits the usage of paddocks as pastures. Forced exclusion of sheep in these sites may also promote the growth of competitively strong grass species.

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Appendix 1

List of sampled sites

Site nr.	Site name (and code)	Coordinates UTM	Farm (Fig. 1)
1	Cerro Caballo 1 (CC1)	19F0368505;4157374	1 Kampenaike
2	Cerro Caballo 2 (CC2)	19F0067775;4156768	
3	Cerro Caballo 3 (CC3)	19F0367047;4157897	
4	Trinchera (T)	19F0365593;4156227	
5	no name (O2)	1970368785;4159390	
6	Cabeza del Mar 1 (CMAR1)	19F0071016;4160004	
7	Cabeza del Mar 2 (CMAR2)	19F0371700;4162460	
8	Vega Josefina (VJ)	19F0362335;4160175	
9	Parque/Josefina (PJ)	19F0370477;4165476	
10	Pesa 2 (PE2)	19F0363954;4163124	
11	no name (Aa)	19F0368063;4160095	
12	Lucho 2 (L2)	19F0071102;4163024	
13	Gali 2 (G2)	19F0366279;4158196	
14	Cerro Redondo 1 (CR-1)	19F0364776;4159884	
15	Cerro Redondo 2 (CR-2)	19F0364537;4160050	
16	no name (M2)	19F0369847;4159742	
17	Campo El Monte 1 (CM2-1)	19F0067913;4162976	
18	Campo El Monte 2 (CM2-2)	19F0369144;4161668	
19	Gali 1–1 (G1-1)	19F0367043;4158832	
20	Gali 1–2 (G1-2)	19F0366976;4158917	
21	Sacrificios (SAC1)	19F0365064;4157370	
22	Los Sauces 1 (S1)	19F0372438;4159941	
23	Los Sauces 2 (S2)	19F0372025;4159996	
24	Consumo (CON)	19F0070527;4159197	
25	Oazy Harbour 1 (OHB1)	19F0391324;4164299	2 Oazy Harbour
26	Oazy Harbour 2 (OHB2)	19F0393351;4164302	
27	Tres Hermanos 1 (TH1)	19F0481983;4075614	3 Tres Hermanos
28	Tres Hermanos 2 (TH2)	19F0484709;4073821	
29	El Álamo (AL)	19F0515511;4066613	4 El Álamo
30	San Isidro (SIS)	19F0520190;4121093	5 San Isidro
31	Quinta Esperanza (QE)	19F0401676;4147744	6 Quinta Esperanza
32	Miriana (MIR)	19F0477485;4132245	7 Miriana
33	Puerto Consuelo (PCONS)	18F0664685;4282915	8 Puerto Consuelo

Appendix 1 (continued)

Site nr.	Site name (and code)	Coordinates UTM	Farm (Fig. 1)
34	Shotel Aike (SHAI)	18F0677397;4311936	9 Shotel Aike
35	El Calafate (CLF)	19F0363249;4169525	10 El Calafate
36	Vega Vieja (VV)	19F0396507;4205526	11 Vega Vieja
37	Estancia Springhill (TF)	19F0477297;4165874	12 Estancia Springhill
38	Domaike 1 (DA-1)	19F0358183;4169455	13 Domaike
39	Domaike 2 (DA-2)	19F0352157;4173300	
40	Domaike 3 (DA-3)	19F0353014;4170020	
41	Los Coipos (COI)	19F0380126;4162433	14 Los Coipos
42	Estancia Josefina (EJ)	19F0362047;4166475	15 Estancia Josefina
43	Laguna Blanca 1 (LBL1)	19F0353128;4202000	16 Laguna Blanca
44	Laguna Blanca 2 (LBL2)	19F0352595;4204986	
45	Laguna Blanca 3 (X1)	19F0361852;4225847	
46	Las Coles (COL)	19F0315295;4176077	17 Las Coles
47	Cerro Castillo (CCAS)	no data	18 Cerro Castillo