

## Wetlands of the Magellanic Steppe (Tierra del Fuego, Argentina)

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**Abstract** Our main objective was to classify vegetation and soils of wetlands in northern Tierra del Fuego (Argentina) along a latitudinal precipitation gradient within the Magellanic Steppe Zone. We presented the first detailed ecological characterization of these wetlands by relating floristic composition to local site conditions, bedrock and climate. The survey consisted of 125 phytosociological censuses and 52 soil profile descriptions. Soils were classified according to FAO, and vegetation samples were explored by applying numeric methods such as cluster analysis and indirect ordination that included a post-hoc correlation with environmental variables. Floristic composition of freshwater communities was strongly related to a latitudinal gradient, and to soil pH, base cations and C/N ratio. Most eutrophic marshes were found on organic soils situated in springs on Tertiary sediments at mid-latitudes. Most acidic marshes occurred within Pleistocene catchment areas at higher latitudes (higher precipitation). Wet grasslands on mineral soils of low C/N ratio within formerly glaciated areas at lower latitudes (lower precipitation) represented the dry end of the moisture gradient covered by this study. Saltwater communities predominated on *playas* of Tertiary sediments and in estuarine systems. They were characterized by alkaline soils and high Na concentrations. Magellanic wetlands form a floristic continuum from the semiarid north to the subarid south with composition not necessarily related to landscape position and soil units, but strongly related to soil variables of secondary taxonomic level. We conclude that at least at the resolution level of our study, floristic composition along the observed gradient is strongly influenced by regional climate.

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**Keywords** Acidity gradient · *Azorella* wet grasslands · Bedrock lithology · *Caltha* marshes · *Carex* fens · Latitudinal gradient · Soil groups

**Plant nomenclature** Correa (1969–1998) for *Poaceae* and *Asteraceae*; Moore (1983) for other families of vascular plants; Matteri and Schiavone (2002) for mosses; Zuloaga et al. (1994), Zuloaga and Morrone (1996, 1999) for nomenclature updating of vascular plants

## Introduction

On an area basis, wetlands cover a small proportion of the land surface of the world (approximately 8–10%), but they support rich biodiversity (Mitsch and Gosselink 2007). They provide many ecological services, including many that can be expressed in economic terms, but they are nevertheless highly threatened by human activities (van Diggelen et al. 2006). In northern Tierra del Fuego (Argentina), wetlands occupy between 5% and 20% of the Magellanic steppe, a semiarid grassy formation covering 5,000 km<sup>2</sup> (Collantes et al. 1999). They are highly valued as habitat and a source of food for wild and domestic ungulates and for many species of migratory shorebirds, and also as a significant carbon pool (de la Balze et al. 2004). These vulnerable habitats are already highly disturbed by sheep grazing (Anchorena et al. 2001; Collantes et al. 2005) and increasingly endangered by other human impacts, including industrial activities, oil extraction and tourist development (Anchorena et al., unpubl.).

Studies on wetlands are mainly conducted on relatively small areas, focused on edaphic factors and productivity, but few have explored the relation between wetland diversity and climate at broader scales (Hájek et al. 2008). In Tierra del Fuego there is a steep climatic gradient imposed by the Andes that controls the transition from steppe to deciduous forest (Frederiksen 1988) but there is no information about the influence of climate on the structure of wetlands along this biome ecotone. Another important control when studying wetlands at the regional scale is bedrock lithology (Hájek et al. 2002; Tahvanainen 2004). A close relation between upland vegetation and bedrock has been shown in a previous survey (Collantes et al. 1999). Because the mineral composition of wetland water is regulated by the geochemistry of the drainage area, we expected that wetland soils and vegetation should also respond to different bedrock lithologies.

The high latitudinal location of Tierra del Fuego, exceptional for the southern hemisphere, has attracted biogeographers and ecologists since the 19th century, especially from northern Europe, looking for homologies and differences between the two circumpolar regions (Tuhkanen et al. 1990; Collantes et al. 1999). Per Dusén, a botanist of the Swedish expedition to Antarctica in 1895/97 (Dusén 1905) was the first to conduct a reconnaissance survey of plant communities, giving an invaluable account of pre-settlement vegetation. Regional inventories were undertaken by Pisano (1973, 1977), who described the vegetation types of southern Chile, including freshwater and saltwater wetlands, and Frederiksen (1988) who surveyed and mapped landscapes and soils for the whole island. In more specific studies, the focus was on peatlands, especially on the ombrotrophic bogs of the humid and perhumid zones. (Bonarelli 1917; Guiñazú 1934; Roivainen 1954; Auer 1965; Blanco and de la Balze 2004; Kleinebecker et al. 2007, 2008). For the semiarid zone of the island, no

integrated description of its wetlands or *vegas* has been published so far. Studies describing similar wetland types outside Tierra del Fuego are those by Roig et al. (1985) in the continental Magellanic steppe, and Clausen et al. (2006) in an Andean region of southern Patagonia. Our objective was to describe and classify the vegetation of the main types of wetlands of the steppe region, and to relate them to environmental features, especially regional climate, bedrock, landform, soil profile and soil variables.

## Material and Methods

### *Study Area*

The steppe region of Tierra del Fuego is part of the Magellanic steppe, a grassy vegetation type extending south of the Patagonian semidesert on the continent, at approximately 51°25' S, and reaching the *Nothofagus* forests at approximately 54° S in the island (Frederiksen 1988; León et al. 1998; Collantes et al. 1999).

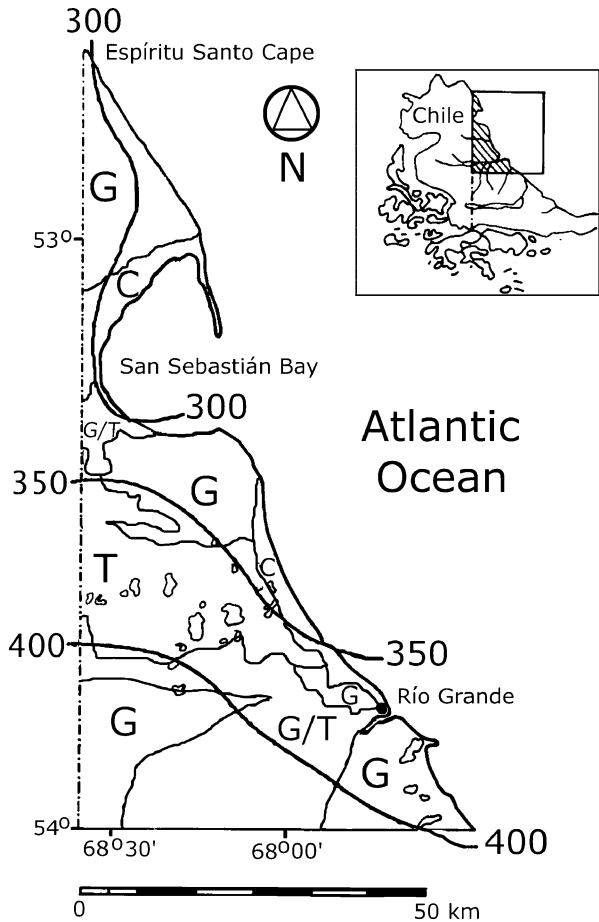
The Magellanic region represents a more humid and oceanic variant of the arid climate that prevails over most of Patagonia. In the Fuegian steppe, daily and seasonal variations of temperature are small (from a mean of 0°C in July to 10°C in January, Anonymous 1986). Cloudiness is high, winds very strong, and the Falklands ocean stream determines a colder climate than that expected from its latitudinal location (Collantes et al. 1999). Spatially, the main climatic gradient has a southwest-northeast direction, due to the rain shadow produced by the Andes on the predominant westerlies. In 115 km, rainfall decreases from 450 mm in the south of the area to 300 mm in the northeastern extreme (Fig. 1). The climatic threshold that causes the change in vegetation from steppe to deciduous forest occurs in the extreme south. Although the scarcity of meteorological stations does not allow the description of these changes, Frederiksen (1988) has classified the steppe area as semiarid and the ecotone as subarid.

The relief of the steppe region is flat to undulating, with some low to medium-height hills. Bedrock lithology is varied (Codignotto and Malumián 1992; Collantes et al. 1999) (Fig. 1). The areas covered by continental glaciation (G) present till and outwash deposits of coarse texture, mainly composed of infertile quartzose sand and hard granite gravel. In contrast, a large area not covered by glaciers or meltwater deposits presents old Tertiary rocks (T) of medium to fine texture (conglomerates, sandstones and claystones), easily weathered and rich in minerals, especially calcite. In the southern half of the area, some landscapes on Tertiary sediments have been covered by a narrow veneer of gravel outwash (G/T). Along the coast, Pleistocene gravel deposits have formed old and active tidal plains, marine terraces, and old coastal shorelines (C).

### *Fieldworks*

The survey covered the area from 52°40' to 54° south latitude (Fig. 1). Using 1:40,000 aerial photographs sampling areas on different types of wetlands were selected according to their extent and the singularity of landscape patterns already described (Anchorena et al. 1991; Collantes et al. 1999).

**Fig. 1** Location of the study area in the Argentine territory of the island of Tierra del Fuego. G – Glacial and meltwater deposits (sand, clay and gravels); C – Coastal Pleistocene deposits (sand, gravels and organic tidal deposits); T – Tertiary rocks (sandstones, claystones and conglomerates); G/T – Outwash deposit over Tertiary rocks. Isohyets from Collantes et al. (1989)



On the ground, each wetland was assigned to a hydrogeomorphic unit (Richardson and Brinson 2001) (Table 1) and was geographically located with a GPS. Vegetation and soil sampling points were selected according to microtopography or observable zonation of soil moisture. These units were afterwards related to hydrogeomorphic subclasses (Table 1). A total of 125 points were sampled in areas ranging from 10 to 25 m<sup>2</sup>, according to previously obtained species/area relationships. At each point, floristic composition, i.e., the cover of vascular plants and mosses was assessed according to the Braun-Blanquet scale modified by Westhoff and van der Maarel (1978). At 52 sites, pits were dug for profile descriptions according to FAO (2006). Profiles were classified according to the IUSS-FAO soil classification (IUSS Working Group WRB 2007) in different Reference Soil Groups (RSG). In addition, depth of the water table was checked, and samples of each horizon were taken for chemical analyses.

### Soil Analyses

Soil samples were air-dried, screened and subjected to the following analyses (according to Jackson 1981): pH in a 1 : 2.5 soil-water mixture, organic C (Walkley-

**Table 1** Wetland hydrogeomorphic classes and subclasses under which each sampled site was classified in the field (modified after Richardson and Brinson 2001)

Class	Subclass	Examples
<i>Riverine</i> Stream channels and their floodplains	<ul style="list-style-type: none"> <li>• <i>Elevated</i>. Coarse to medium-textured deposits of the floodplain, flat to convex</li> <li>• <i>Depressed</i>. Fine-textured deposits of the floodplain, flat to concave</li> <li>• <i>Discharges</i> on valley escarpment, fine-textured</li> </ul>	Point bars, meander scrolls, natural levees Oxbow lakes, backswamp plains Springs
<i>Depressional</i> Small basins below the surrounding topography	<ul style="list-style-type: none"> <li>• <i>Borders</i>. Medium-textured soils</li> <li>• <i>Centers</i>. Fine-textured soils</li> </ul>	Edges of temporary ponds (glacial terrain) Center of temporary ponds (glacial terrain)
<i>Lacustrine</i> Large temporary lakes	<ul style="list-style-type: none"> <li>• <i>Discharge</i>. Areas of stream discharge in <i>playas</i></li> <li>• <i>Recharge</i>. Areas of inundation-desseccation</li> </ul>	Fringe areas between freshwater and saltwater <i>Playas</i>
<i>Organic Flats</i> Flat terrain in areas of relatively high precipitation, with organic soils	-	Peatlands
<i>Estuarine</i> Alluvial and marine sediments flooded periodically by tidal waters	<ul style="list-style-type: none"> <li>• Low areas of daily tidal inundation</li> <li>• High areas of intermittent tidal inundation</li> </ul>	Mud flats and tidal marshes Saline shrublands and prairies
<i>Slope</i> Concave convergent positions on landscapes	-	Topographic swales

Black), total N (Kjeldahl modified by Ritcher 1980), extractable P (Kurtz and Bray I), exchangeable cations (extracted with ammonium acetate 1 N, pH=7 and quantified by atomic absorption). The analytical data was used to confirm the RSG and to refine the soil classification by adding one or more qualifiers to the RSG. For profiles lacking the needed chemical data, classification was inferred from pH data or from similar classified profiles in the same type of geomorphic setting.

### Statistical Analyses

A vegetation data matrix of 125 samples and 118 species was classified with “Two-Way Indicator Species Analysis” (Twinspan) using PCORD version 5 (McCune and Grace 2002). Twenty-seven species with single appearances and low cover values were excluded from the analysis. Alphanumeric values of species abundance recorded in the field were transformed into numeric values from 1 to 9. Nine pseudospecies and five cut levels were used. Diversity ( $N_2$ , the inverse of the

Simpson index), richness, mean species cover and species constancy were calculated for each community.

While the environmental setting of saltwater wetlands was relatively easy to recognize, freshwater communities seemed to occur along complex gradients. To investigate environmental gradients, we used 25 out of a total of 36 samples of freshwater wetlands with complete soil analyses and occurring in the southern half of the area, where the precipitation gradient is noticeable and the rock substrate most variable (see Fig. 1). We performed correspondence analysis (CA) with down-weighting of rare species by PC-ORD version 5 (McCune and Grace 2002). The resulting floristic ordination was interpreted in relation to soil variables and latitude using Kendall's rank correlation coefficients. Two ordinal variables were used to represent the thickness of peat and the depth of the water table (Table 2). For comparisons of soil variables and vegetation attributes with bedrock classes and community types, standard statistical methods were performed by InfoStat (2008), and the non-parametric Kruskal-Wallis test was used to indicate the significance of differences. To see the pattern of categorical variables (bedrock areas, soil groups and hydrogeomorphic classes) in relation to the ordination of samples and species by CA, categories were overlaid on each point of the ordination.

## Results

### *Wetland Soils*

Most profiles were classified in the gleysol and histosol soil groups with some fluvisols, solonetz and solonchaks (Table 3). Gleysols (20 profiles) were found in most wetlands over the whole area. Histosols (15 profiles) appeared in organic flats and depressed riverine wetlands, mostly in the southern part of the study area. Fluvisols (11 profiles) with poor development appeared in riverine systems on areas with over-bank flow from streams and on low tidal landforms. Solonetz and solonchaks (three profiles each) dominated the saline environment in lacustrine wetlands, old tidal plains and elevated tidal landforms. While profile morphology is the main criterion in separating RSGs, there were important differences in chemical properties between soils of the same or related RSGs, as denoted by the eutric and dystic qualifiers for a given RSG, or the differences in C and N between histic and

**Table 2** Ordinal scales to estimate peat thickness and water table level

Scale	Peat depth	Water level at summer
0	no peat	>100 cm below surface
1	<20 cm	70–100 cm
2	20–40 cm	40–70 cm
3	40–60 cm	20–40 cm
4	60–80 cm	20–40 cm
5	>80 cm	0–20 cm

**Table 3** Reference Soil Groups (RSG) (IUSS-FAO) in which a total of 52 wetland soil profiles were classified

	<i>n</i>	pH	C (g/kg)	N (g/kg)	C/N	Ca (cmolc/kg)	Mg (cmolc/kg)	Na (cmolc/kg)	K (cmolc/kg)
Fibric Histosol	3	5.1±0.1	667.97±331.92	21.83±2.14	30.57±18.43	9.58±0.85	1.77±0.42	0.46±0.28	0.28±0.14
Hemic Histosol	3	5.3±0.6	465.14±20.32	23.11±1.63	20.10±2.31	4.5±3.40	1.30±0.14	0.70±0.00	0.57±0.57
Sapric Histosol (dystic)	4	5.1±0.2	453.83±71.74	22.29±3.09	20.37±2.66	4.4*	0.9*	0.3*	0.2*
Sapric Histosol (eutric)	5	6.6±0.4	397.47±85.70	28.81±3.46	13.80±4.44	47.66±10.32	14.36±2.22	6.92±3.47	2.19±3.74
Histic Gleysol	7	5.2±0.3	349.18±97.53	16.68±4.76	20.89±10.46	9.53±4.55	0.79±1.03	0.49±0.47	0.88±0.68
Mollic Gleysol	7	6.3±0.9	103.39±95.39	3.29±2.40	9.91±0.64	29.34±15.20	10.96±5.80	1.92±2.69	2.59±0.28
Fluvisol (dystic)	3	4.7±0.2	210.13±155.01	11.82±9.81	17.76±1.88	10.09±4.00	1.7±1.07	0.70±0.45	0.50±0.37
Fluvisol (eutric)	3	6.4±0.2	46.07±8.38	4.52±1.47	10.03±2.16	22.45±4.35	5.55±0.92	1.06±0.15	0.44±0.21
Fluvisol (tidalic)	4	8.0±0.8	49.5*	2.15*	22.3*	3.6*	5.8*	26.9*	4.6*
Solonetz	3	7.2±0.4	127.57±62.53	7.30±11.17	17.47±18.92	21.32±11.90	14.03±13.11	8.59±31.53	4.36±0.69
Solonchak	3	8.2±0.6	91.32±280.72	5.32±11.72	17.16±7.21	17.00±13.93	8.32±0.92	23.43±10.82	3.74±1.55

\* Only one sample was analyzed

mollic gleysols (Table 3). Both climatic and lithological factors might be associated with these differences (Table 4). In the semiarid zone (300–350 mm annual precipitation), C and N content of wetland soils in areas of glacial deposits (G) were significantly lower than in wetlands underlain by any type of bedrock in the higher rainfall zone (350–400 mm). In this less xeric climate, wetlands on watersheds over Tertiary sediments (T) presented soils with higher pH and base concentration, while those from the area of glacial deposits (G) had the lowest values. Where a narrow outwash deposit covered the Tertiary rocks (G/T), wetlands presented soils with intermediate pH and base concentration. Although not all values differed significantly, the tendency was consistent.

### Plant Communities

Six freshwater communities and three saltwater communities resulted from the Twinspan classification analysis (Fig. 2). Twelve groups of species, each having a close relationship with the indicator species of each cut level of the Twinspan (Fig. 2), were arranged in Table 5. Groups 1 and 2 are mosses, sedges and grasses of generally very wet conditions. Group 3 contains very short graminoids and herbs. Group 4 supports species resistant to saline or alkaline conditions. Groups 5 and 6 are composed of species of high ecological amplitude, including some exotic or cosmopolitan species that increase after disturbance. Groups 7 and 8 contain species common in dry, non-wetland habitats. Groups 9 to 12 characterize the saline environment. Differences in community attributes (total cover, richness, diversity) and soil pH between community types were significant at  $P < 0.0001$  for the overall comparison with the Kruskal-Wallis test. Different letters in Table 6 indicate significant differences at  $P < 0.05$ .

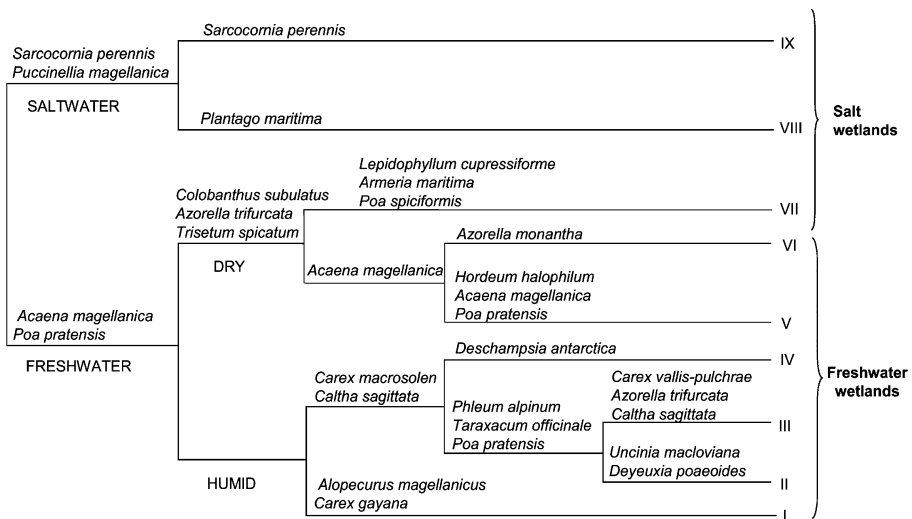
### Environmental Gradients of Freshwater Wetlands

The first CA axis (eigenvalue 0.45) explains 20% of the total variance. In the ordination, the freshwater community types (I–V) are arranged along an acidity-

**Table 4** Differences in wetland soil chemistry between bedrock areas and rainfall zones. Different letters indicate significant differences ( $P < 0.05$ ) shown by Kruskal-Wallis test

	Glacial deposits (G) 300–350 mm	Glacial deposits (G) 350–400 mm	Glacial cover on Tertiary rocks (G/T) 350–400 mm	Tertiary rocks (T) 350–400 mm
pH	6.4±0.1 bc	4.9±0.2 a	5.5±0.6 ab	6.9±0.3 c
Ca (Cmolc/kg)	21.9±3.22 b	8.19±2.96 a	25.29±19.66 b	42.94±16.46 b
Mg (Cmolc/kg)	5.13±0.31 ab	1.36±0.87 a	6.75±6.16 ab	13.54±4.15 b
Na (Cmolc/kg)	1.13±0.21 ab	0.54±0.27 a	3.65±4.32 b	6.62±4.56 b
Base cations (Cmol/kg)	28.67±3.61 b	10.83±4.03 a	38.18±28.56 b	64.60±21.75 b
C (g/kg)	45.03±7.02 a	339.96±151.59 b	320.46±153.85 b	303.52±327.00 b
N (g/kg)	4.63±1.42 a	16.61±7.05 b	19.58±9.22 b	23.72±10.58 b
<i>n</i>	3	7	10	5





**Fig. 2** Successive divisions of vegetation samples in the Twinspan classification, with the indicator species for each cut level and the nine community types obtained

alkalinity gradient (Fig. 3) defined by strong positive correlations with pH and base cations and negative correlations with latitude and C/N ratio (Table 7). Sixteen percent of the total variance is explained by axis II (eigenvalue 0.37) which is highly correlated with the position of the water table, total nitrogen and peat depth (Table 7). From left to right along axis I, species groups associated with wet and acid conditions (1 and 2) are followed by species of high amplitude (5 and 6) and then, by the group of dwarf life forms (group 3). The eutrophic (4) and the steppic (8) groups merge at the end of axis I, but are separated along axis II.

Overlays of bedrock, hydrogeomorphic classes and soil groups on the ordination revealed relationships among vegetation type, mineral richness and hydrology. Bedrock types form a kind of gradient along axis II. Tertiary rocks, associated with the eutrophic *Caltha* marshes (type IV) at the axis bottom, are followed by sediments of mixed lithology (G/T) associated with community types II and III, and part of I, and finally by the association of glacial deposits (G) with community types I and V (Fig. 4a). In response to landform and soil, the *Azorella* wet grassland (type V) is associated with dry, elevated geoforms of riverine systems (Fig. 4b) and mollic gleysols (Fig. 4c), while the eutrophic *Caltha* marsh (type IV) is associated with springs in valley borders (Fig. 4b) and sapric histosols (eutric) (Fig. 4c). The most acidic community, the acidic tall sedge marsh with mosses (type I), is associated with organic flats and riverine depressed forms, although some elevated forms also occur (Fig. 4b). Their soils are varied, including the most acidic histosols (fibric and hemic histosols) (Fig. 4c).

### Description of Community Types

The nine plant communities obtained by the Twinspan method and analyzed in relation to environmental gradients with the CA are described below following Table 5 and Figs. 3 and 4.

**Table 5** Shortened synoptic table of species occurrence in percentage (bold type arabic digits) and mean cover (normal type digits) in nine wetland community types resulting from the Twinspan classification. The species groups (1–12) and the community types (I–IX) are described in the text

	Tall sedge marshes		<i>Caltha</i> marshes				Azorella wet grasslands		Salt shrubl.	Salt marsh	Salt carpet							
	with mosses		acidic	eutrophic		acidic	eutrophic											
	I	II	III	IV	V	VI	VII	VIII				IX						
1 <i>Polytrichum juniperinum</i>	<b>43.8</b>	34.9			<b>10.5</b>	2.6	<b>9.1</b>	0.5										
<i>Syntrichia robusta</i>	<b>5.3</b>	37.5																
<i>Sanionia uncinata</i>	<b>12.5</b>	50.0			<b>21.1</b>	1.4	<b>9.1</b>	0.5										
<i>Carex magellanica</i>	<b>6.3</b>	0.5																
2 <i>Carex gayana</i>	<b>56.3</b>	44.0	<b>23.1</b>	21.8														
<i>Carex curta</i>	<b>50</b>	9.5	<b>23.1</b>	2.7	5.3	0.5												
<i>Carex decidua</i>	<b>50</b>	3.3	<b>7.7</b>	0.5														
<i>Carex atropicta</i>	<b>25</b>	10.2	<b>23.1</b>	6.6	5.3	0.5												
<i>Carex capitata</i>	<b>6.3</b>	0.1	<b>7.7</b>	37.5														
<i>Carex macloviana</i>	<b>56.3</b>	24.6	<b>46.2</b>	19.4	<b>21.2</b>	1.0		<b>24.1</b>	1.1									
<i>Deyeuxia poaeoides</i>	<b>56.3</b>	31.2	<b>46.2</b>	17.6			<b>36.4</b>	0.1										
<i>Alopecurus magellanicus</i>	<b>81.3</b>	12.8	<b>100</b>	2.4	<b>57.9</b>	1.4	<b>45.5</b>	1.3	<b>31</b>	1.2	<b>20</b>	0.5	<b>14.3</b>	0.5				
<i>Stellaria debilis</i>	<b>37.5</b>	1.8	<b>23.1</b>	1.2			<b>45.5</b>	1.6										
<i>Ucinia macloviana</i>	<b>6.3</b>	5.0	<b>61.5</b>	14.7	5.3	8.8												
3 <i>Caltha sagittata</i>	<b>37.5</b>	2.5	<b>92.3</b>	11.5	<b>94.7</b>	41.4	<b>72.8</b>	16.4	<b>48.3</b>	11.9	<b>20</b>	0.5						
<i>Juncus scheuchzerioides</i>	<b>18.8</b>	6.6	<b>69.2</b>	23.2	<b>47.4</b>	4.4	<b>81.9</b>	24.1	<b>27.6</b>	0.9	<b>30</b>	14.3		<b>10</b>	37.5			
<i>Carex vallis-pulchrae</i>	<b>12.5</b>	2.5	<b>15.4</b>	0.5	<b>73.7</b>	6.5	<b>63.7</b>	29.1	<b>13.8</b>	1.5								
<i>Carex macrosolen</i>	<b>18.8</b>	4.8	<b>76.9</b>	7.0	<b>73.7</b>	8.3	<b>90.9</b>	17.2	<b>65.5</b>	7.9	<b>60</b>	12.8	<b>14.28</b>	0.5	<b>10</b>	0.5		
4 <i>Deschampsia antarctica</i>			<b>15.4</b>	9.4	<b>52.6</b>	0.7			<b>40</b>	2.8				<b>10</b>	2.5			
<i>Eriachneium magellanicum</i>							<b>63.6</b>	11.1	<b>24.1</b>	0.7	<b>40</b>	2.8		<b>20</b>	19.8			
<i>Hordeum lechleri</i>	<b>25</b>	11.8	<b>7.7</b>	18.8	<b>10.5</b>	0.5	<b>54.5</b>	6.3	<b>3.4</b>	5.0	<b>30</b>	21.7	<b>42.9</b>	2.7	<b>90</b>	13.3	<b>50</b>	5.5
<i>Pratia repens</i>	<b>12.5</b>	0.5	<b>46.2</b>	0.8	<b>73.7</b>	0.7	<b>81.8</b>	4.3	<b>51.7</b>	0.7	<b>60</b>	19.9						
5 <i>Phleum alpinum</i>	<b>68.8</b>	5.4	<b>84.6</b>	2.4	<b>68.4</b>	1.5	<b>9.1</b>	0.5	<b>58.6</b>	1.3	<b>30</b>	0.5	<b>28.6</b>	0.3				
<i>Koeleria fueguina</i>	<b>68.8</b>	2.3	<b>46.2</b>	11.1	<b>57.9</b>	4.2	<b>27.3</b>	1.2	<b>27.6</b>	7.7								
<i>Hordeum halophilum</i>	<b>56.3</b>	2.3	<b>69.2</b>	4.1	<b>52.6</b>	10.4	<b>45.5</b>	15.6	<b>62.1</b>	9.5								
6 <i>Acaena magellanica</i>	<b>81.3</b>	5.5	<b>76.9</b>	3.0	<b>78.9</b>	2.7	<b>81.9</b>	5.3	<b>96.6</b>	15.2	<b>30</b>	3.9	<b>14.3</b>	0.5				
<i>Poa pratensis</i>	<b>68.8</b>	5.6	<b>100</b>	16.9	<b>94.8</b>	5.3	<b>54.5</b>	11.4	<b>82.8</b>	4.7	<b>20</b>	0.5	<b>28.6</b>	1.3				
<i>Taraxacum officinale</i>	<b>68.8</b>	7.8	<b>69.2</b>	2.8	<b>63.2</b>	3.7	<b>27.3</b>	0.1	<b>48.3</b>	8.5	<b>60</b>	3.6	<b>71.4</b>	2.1	<b>30</b>	1.2		
<i>Trisetum spicatum</i>	<b>31.3</b>	0.5	<b>69.2</b>	1.2	<b>42.1</b>	1.5	<b>27.3</b>	0.4	<b>93.1</b>	5.6	<b>80</b>	3.6	<b>71.4</b>	2.7	<b>40</b>	6.2		
<i>Azorella filamentosa</i>	<b>18.8</b>	0.5	<b>23.1</b>	1.2	<b>52.6</b>	9.3			<b>67</b>	5.5	<b>60</b>	3.1	<b>28.6</b>	0.5	<b>30</b>	2.0		
<i>Hordeum pubiflorum</i>	<b>6.3</b>	0.5	<b>7.7</b>	8.8	<b>26.3</b>	3.2	<b>36.4</b>	4.5	<b>44.9</b>	13.0	<b>50</b>	3.5	<b>28.6</b>	2.8	<b>10</b>	37.5	<b>30</b>	7.8
7 <i>Azorella trifurcata</i>	<b>6.3</b>	0.1	<b>7.7</b>	0.5	<b>63.2</b>	1.0	<b>54.5</b>	3.6	<b>82.8</b>	12.6	<b>80</b>	25.2	<b>28.6</b>	5.0				
8 <i>Colobanthus subulatus</i>					5.3	0.5			<b>62.1</b>	1.5	<b>30</b>	1.8	<b>71.4</b>	1.3	<b>10</b>	0.5		
<i>Azorella monantha</i>									<b>31</b>	1.1	<b>60</b>	8.5	<b>57.1</b>	5.1	<b>20</b>	1.5		
<i>Deschampsia patula</i>					<b>10.5</b>	0.5			<b>51.7</b>	3.2	<b>10</b>	0.5	<b>42.9</b>	0.5	<b>20</b>	0.5		
<i>Poa spiciformis</i>	<b>6.3</b>	0.1			<b>10.5</b>	2.8			<b>20.7</b>	3.2	<b>40</b>	15.3	<b>85.7</b>	3.3	<b>30</b>	0.5		
<i>Azorella fueguiana</i>					5.3	18.8			<b>31</b>	2.7			<b>14.3</b>	0.5				
<i>Festuca gracillima</i>	<b>6.3</b>	0.1							<b>24.1</b>	1.1			<b>57.1</b>	8.7				
9 <i>Armeria maritima</i>	<b>6.3</b>	0.1			5.3	0.5			<b>10.3</b>	0.4			<b>71.4</b>	1.3	<b>40</b>	0.4	<b>50</b>	0.5
10 <i>Lepidophyllum cupressiforme</i>													<b>57.1</b>	40.8	<b>30</b>	9.2		
<i>Plantago maritima</i>									<b>30</b>	3.9			<b>42.9</b>	1.2	<b>70</b>	3.4		
<i>Lepidium pseudo-didymus</i>													<b>14.3</b>	0.5	<b>20</b>	0.5		
11 <i>Poa atropidiformis</i>									<b>13.8</b>	7.5	<b>30</b>	3.3			<b>60</b>	1.6	<b>40</b>	4.2
<i>Puccinellia magellanica</i>											<b>20</b>	19.0	<b>28.6</b>	1.5	<b>90</b>	18.6	<b>50</b>	19.8
<i>Puccinellia pusilla</i>											<b>20</b>	0.5	<b>14.3</b>	5.0	<b>30</b>	1.8	<b>40</b>	7.2
<i>Rumex crispissimus</i>															<b>10</b>	0.1		
12 <i>Sarcocornia perennis</i>															<b>40</b>	17.5		
<i>Puccinellia biflora</i>																	<b>100</b>	40.6
<i>Sedum acre</i>																	<b>40</b>	27.5
																	<b>10</b>	0.5

**Table 6** Mean values  $\pm$  s.d. of some vegetation attributes and soil pH of the nine community types classified with Twinspan. Different letters indicate significant differences ( $P < 0.05$ ) shown by Kruskal-Wallis test

	Tall sedges marshes		<i>Caltha</i> marshes		<i>Azorella</i> wet grasslands		Salt shrubl.	Salt marsh	Salt carpet
	with mosses	with <i>Caltha</i>	acidic	eutrophic	acidic	eutrophic			
	I	II	III	IV	V	VI	VII	VIII	IX
<i>n</i>	16	13	19	11	29	10	7	10	10
Total vegetation cover	96.44 c	97.23 c	95.59 bc	99.55 c	86.14 a	88.13 ab	70.71 a	70.5 a	70.5 a
Richness	16.94 cd	17.23 cd	18.53 d	13.09 bc	19.45 d	16.5 cd	17.86 cd	9.9 ab	4.3 a
Diversity	11.99 bc	13.32 cd	13.53 cd	10.01 bc	15.68 d	12.91 bc	12.99 bc	7.76 ab	3.63 a
pH	5.1 a	5.5 ab	6.0 bc	6.7 cd	6.3 bc	6.9 cd	7.0 d	8.2 d	8.0 d

### *I and II) Tall sedge marshes*

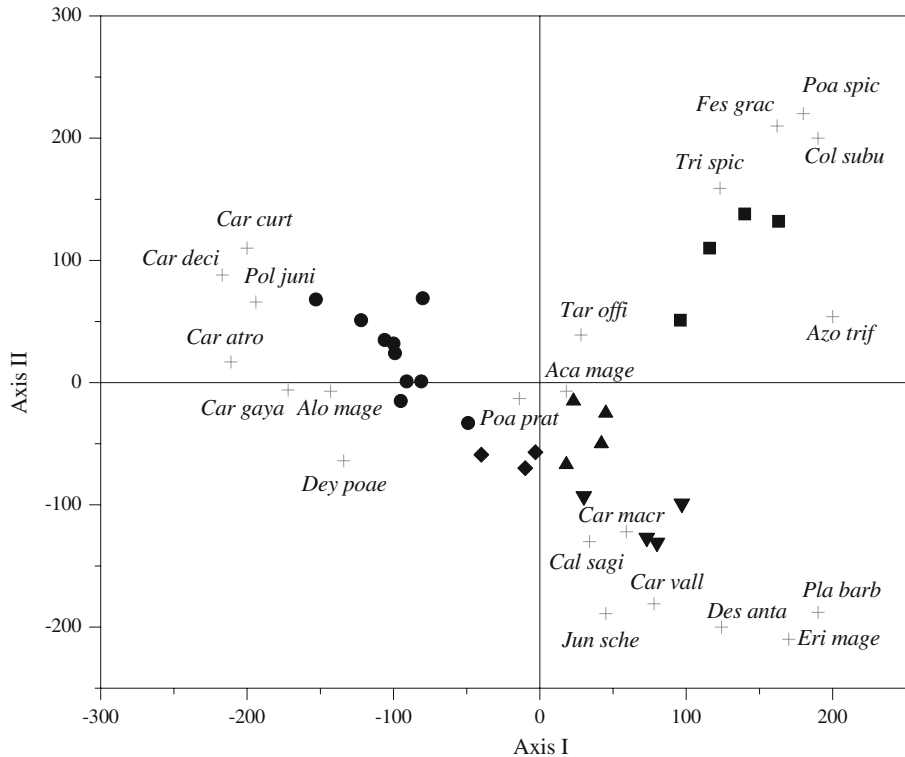
Various *Carex* species, especially *Carex gayana*, and the grasses *Deyeuxia poaeoides* and *Alopecurus magellanicus* (species group 2) characterize these marshes in the southernmost sector of the area. They prevail on organic flats and on depressed riverine landforms, with the water table at 0–20 cm. The most frequent soils are fibric or hemic histosols and histic gleysols. They include two communities: I) Tall sedge marshes with mosses, with different mosses (group 1), and a mean soil pH of 5.1; II) Tall sedge marshes with *Caltha*, in which the tall sedges decrease and dwarf sedges/rushes and *Caltha sagittata* (group 3) increase, with higher mean pH (5.5).

### *III and IV) Caltha marshes (dwarf-sedge marshes)*

These are two types of marshes characterized by very short turf, and dominated by species group 3. They are probably influenced by historical grazing and occur throughout the study area but prevail in mid latitudes where annual precipitation is 350–400 mm. The two communities are distinguished by the presence of species group 4: an acidic one III) with group 4 scarcely represented, on riverine depressed landforms and small depressions on meltwater plains (water table at 20–50 cm in summer), having histic gleysols and sapric histosols, with a mean pH of 6.0; and an eutrophic one IV) with species of group 4, especially *Deschampsia antarctica*, mainly on springs from valley escarpments, with sapric histosols, with a mean pH of 6.7.

### *V and VI) Azorella wet-grasslands*

Related to valley positions that are inundated only a few days a year, with the water table generally deeper than 70 cm in summer, these grasslands are dominated by the cushion shrub *Azorella trifurcata* (group 7). Steppic indicators (group 8) are also present, as is the “increaser” group 6, especially *Acaena magellanica*. These



**Fig. 3** Correspondence analysis ordination diagram of samples and species of freshwater communities (first two axes). The full symbols indicate the Twinspan community types: *circles* – tall sedge marshes with mosses; *diamonds* – tall sedge marshes with *Caltha*; *upward-pointing triangles* – acidic *Caltha* marshes; *downward-pointing triangles* – eutrophic *Caltha* marshes; *squares* – acidic *Azorella* wet grasslands. The crosses indicate species: *Aca mage*: *Acaena magellanica*, *Alo mage*: *Alopecurus magellanicus*, *Azo trif*: *Azorella trifurcata*, *Car atro*: *Carex atropicta*, *Car curt*: *Carex curta*, *Car deci*: *Carex decidua*, *Car gaya*: *Carex gayana*, *Car macr*: *Carex macrosolen*, *Cal sagi*: *Caltha sagittata*, *Col subu*: *Colobanthus subulatus*, *Car vall*: *Carex vallis-pulchrae*, *Des anta*: *Deschampsia antarctica*, *Dey poae*: *Deyeuxia poaeoides*, *Eri mage*: *Eriachanum magellanicum*, *Fes grac*: *Festuca gracillima*, *Jun sche*: *Juncus scheuchzerioides*, *Pla barb*: *Plantago barbata*, *Poa prat*: *Poa pratensis*, *Poa spic*: *Poa spiciformis*, *Pol juni*: *Polytrichum juniperinum*, *Tar offi*: *Taraxacum officinale*, *Tri spic*: *Trisetum spicatum*

communities occupy the border zone between the more humid *Caltha* marsh and the upland steppe vegetation on depressional wetlands and on the coarser deposits of floodplains. They are the most common wetlands in the semiarid zone (300–350 mm rainfall). Soils are luvic mollic gleysols and fluvisols (eutric). Two communities (V and VI) were separated by Twinspan in accordance with the differential presence of the eutrophic group 4.

#### VII) Salt shrublands

A very diverse community, salt shrublands occur on relatively dry soils and sand deposits of estuarial and lacustrine wetlands that are probably rarely inundated. Characteristic species are steppic indicators (group 8), some salt indicators

**Table 7** Kendall's tau correlation coefficient of latitude (LAT) and soil variables with axes I and II of the CA ordination

	Axis I	Axis II	<i>n</i>
LAT	-0.765***	0.148	25
pH	0.678***	-0.253	25
Ca	0.518***	-0.309*	25
Mg	0.492***	-0.296*	25
C/N	-0.507***	-0.144	25
C total	-0.327*	-0.271	25
N total	-0.093	-0.479***	25
Peat depth	-0.224	-0.378*	25
Water table	-0.233	-0.510***	25

\* –  $P \leq 0.05$ ; \*\*\* –  $P \leq 0.001$

(*Hordeum lechleri*, *Puccinellia* spp., *Plantago maritima*) and the frequent medium-height shrub *Lepidophyllum* forming shrubby steppes or shrublands. Soils are mainly haplic solonetz or luvic gleysol (sodic) with a mean pH of 7.0.

#### VIII) Salt marshes

They are grassy marshes characterized by groups 4 and 11, especially by *Hordeum lechleri* and *Puccinellia* spp. They occur where water discharges in the *playas* of the Tertiary landscape and on small lakes and swales of the higher tidal plains. Soils are solonchacks with a high mean pH (8.2).

#### IX) Salt carpet

This is a prostrate community dominated by the succulent halophyte *Sarcocornia perennis*. It occupies low flat areas under the influence of ocean tides in fluvisols (tidalic) with a mean pH of 8.0.

### Discussion

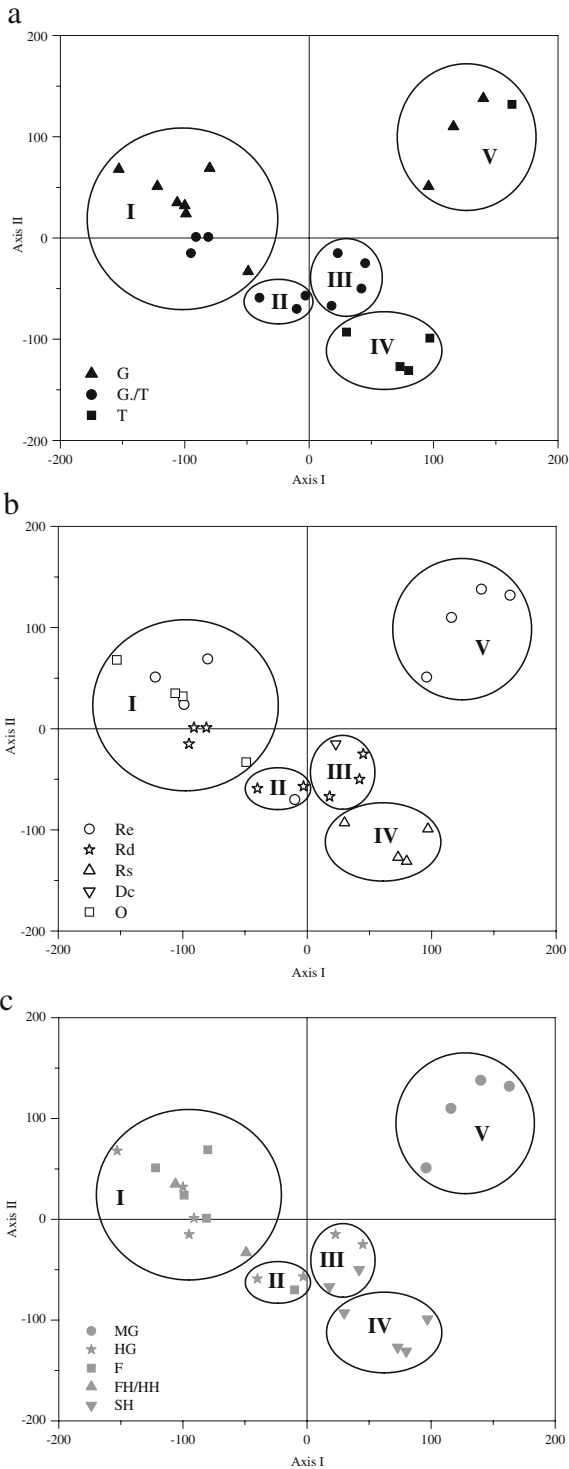
Although the Fuegian flora has affinities with that of the Patagonian region and also extends northwards along the Andes at gradually higher altitudes (Moore 1983), a large part of the native species occur only south of 51–52° S, which may indicate a limit between neotropical and antarctic elements (Tuhkanen et al. 1990). As previously reported for the steppe vegetation (Collantes et al. 1999), the Magellanic wetlands also share several species with the Northern Hemisphere. Most of the disjunct bipolar species (Dahl 1998) are wetland species present in our survey, especially sedges: *Carex curta*, *C. macloviana*, *C. magellanica*, *C. microglochin*, *Phleum alpinum*, *Trisetum spicatum*, and *Plantago maritima*. However, no climatic counterparts of semiarid Tierra del Fuego exist in the Northern Hemisphere, and the

**Fig. 4** Overlays of environmental categories on the correspondence analysis ordination. Loops enclose community types I to V classified by Twinspan. **a** *Bedrock areas*: G – glacial deposits; G/T – outwash veneer over Tertiary rocks; T – Tertiary rocks. **b** *Geoforms*: Re – riverine elevated; Rd – riverine depressed; Rs – riverine spring; Dc – depressional (center); O – organic flats. **c** *Soil groups (RSG)*: MG – mollic gleysol; HG – histic gleysol; F – fluvisol; FH/HH – fibric and hemic histosols; SH – sapric histosol (eutric)

vegetation resemblances in Europe take place in areas located at considerably higher latitudes (Tuhkanen et al. 1990) or altitudes (Dahl 1998).

The main wetland vegetation we found consisted of marshes of sedge/rushes, sometimes with high abundance of prostrate herbs, mainly *Caltha sagittata*, and wet grasslands with cushion shrub encroachment, especially of *Azorella trifurcata*. Many of the sedge/rush marshes had organic soils and qualify as fens. The absence of bogs in our study area was already recorded in the small-scale maps of the early peatland studies (Guiñazú 1934; Roivainen 1954; Auer 1965) which locate *Sphagnum* bogs at higher latitudes than our southern limit (54° S). Certainly, the ombrotrophic *Sphagnum* bogs can be found as far north as 52° S but only near the Pacific coast under more oceanic conditions and 600–1500 mm/year of rainfall (Kleinebecker et al. 2007). The *Carex* peatlands mapped by the aforementioned authors over different sectors of the steppe area would correspond to our communities on histosols, i.e., all of the tall sedge fens (I–II) and some of the dwarf sedge fens (III–IV). The most northerly located *Carex* fen in our study area was at the latitude 52°59'02" S.

Freshwater community types I–VI differ in soil pH (Table 6) and form an ecocline along CA axis I (Fig. 3) that is related to pH, base richness and C/N ratio (Table 7). The high negative correlation of axis I with latitude suggests the climatic control of the ecocline. This latitudinal gradient probably influences floristic composition through both groundwater and temperature regimes. However, the water table level and peat depth are not related to axis I (Table 7), suggesting that temperature *per se* could be a stronger influence than water regime. This seems more evident in the south of the area (negative extreme of axis I) where the highly acidic community I, the “tall sedge marsh with mosses”, occupies both wet and relatively dry sites (Fig. 4b), on organic and mineral soils, respectively (Fig. 4c). At that latitude the decrease in temperature related to the sun position is magnified by the cooling effect of the Andes (Moore 1983), probably imposing physiological constraints to species that are common further north. It is accepted that geographical distribution of species, especially at high latitudes, is mainly governed by temperature parameters (Dahl 1998). Species turnover along axis I seems to be consistent with geographical distribution on a larger scale. Species of the tall sedge marsh in the negative sector of axis I, such as *Carex magellanica*, *Carex curta*, *C. microglochin*, *Uncinia macloviana* (from species groups 1 and 2 of Table 5), are also common species of the *Sphagnum* or *Massipospermum* bogs further south and west, outside the study area (Moore 1983; Roig et al. 2004), but are absent or very rare in the steppe zone (Moore 1983; Boelcke et al. 1985). Species of groups 3–6, that occupy the central sector of axis I, like *Caltha sagittata*, *Carex vallis-pulchrae*, *Juncus scheuchzerioides*, *Deschampsia antarctica*, *Deyeuxia poaeoides*, *Poa pratensis*, *Phleum alpinum*, are found all over the island (Moore 1983), but only in the more humid and oceanic areas of the continental Magellanic steppe (Boelcke et al. 1985). Species of group 8 (*Festuca gracillima*, *Poa spiciformis*, *Colobanthus subulatus*, *Azorella*



*monantha*), at the drier positive extreme of axis I, predominate in the insular and continental steppe areas, while in the south and west portions of the island occur only in dry habitats (Moore 1983; Boelcke et al. 1985). More than a decrease in annual temperatures, the key parameter with increasing latitude could be lower summer temperatures, considering that many species that appear when entering the deciduous forest zone from the steppe can occur further north in the moorlands of the Pacific coast, under a pronounced oceanic climate (Moore 1983). Thus, although the impacts of climate should be less severe in wetlands than in adjacent zonal vegetation, some groups of wetland species seem to behave as phytogeographical elements. Other broad scale studies have found climate as a primary determinant of wetland floristic diversity, with groups of wetland species characterizing different floristic regions (Hájek et al. 2008; Naqinezhad et al. 2009).

The decrease in temperature with latitude probably causes a decrease in biological activity in the soil that retards decomposition of organic matter (Jenny 1950; Tate 1987), a trend reflected by the observed increase in C/N ratio with increasing latitude along CA axis I (Table 7). The accompanying decrease in pH may be determined by a simultaneous increase of rainfall with latitude, causing strong leaching of base cations (Table 7), as shown for some climatically induced soils (Duchaufour 1977).

Bedrock lithology seems to interact with climate in affecting soil chemistry and floristic composition. The higher Ca and Mg concentrations in wetland soils of landscapes on Tertiary rocks with calcareous minerals, compared to other less cation-rich bedrock areas (Table 4), probably determines the close association of bedrock zones with community types (Fig. 4a). Other studies report similar relations between bedrock quality and gradients of poor-rich wetland or mire vegetation (Vitt et al. 1995; Hájek et al. 2002; Tahvanainen et al. 2002).

The positive extreme of axis I is not only related to a drier and warmer climate but also to drier topography. All samples belong to the *Azorella* wet grasslands (Fig. 3) and are on elevated riverine landforms and mineral soils (Fig. 4b and c). This holds for the southern half of the study area, from which the samples for the CA were selected. These species could probably occupy more hydric soils and landforms in lower latitude wetlands. The topographic gradient is best expressed by axis II, which has significant relationships with the height of the water table and with peat depth. As shown in Fig. 3, axis II has in its “dry” positive extreme the *Azorella* wet grassland and in its negative “wet” extreme the “eutrophic *Caltha* marsh”, a rich spring fen community growing on sapric histosols (Fig. 4c); these two wetland types share the same intermediate latitudes and similar climate, but contrasting moisture relations. Also at the site level, there is a significant correlation of axis II with N content (Table 7) that may be explained by a positive relation between pH/ base content and N pools and fluxes, as Bridgham et al. (2001) found in high latitude wetland soils. No relationship between sample positions and these soil factors was detected in the middle part of the gradient.

Finally, the importance of grazing on the structure of these communities should be pointed out. The extensive dominance of *Caltha sagittata* in marshes and of *Azorella trifurcata* in wet grasslands seems to be an indication of overgrazing (Díaz Barradas et al. 2001). This is supported by censuses made in wetlands before sheep



introduction, which showed low cover values for the two species (Dusén 1905). Short height, hard leaves, large rhizomes or cushion growth form are among the attributes permitting escape from grazing by *Caltha* and *Azorella*, allowing them to compete for light with taller but less grazing-tolerant plants (Díaz Barradas et al. 2001). The ecology of *Caltha sagittata* resembles that of its boreal relative *Caltha palustris*, frequent in European fens (Grootjans et al. 1985), in that both are concentrated on humid soils with high base content but avoid permanently inundated soils. Artificial drainage for agriculture in European very humid fens has caused the enhancement of nitrification and a large increase in the abundance of *Caltha* (Grootjans et al. 1985; van der Hoeck and Sýkora 2006). Heavy grazing in Magellanic very humid wetlands probably caused similar effects as a result of soil compaction and abundant dung deposition. Another indicator of the process is the increase in nitrophilous species such as *Poa pratensis* and *Taraxacum officinale*, exotics that belong to the highly productive class *Molinio-Arrhenaeteretea* of Europe (Roig et al. 1985). The higher diversity of *Caltha* and *Azorella* wetlands (Table 6) could be a direct consequence of grazing, as Díaz Barradas et al. (2001) has proposed more generally. As shown in Fig. 3, the wetlands presumed to have been disturbed (communities III, IV, V and VI) occur at medium and positive positions of axis I, i.e. at mid and lower latitudes, where grazing regimes have been longer and heavier, in part because seasonal access to wetlands is expanded due to the drier climate (Anchorena et al. 2001).

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