



Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast

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ABSTRACT

Aim To produce an inventory of south-west Atlantic saltmarshes (from latitude 31°48' S to 43°20' S) using remotely sensed images and field sampling; to quantify their total area; to describe the biogeographical variation of the main habitats characterized by dominant vascular plants, in relation to major environmental factors; to test the hypothesis of predominance of the reversal pattern in plant distribution (sedges and grasses dominate the lower, regularly inundated zones, while the upper zones are occupied by more halophytic species) previously described; and to compare these south-west Atlantic saltmarshes with others world-wide.

Location South-western Atlantic saltmarshes

Methods Field samples of dominant emergent plant species positioned by the global positioning system (GPS) were obtained from most coastal saltmarshes (14) between southern Brazil and northern Patagonia, Argentina. Landsat satellite images were obtained and coastal saltmarsh habitats were quantified by supervised classification, utilizing points gathered in the field.

Results Three main plant species dominated the low and middle intertidal saltmarsh, *Spartina alterniflora* Loesel., *Spartina densiflora* Brong. and *Sarcocornia perennis* (P. Mill.) A.J. Scott. The total area of the studied coastal saltmarshes was 2133 km², comprising 380 km² of *Sp. alterniflora* marsh, 366 km² of *Sp. densiflora* marsh, 746 km² of *Sar. perennis* marsh and 641 km² of brackish marsh (dominated by *Juncus acutus* L., *Juncus kraussii* Hochst., *Scirpus maritimus* L., *Scirpus americanus* Pers. and *Phragmites australis* (Cav.) Trin.). Cluster analysis showed three habitat types: saltmarshes dominated by (1) *Sp. densiflora* and brackish species, (2) *Sp. alterniflora* and *Sar. perennis* and (3) *Sp. densiflora* only. The analysis of abiotic variables showed significant differences between groups of habitats and coordinated gradients of the abiotic variables. The south-west Atlantic coast showed decreasing mean annual rainfall (1200 to 196 mm) and increasing mean tidal amplitude (< 0.5 to > 2.5 m) from latitude 31° to 43°.

Main conclusions South-west Atlantic saltmarshes are globally important by virtue of their total extent. Remote sensing showed that the reversal pattern in plant distribution is not widespread. Indeed, south-west Atlantic saltmarshes are better characterized by the presence of the halophytic genera *Spartina* and *Sarcocornia*. Our results support the interpretation that south-west Atlantic saltmarshes constitute a class of temperate type (*sensu* Adam, 1990) with transitional characteristics between Australasian–South African saltmarshes and west Atlantic saltmarshes.

Keywords

Argentina, Brazil, coastal saltmarsh, *Sarcocornia*, south-west Atlantic coast, *Spartina*, Uruguay, zonation.

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INTRODUCTION

Saltmarshes are intertidal ecosystems, backed up against the land on one side while open to the sea on the other (Wiegert *et al.*, 1981). They embody environmental characteristics of both terrestrial and marine communities. They are plastic coastal features, shaped by the interaction of water, sediments and vegetation. For stability, they require protection from high-energy waves and therefore usually develop in sheltered sites. In some parts of the world they show extremely diverse vegetation (boreal type *sensu* Adam, 1990), while in other regions they are dominated by a few plant species, usually grasses (west Atlantic type *sensu* Adam, 1990).

As for other continents (Adam, 2002), there is no reliable inventory of coastal saltmarsh area for South America. West (1977) pointed out that between southern Brazil and northern Patagonia (south-west Atlantic region) there are extensive saltmarshes on estuaries with large discharges and prevailing brackish conditions. An important feature of saltmarshes is variation in the species composition of vascular plants with elevation (Adam, 1990), but although these zonation patterns are also used for classification of coastal saltmarshes throughout the world (Adam, 1990), few syntheses of Latin American saltmarsh vegetation have been attempted (West, 1977; Costa & Davy, 1992). Early classifications of coastal saltmarshes of the world (Chapman, 1960) included the coasts of Argentina, Uruguay and the south of Brazil within a group denominated South American. West (1977) described zonation patterns that occur on a grand scale in these estuaries, where sedges and grasses dominate the lower, regularly inundated zones, and the upper zones are occupied by more halophytic species. Thus, although these marshes show affinities with temperate marshes elsewhere, based on the perception of an inverted zonation pattern, they have been recognized as a separate type (see Adam, 1990). However, descriptive studies of south-west Atlantic saltmarsh vegetation (Ringuelet, 1938; Chebataroff,

1952, 1953; Verettoni, 1961; Vervoort, 1967; Costa & Davy, 1992; Cagnoni & Faggi, 1993; Isacch, 2001; Costa *et al.*, 2003) and our observations suggest that the inversion of zonation pattern is restricted to small areas of the most extensive saltmarshes or to the upper estuaries of rivers influenced by fresh water. Therefore interpretation of the relationship between south-west Atlantic marshes with others world-wide is unclear.

The purpose of this work was to produce an inventory of south-west Atlantic coastal saltmarshes using a combination of remotely sensed images and field sampling. We aimed to quantify their total area and to describe regional variation of the main habitats characterized by dominant vascular plants, in relation to major environmental factors. We test the hypothesis of predominance of reversal in the pattern of plant distribution described by West (1977). This should enable comparison of south-west Atlantic coastal saltmarshes with others world-wide.

METHODS

Study area

The study area included coastal saltmarshes from southern Brazil (from 31°), Uruguay and Argentina (to 43° S; Table 1) including 14 different sites. This region has one of the widest and flattest continental shelves anywhere (the Southwest Atlantic Shelf) and it includes the coastal area of the confluence of the southward Brazil Current and northward Malvinas (Falkland) Current (Costa & Davy, 1992; Longhurst, 1998). The Subtropical Confluence occurs at the latitude of La Plata River, which generates an offshore flux whose location is seasonally variable and determined by the relative flux strengths of the two currents (Longhurst, 1998). From a terrestrial point of view, the study area crosses three large biogeographical provinces (Cabrera & Willink, 1973): Pampas

Table 1 Data of satellite imagery selected for the classification of coastal saltmarshes from Brazil, Uruguay and Argentina: L7, Landsat 7 (ETM+); L5, Landsat 5 (TM)

Site	Satellite	Path-row	Date	Latitude
Brazil				
Lagoa dos Patos	L7	221-82	12 November 2002	31°48'–32°11'
Uruguay				
Arroyo Maldonado	L7	222-84	18 March 2000	34°53'
Laguna José Ignacio	L7	222-84	18 March 2000	34°53'
Argentina				
Bahía Samborombón	L7	224-85	30 January 2001	35°13'–36°18'
Laguna Mar Chiquita	L5	223-86	3 February 2002	37°29'–37°46'
Bahía Blanca	L7	226-87	3 February 2003	38°41'–39°30'
Río Colorado	L7	226-88	15 January 2002	39°34'
Bahía Anegada	L7	226-88	15 January 2002	39°48'–40°42'
Río Negro	L7	226-88	30 October 2002	41°00'
Caleta de los Loros	L7	227-89	10 February 2003	41°01'
Bahía San Antonio	L5	228-88	5 January 2002	40°42'–40°50'
Riacho San José	L7	227-89	10 February 2003	42°24'
Caleta Valdés	L7	227-89	10 February 2003	42°15'–42°27'
Río Chubut	L7	227-90	10 February 2003	43°20'

	Mean tidal amplitude (m)	Run-off volume (m ³ s ⁻¹)	Annual rainfall (mm)	Phytogeographical province*
Brazil				
Lagoa dos Patos	0.47	2000†	1200	Pampas
Uruguay				
Arroyo Maldonado	0.31	14‡	1020	Pampas
Laguna José Ignacio	0.31	7‡	1020	Pampas
Argentina				
Bahía Samborombón	0.75	22,031§	950	Pampas
Laguna Mar Chiquita	0.79	20¶	920	Pampas
Bahía Blanca	2.44	–	645	Espinal and Pampas
Río Colorado	1.64	319§	600	Espinal and Monte
Bahía Anegada	1.64	–	500	Monte
Río Negro	2.94	858§	380	Monte
Caleta de los Loros	6.04	–	300	Monte
Bahía San Antonio	6.44	–	248	Monte
Riacho San José	3.00	–	225	Monte
Caleta Valdés	2.70	–	225	Monte
Río Chubut	2.77	47§	196	Monte

*After Cabrera & Willink (1973).

†Fernandes *et al.* (2002).

‡Unpublished report from the Ministerio de Transporte y Obras Públicas from Uruguay Conservación y Mejora de Playas. MTOP/PNUD/UNESCO, Report URU 73.007 (1979).

§Calcagno *et al.* (2000).

¶Estimated value after Fasano *et al.* (1982).

(dominated by grasslands), Espinal (dominated by thorn trees) and Monte (dominated by bushes) (Table 2). The annual mean precipitation increases from 250 mm in the south (Río Chubut) up to 1200 mm in the northern part of our study area (Lagoa dos Patos). Astronomical microtides (up to 0.5 m) on the southern Brazilian and Uruguayan coast contrast with meso-macrotides (2.7–6.4 m) dominating the coast to the south, in northern Patagonia. Sediments from saltmarshes of Argentina, Uruguay and Brazil have variable quantities of sand, shells and boulders, but mud always represents the highest percentage (Urien & Ewing, 1974; Fasano *et al.*, 1982; Calliari, 1998; Yorio, 1998). Light cattle grazing on coastal saltmarshes can occur at a low frequency (Bilenca & Miñarro, 2004; Isacch *et al.*, 2004).

Definition of main habitats and field sampling

Phytosociological studies have been carried out in southern Brazil (Reitz, 1961; Danilevicz, 1989; Costa, 1997), Uruguay (Chebataroff, 1952, 1953) and Argentina (Ringuelet, 1938; Parodi, 1940; Verettoni, 1961; Vervoort, 1967; Faggi, 1985; Cagnoni & Faggi, 1993) characterizing dominant taxa and their associated species. Since the south-west Atlantic is a warm temperate biogeographical transition zone, some elements of the flora are restricted to the north subtropical border (e.g. *Acrosticum* spp., *Paspalum vaginatum*) and others to the southern cold temperate zone (e.g. *Puccinellia* spp.). Nevertheless, regionally, consistent dominant taxa can be

Table 2 Physical factors and phytogeographical regions of the coastal saltmarshes from Brazil, Uruguay and Argentina

recognized as indicators of species assemblages clearly related to topography and salt stress (Costa, 1997; Yorio, 1998) and responsible for distinctive landscape habitat units. Previous studies of Isacch (2001) and Nogueira & Costa (2003) demonstrated that spectral channels in the visible and reflected infrared region of digital images allowed a clear delimitation of water, non-vegetated tidal flats, uplands and marsh vegetated habitats dominated by *Spartina alterniflora* Loesel., *Spartina densiflora* Brong., *Sarcocornia perennis* (P. Mill.) A.J. Scott and brackish marsh species.

There is no coherent systematic treatment of the flora of Latin America and so, along the Atlantic coast, *Sp. alterniflora* and *Sp. densiflora* have been variously classified into several varieties, different species and hybrids, mainly based on differences of certain inflorescence features (Mobberley, 1956; Cabrera, 1970). Similar taxonomic uncertainties and ambiguities are observed for *Sar. perennis* (Reitz, 1961; Natural Resource Conservation Service, 2004). In order to map and categorize consistently the saltmarsh habitats characterized by their dominant cover along the coasts of southern Brazil, Uruguay and Argentina we considered here *Sp. densiflora* Brong. to be synonymous with *Spartina montevidensis* Arch., *Sp. montevidensis* (Arch.) St. Yves, *Spartina patagonica* Speg. and *Spartina juncea* Willd. var. (Cabrera, 1970); *Sp. alterniflora* Loesel. considered synonymous with *Spartina brasiliensis* Raddi and *Spartina maritima* var. *brasiliensis* (Raddi) St. Yves (Cabrera, 1970); *Sar. perennis* (P. Mill.) A.J. Scott to be synonymous with *Sarcocornia fruticosa* (= *Salicornia fruticosa*

L.), *Salicornia ambigua* Michx., *Salicornia gaudichaudiana* Mog. and *Salicornia virginica* L. (Reitz, 1961; Natural Resource Conservation Service, 2004).

All 14 sites within the study area with patches of saltmarsh vegetation recognized by the Landsat image (spatial resolution 30×30 m) were sampled between December 2002 and March 2004. Because of the great variability of extent of marsh and the complex environmental gradients for salinity and topography among study sites, geolocated (global positioning system, GPS) point samples were selected following a stratified random sampling scheme (Manly, 1993). The number of samples at each site was proportional to the area of saltmarsh. Data were gathered by selecting quadrats of 1×1 m within each type of habitat. Totals of 230, 85 and 735 quadrats were recorded for the occurrence of dominant and associated species, and visually estimated canopy cover at sites located in Brazil, Uruguay and Argentina, respectively. All the range of vegetated and non-vegetated intertidal habitats was surveyed by walking and/or using small low-speed planes in some cases. Non-vegetated habitats were denominated by tidal flats. All marshes dominated by species of *Scirpus*, *Juncus*, *Cortaderia* and *Phragmites* species, commonly associated with freshwater input to saltmarshes (Adam, 1990; Costa, 1997; Haacks & Thannheiser, 2003), were considered brackish marshes. Additional information about associated species was obtained from bibliographic references.

Remote sensing analysis

Data acquisition

The satellite imagery used was recorded by the Landsat Thematic Mapper (TM) sensor on board Landsat 5, and the Enhanced Thematic Mapper-plus (ETM+) sensor on board Landsat 7. We selected only those images taken at the lowest tidal levels, when the whole marsh would have been exposed, from the pool of satellite images for each site. Images of different sites were obtained between March 2000 and February 2003 (see Table 1 for details).

Image pre-processing procedures

The satellite images were geocoded to a Gauss Kruger (Campo Inchauspe datum for Argentine images) or UTM (Yacaré datum for Uruguay images and WGS-84 datum for Brazil images) coordinate system using a first-order transformation and nearest-neighbour resampling. The pixel size after resampling was 30×30 m and the root-mean squared errors achieved were always lower than 1.5 pixels. We used field and map points for georeferencing. At a few sites where the access was difficult and thus GPS data were impossible to get, data were acquired from topographic maps (scale 1 : 50,000).

Classification procedure and accuracy assessment

We used a supervised classification to identify coastal saltmarsh habitats (Campbell, 2002) for all saltmarshes within

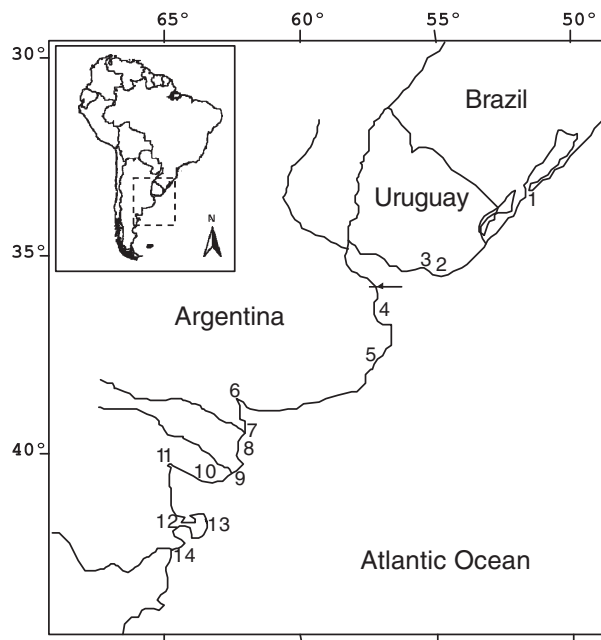


Figure 1 Saltmarshes of the south-west Atlantic coast. For details of sites (numbers) see Table 1. Arrow indicates Punta Indio.

the study area recognized by the spatial resolution of Landsat images (see Fig. 1). In this case we used one set of GPS points gathered in the field to generate the training sites, and the others were reserved to assess the accuracy of classifications. For the classification procedure we used a maximum likelihood probability algorithm (Richards, 1986), which is based on the probability density function associated with a particular training site signature. Pixels are assigned to the most likely class based on a comparison of the posterior probability that it belongs to each of the signatures being considered. The area of tidal flats and vegetated habitats from classified images for each saltmarsh were used for posterior analysis. We used an error matrix analysis to assess the accuracy of the classification procedure, using the kappa index of agreement and overall accuracy error (Rosenfield & Fitzpatrick-Lins, 1986). The number of reference test pixels used for the assessment of accuracy varied with the representatives of each class into the subset of the image (i.e. more cover more pixels). The environment of Idrisi 32 (Clark Labs, Worcester, MA, USA) was used for the analysis of satellite images.

Given that it may be difficult to detect the magnitude of zonation pattern directly from the classified satellite images, we designed a sampling scheme based on the satellite images. Using systematic sampling (Manly, 1993) of the classified satellite images, we sampled equidistant strips (vector lines) perpendicular to the coast of the marshes from the lower to the upper estuarine part of each site ($n = 30$; including all the gradient from saltwater-dominated to freshwater-dominated habitats to the upland border). Finally, the occurrence of a lower marsh halophytic–upper marsh brackish species zonation, or inverse zonation pattern (*sensu* West, 1977),

Table 3 Areas of different habitats from saltmarshes of the western south Atlantic coast, dominant species of brackish marsh and inverse zonation percentage (%). The kappa index of agreement and overall accuracy error for the classifications of saltmarshes habitats are also shown. Key: Sa, *Spartina alterniflora* Loesel.; Sd, *Spartina densiflora* Brong.; Sp, *Sarcocornia perennis* (P. Mill.) A.J. Scott; Sc, *Scirpus maritimus* L.; Se, *Scirpus americanus* Pers.; Jk, *Juncus kraussii* Hochst.; Ju, *Juncus acutus* L.; Co, *Cortaderia celloana* (Schult.) Asch. et Graeb.; Ph, *Phragmites australis* (Cav.) Trin. (+) Means recorded in the field but not with the satellite image analysis. (–) Means not recorded

	Surface covered (ha)					Species in brackish marsh	Inverse zonation (%)	Accuracy assessment	
	Sa marsh	Sd marsh	Sp marsh	Brackish marsh	Tidal flat			Kappa index (%)	Overall accuracy (%)
Brazil									
Lagoa dos Patos	53	619	+	5551	+	Sc, Jk	3.3	75.1	86
Uruguay									
Arroyo Maldonado	+	550	111	1222	+	Sc, Se, Ju	6.7	95.1	97.6
Laguna José Ignacio	–	178	2	469	+	Sc, Se, Ju	3.3	95.1	97.6
Argentina									
Bahía Samborombón	5060	26314	8336	42345	14046	Sc, Ju, Co	6.7	76.5	94.8
Laguna Mar Chiquita	–	3882	304	7382	143	Ju, Co	6.7	98.7	99.3
Bahía Blanca	9193	65	20376	+	60973	Ju, Ph	0	83.4	97.9
Río Colorado	397	1344	731	4548	1807	Ph	6.7	90.3	95.5
Bahía Anegada	20503	2908	42060	2492	62797	Ph	0	90.3	95.5
Río Negro	47	656	+	49	+	Ph	3.3	98.4	98.9
Caleta de los Loros	440	+	30	–	1144	–	0	98.7	99.5
Bahía San Antonio	2068	+	2124	–	10111	–	0	98.2	98.8
Riacho San José	108	23	225	–	633	–	0	91.2	95.8
Caleta Valdés	89	25	329	–	2747	–	0	91.2	95.8
Río Chubut	–	18	+	–	+	–	0	87.7	94.8

was assigned to each strip, and the frequency of inverse zonation patterns was estimated for each of the 14 sites.

Statistical analysis

The percentage coverage of tidal flats and vegetated habitats in each saltmarsh was used to classify sites in a clustering procedure. A Euclidean distance algorithm was used to calculate dissimilarity indexes between all pairs of saltmarshes (following Hair *et al.*, 1995). We also used a bootstrapping technique to identify statistically significant groups of sites (Jaksic & Medel, 1990). The cluster analysis procedure was repeated 1000 times for each of the new matrices generated with the bootstrapping technique (following Caswell, 1989). Each iteration gave six node values, and then from the resulting distribution of the 6000 pseudovalues (nodes) the program gave a cut-off threshold for significantly distant values. We chose the fifth percentile of the distribution of node values; therefore, habitat coverage groups of saltmarsh sites obtained at distance values lower than the cut-off ($P < 0.05$) were considered significantly different.

Discriminant analysis (Hair *et al.*, 1995) of standardized values of abiotic variables was used to test the hypothesis that the abiotic factors distinguished the groups of saltmarshes obtained by cluster analysis. Rainfall data were obtained from the US Department of Commerce, National Oceanic and Atmospheric Administration (NOAA), National Environmental Satellite, Data, and Information Service Office, National

Climatic Data Center (<http://lwf.ncdc.noaa.gov/oa/climate/climatedata.html>). Freshwater run-off data were $\log_{10}(x + 1)$ transformed to increase homogeneity of variance and normality. The discrimination between centroids was tested at the 5% significance level by Wilk's lambda statistics and Rao's 'V' statistics, showing the multidimensional distance between groups of saltmarshes (Klecka, 1975).

RESULTS

Three main plant species dominated the low and middle intertidal saltmarshes of the coastal south-west Atlantic: *Sp. alterniflora*, *Sp. densiflora* and *Sar. perennis* (Table 3; Figs 2 & 3). *Spartina alterniflora* was always in the mid-intertidal (inundated by all high tides) oceanic front of the saltmarsh as monospecific stands. The other two species frequently occupied upper levels in the intertidal area (inundated mainly during spring high tides) and presented three different patterns: (1) *Sp. densiflora* only, (2) *Sar. perennis* only and (3) a mixture of *Sp. densiflora* and *Sar. perennis*. In these three types of saltmarsh stand other species mainly occupied a zone a few metres wide between *Sp. densiflora* and brackish marsh (Table 4), or were in the upper border of *Sar. perennis*-dominated marshes from Bahía Blanca to Río Chubut. In the area located at the upper part of *Sar. perennis* marshes from Bahía Blanca to Río Chubut, associated species were similar (*Heterostachys rytteriana* (Moq.) Ung. Stern, *Limonium brasiliensis* (Boiss.) O. Kuntze., *Atriplex* spp.,

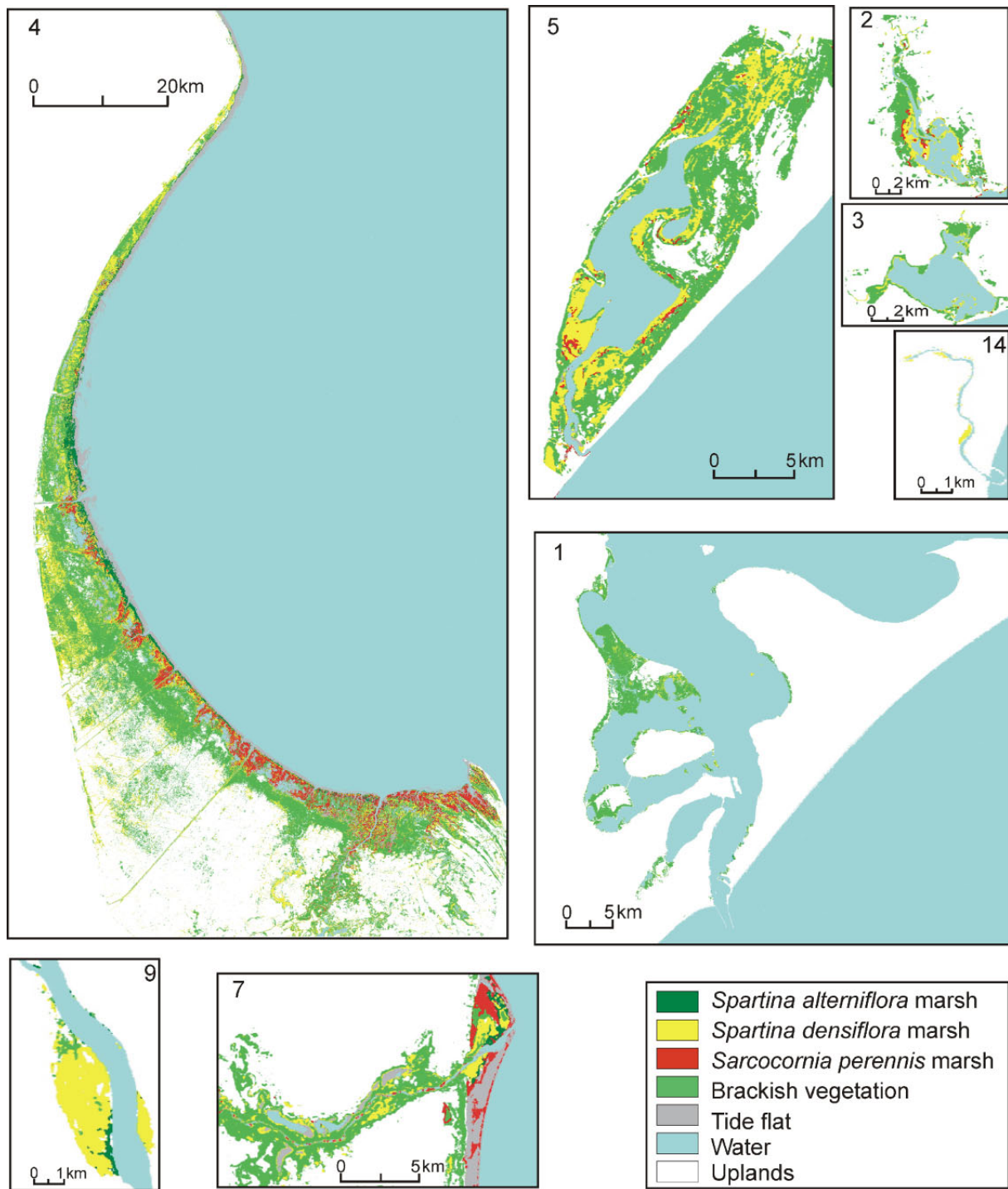


Figure 2 Saltmarshes of the south-west Atlantic coast characterized by the influence of freshwater. For references to sites (numbers) see Table 1.

Lycium chilensis Miers, *Suaeda patagonica* Speg., *Suaeda divaricata* Moq.; Verettoni, 1961; Yorio, 1998; and personal observation). Brackish vegetation was frequently recorded on the landward side of the three former species zones. Also, brackish marshes were found on the leading edge of saltmarshes with freshwater input, but always in the upper

estuarine part of rivers and coastal lagoons where the influence of fresh water was marked. Although inverse zonation patterns were recorded in a few saltmarshes with freshwater input, their frequency was lower than 7% (Table 3).

The total area covered by coastal saltmarshes in the studied area is 2133 km² (Argentina 2045 km², Uruguay 25 km²,

Table 4 The most common associated species present within *Spartina densiflora* marshes and brackish marshes for the different coastal saltmarshes of the south-west Atlantic characterized by the influence of fresh water

Region	Species	References
Brazil (Lagoa dos Patos)	<i>Scirpus maritimus</i> L., <i>Vigna luteola</i> (Jacq.) Benth., <i>Rumex paraguayensis</i> D. Parodi, <i>Aster squamatus</i> (Spreng.) Hier., <i>Paspalum vaginatum</i> Swartz, <i>Polygonum neglectum</i> L. and <i>Eclipta prostrata</i> (C.) Hassk.	Danilevicz (1989), Costa & Davy (1992), Costa (1997)
Uruguay (Arroyo Maldonado, Laguna José Ignacio)	<i>Scirpus maritimus</i> L., <i>Scirpus americanus</i> Pers., <i>Juncus acutus</i> L.	This study
Argentina (Bahía Samborombón, Laguna Mar Chiquita)	<i>Distichlis spicata</i> (L.) Green, <i>Apium leptophyllum</i> (Pers.) F. Muell., <i>A. sellowianum</i> Hoff, <i>Sarcocornia perennis</i> (P. Mill.) A.J. Scott, <i>Juncus acutus</i> L.	Cagnoni & Faggi (1993), Isacch <i>et al.</i> (2004)

Brazil 62 km²), 380 km² being dominated by *Sp. alterniflora*, 366 km² by *Sp. densiflora*, 746 km² by *Sar. perennis* and 641 km² by brackish marshes. The dominant brackish marsh species were *Juncus acutus* L., *Juncus kraussii* Hochst., *Scirpus maritimus* L., *Scirpus americanus* Pers., *Cortaderia selloana* (Schult.) Asch. et Graeb. and *Phragmites australis* (Cav.) Trin. (Table 3). Additionally, the total area of non-vegetated tidal flats at low tide was 1544 km².

Cluster analysis and bootstrap procedures identified three significantly distinct coverage groups of saltmarsh habitat (Fig. 4). The first group (all northern marshes between Lagoa dos Patos and Laguna Mar Chiquita and also the Río Colorado) was characterized by the dominance of *Sp. densiflora* at the oceanic leading edge of the marshes and brackish marshes covering the inland border (Fig. 2). The second group (marshes between Bahía Blanca and Caleta Valdés) was composed of *Sp. alterniflora* low marshes and *Sar. perennis* upper marshes (Fig. 3). The third group (Río Negro and Río Chubut) included saltmarshes where *Sp. densiflora* spread over most of the intertidal zone, either monospecifically or associated with a few other species (Fig. 2).

The analysis of abiotic variables showed significant differences between habitat coverage groups for saltmarshes and correlated gradients between the abiotic variables (Table 5, Fig. 5a). The main coordinated gradient was identified by the abiotic discriminant function 1 (AF1). AF1 was positively correlated with latitude and mean tidal amplitude of the saltmarshes and negatively correlated with mean annual rainfall (Table 5). The south-west Atlantic coast showed decreasing mean annual rainfall ($r^2 = 0.95$, $n = 14$, $P < 0.001$) and an increasing mean tidal amplitude ($r^2 = 0.45$, $n = 14$, $P = 0.009$) from latitude 31° to 43° S (Fig. 5). The AF1 discriminated both southern marsh groups 2 and 3 from the northern group 1 (Figs 4 & 5a). Groups 2 and 3 were separated by AF2, which described the significant ecological effect of freshwater run-off into the dry southern coast, differentiating Río Negro and Río Chubut saltmarshes from the others (Table 5, Fig. 5a). Together the discriminant functions AF1 and AF2 accounted for 100% of the explained

variance and classified the saltmarshes with 100% accuracy. Differences in the area covered by dominant saltmarsh plants identified abiotically distinct sites, characterized by decreasing annual rainfall, increasing latitude and mean tidal amplitude (Fig. 5a–c).

DISCUSSION

Our study combined field data and remote sensing technology to generate an inventory of south-west Atlantic coastal saltmarshes. These procedures have already been used to survey and classify saltmarsh habitats (see Klemas, 2001), Landsat TM and ETM+ being the most widely used satellites to identify vegetation types, because of their high-quality data for these targets (Campbell, 2002). TM satellites are able to separate salt-marsh vegetation communities (Donoghue & Shennan, 1987) and identify brackish water marshes (Bailey, 1997; Zhang *et al.*, 1997), although Landsat sensors had some difficulty in classifying the vegetation types of brackish marshes. Recently, there have been studies using remote sensors with higher spatial resolution to identify saltmarsh habitats (Bajjouk *et al.*, 1996; Eastwood *et al.*, 1997; Smith *et al.*, 1998; Silvestri *et al.*, 2002), which unfortunately are expensive and available for few sites in South America. However, because of the extensive area cover by south-west Atlantic marshes, we are confident that the spatial resolution (30 × 30 m) of Landsat TM and ETM+ sensors provides a very reliable tool.

Our inventory demonstrates that south-west Atlantic coastal saltmarshes are globally important by virtue of their great extent (Table 6). Buenos Aires Province, in Argentina, includes 93% of the total saltmarsh area surveyed and the three main sites of Bahía Samborombón, Bahía Blanca and Bahía Anegada together represent 84% of the total inventory. Only the first of these sites has important freshwater input and the other two are associated with coasts containing extensive tidal flats with an average annual rainfall of less than 600 mm.

The south-west Atlantic coastal saltmarshes are diverse from a geomorphological standpoint; they develop on areas dom-

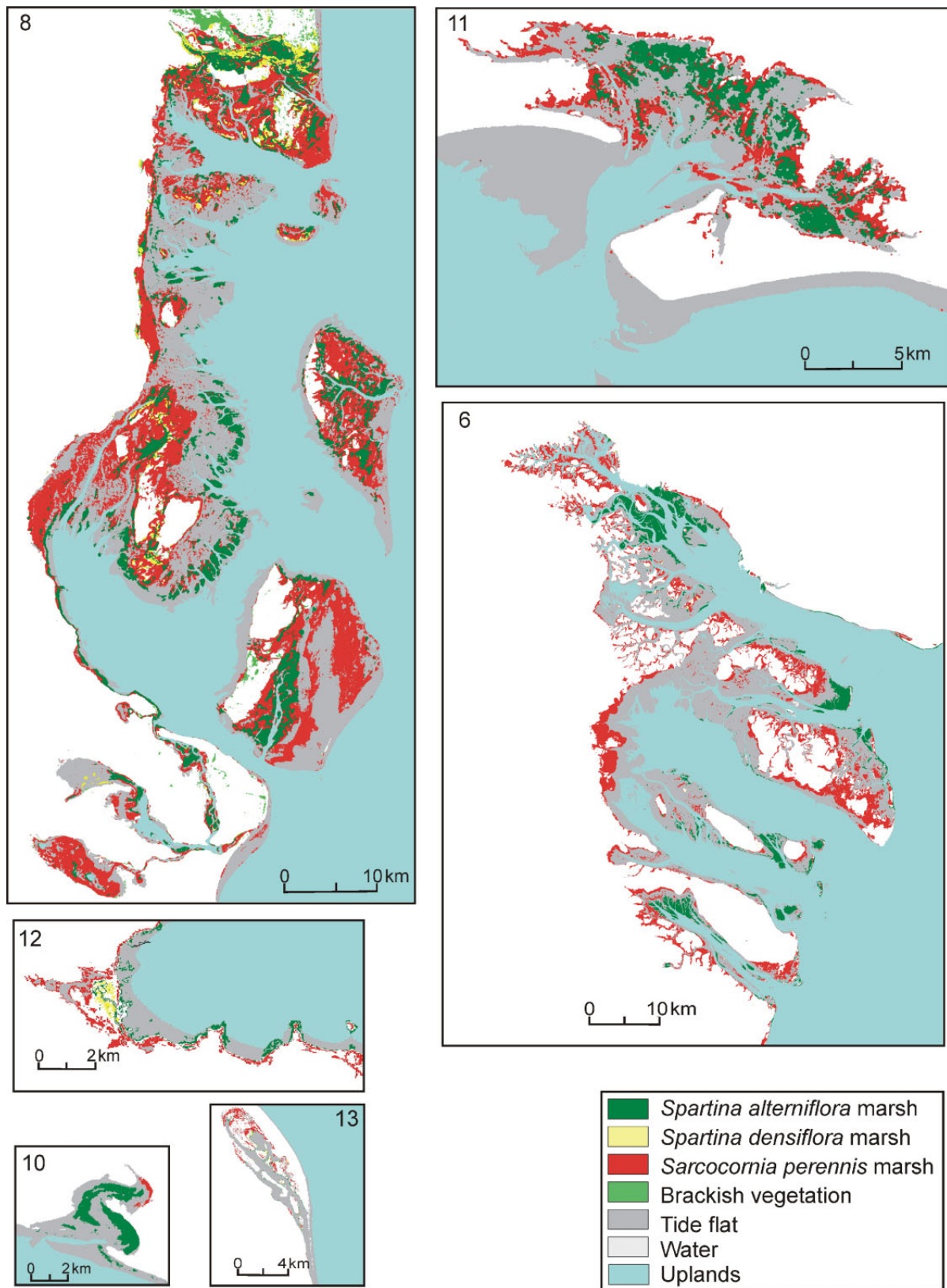


Figure 3 Saltmarshes of the south-west Atlantic coast characterized only by the influence of seawater. For references to sites (numbers) see Table 1.

Table 5 Abiotic discriminant analysis of the habitat coverage groups of coastal saltmarshes of the south-west Atlantic. Significant discriminant function, explained variance, correlation coefficients (*R*) and the canonical discriminant functions of the abiotic variables that discriminated the habitat coverage groups are shown. Wilk's lambda = 0.086, $F_{8,16} = 4.839$, $P < 0.004$

d.f.	Explained variance (%)	Abiotic variables	<i>R</i>	Canonical discriminant functions	
				Root 1	Root 2
1	83.4	Latitude	0.860	-1.052	0.930
		Annual rainfall	-0.922	-1.732	0.134
		Mean tide	0.822	-0.029	-0.145
2	16.6	Run-off volume	0.546	-0.610	0.843

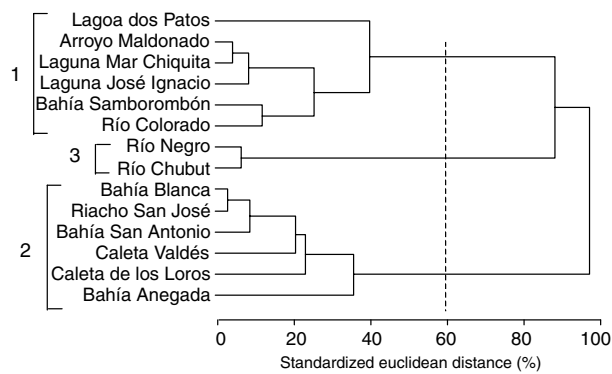


Figure 4 Unweighted Pair Group Method with Arithmetic Mean (UPGMA) distance dendrogram from cluster analysis of 14 saltmarsh sites based on the percentage of cover of different habitats. The vertical line was obtained from a bootstrap procedure and indicates that groups of sites to the left of the line are significant at $P < 0.05$. Numbers (1–3) represent different habitat coverage groups.

inated by tidal flats of rivers, lagoons, creeks, coves and bays. However, three groups of habitat coverage can be identified. Two major habitat coverage groups were separated geographically; brackish and marine waters dominate the northern and southern parts, respectively, of the latitudinal gradient studied. Brackish waters are related to areas of high rainfall (mostly 920 to 1200 mm year⁻¹) and estuarine regions of large watersheds (Costa & Davy, 1992; Costa *et al.*, 2003). The southern part is characterized by low rainfall (< 650 mm year⁻¹) and the presence of large bays, some of them originating from extinct or almost extinct large rivers (e.g. Río Colorado; Spalleti & Isla, 2003). Dry coastal areas with a mean freshwater input of 50–850 m³ s⁻¹ and mesotides (Río Chubut and Río Negro) produce a third group that has intermediate characteristics. In contrast to the conclusion of West (1977) the southern part of the south-west Atlantic coast is dominated by typical saltmarsh vegetation. Indeed, *Sp. alterniflora*, *Sp. densiflora* and *Sar. perennis* cover dominates 70% of saltmarshes of the south-west Atlantic coast.

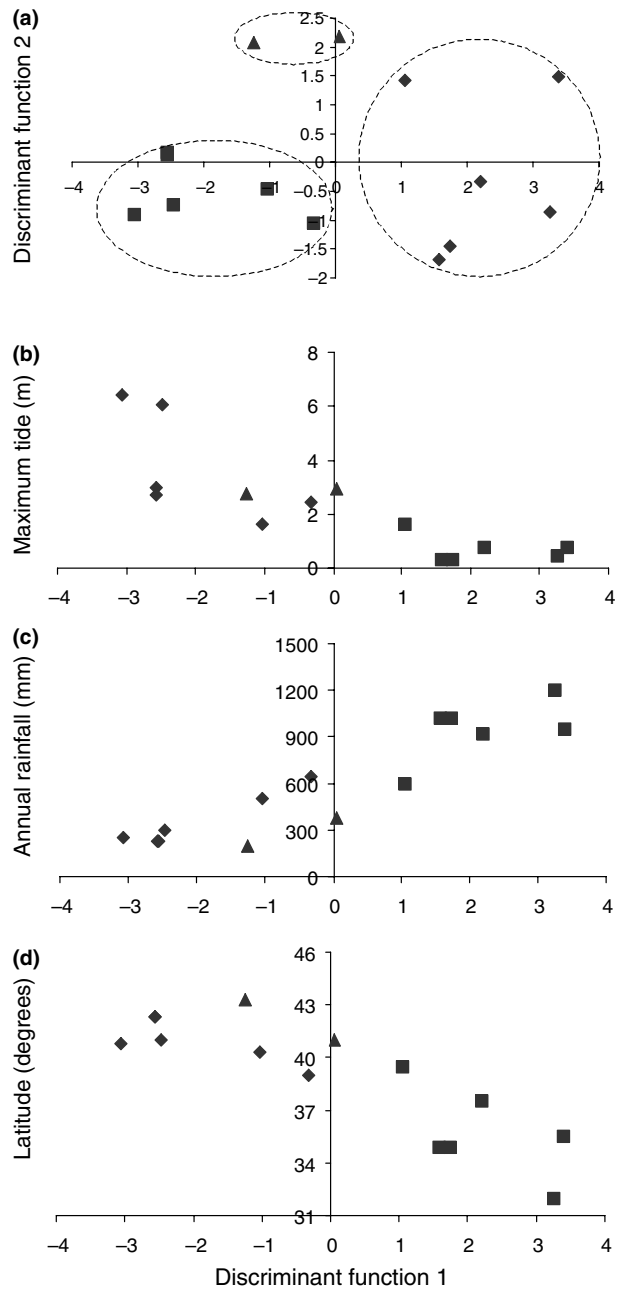


Figure 5 (a) Ordination of coastal saltmarshes of the south-west Atlantic according to the abiotic discriminant functions (DF) and relationship between DF1 and (b) latitude, (c) annual rainfall and (d) mean tidal amplitude for 14 saltmarshes of southern Brazil, Uruguay and Argentina. Similar symbols indicate saltmarshes from the same habitat coverage group. Squares, diamonds and triangles represent sites from groups 1, 2 and 3 listed in Fig. 4, respectively.

Biogeographical variation of saltmarshes along a large latitudinal range has also been recognized by Chapman (1960) and Adam (1990) for the North American west Atlantic saltmarshes, but has mainly been interpreted as the result of differences in solar energy received. Considering the dominant species and the floristic species, both authors distinguish a cold

Table 6 Area of saltmarsh for large regions of the world

Region	Tidal marsh area (km ²)	Reference
Gulf Coast (North America)	9880	Field <i>et al.</i> (1991)
Atlantic coast (North America)	5000–6000	Field <i>et al.</i> (1991)
Pacific coast (North America)	440	Field <i>et al.</i> (1991)
British Isles	450	Dijkema (1990)
Western Europe	950	Dijkema (1990)
Australia	6020*	N. Montgomery, OzEstuaries (pers. comm.)
South-west Atlantic coast (Brazil, Uruguay and Argentina)	2133	This study

*That value includes saltmarshes and salt flats (N. Montgomery, OzEstuaries pers. comm.).

temperate northern type (e.g. the Bay of Fundy) and a warm temperate–subtropical coastal plain (southward from North Carolina). Similar changes of solar radiation or temperature seem not to be responsible for observed biogeographical changes in south-west Atlantic marshes, since the low-latitude dominant species *Sp. densiflora* is able to withstand lower average temperatures than *Sp. alterniflora* (southern dominant species). The southernmost populations of *Sp. densiflora* and *Sp. alterniflora* are found at Río Gallegos (51° S; West, 1977) and Valdés Peninsula (42° S, this study) where average temperatures are 12–1 °C (summer–winter) (Faggi, 1985) and 18–7 °C (summer–winter) (Paruelo *et al.*, 1998), respectively. Consequently, the dominance or co-dominance of *Sp. alterniflora* and *Sar. perennis* along most of the northern Patagonian coast seems related to the prevalence of euhaline conditions and is not explained by the latitudinal variation of temperature or radiation.

A marked gradient of increasing aridity and tidal amplitude can be observed from southern Brazil (31° S) to the Valdés Peninsula (43° S) and is associated with changes of the saltmarsh communities. Two large groups of coastal saltmarshes are recognized, and their boundary occurs between Laguna Mar Chiquita and Bahía Blanca (approximately between 38° S and 39° S). This coincides with the limit between the Pampas and Espinal–Monte biogeographical provinces described by Cabrera & Willink (1973), which are characterized by decreasing rainfall southward. In the northern part of this region, the coastal brackish water marshes of the Lagoa dos Patos and Río de la Plata estuaries are dominated by mixed and monospecific stands of *Sp. densiflora* (Cagnoni & Faggi, 1993; Costa, 1997; Costa *et al.*, 2003), whereas in the southern part seasonally hypersaline semi-arid bays are dominated by *Sp. alterniflora* and *Sar. perennis*. The large low-energy flats in the southern part also facilitate colonization by *Sp. alterniflora* of the low intertidal area that is flooded by all tides (Adam, 1990), while *Sp. densiflora* and/or *Sar. perennis* dominate the upper marshes (Yorio, 1998). The existence of an intermediate group in middle latitudes (*Sp. densiflora*-domin-

ated marshes between 41 and 43° S; at Río Negro and Río Chubut) shows the determinant forcing factor of freshwater input on south-west Atlantic saltmarshes. Monopolization by *Sp. alterniflora* of those estuarine intertidal areas dominated by seawater may not only be a question of salt tolerance. A recent reciprocal transplantation experiment in southern Brazil showed that *Sp. densiflora* is highly competitive in irregularly flooded estuaries subjected to marked freshwater discharge extending over low and middle marshes (Costa *et al.*, 2003). Elsewhere it has been demonstrated that biological interactions between saltmarsh plants are sensitive to numerous aspects of the physicochemical environment and this may affect their relative distributions (Adam, 1990, 2002).

The northern part of the study site is the coastal area of the large Pampas plains (Soriano *et al.*, 1991). The dominant landforms are lowlands characterized by saline soils. However, small coastal areas may show the local influence of freshwater conditions, producing local inverse patterns in plant zonation. In these areas, halophytic vegetation may grow in the upper marsh and inland while freshwater marsh vegetation may dominate the low tidal marsh. The inverse pattern cited by West (1977), following Parodi, 1940) corresponds with a particular site of the Río de la Plata coast (Punta Indio, 37°16'24" S 57°13'34" W; Fig. 1). Following West (1977), Adam (1990) assumed that, in spite of the affinities with temperate types, a widespread reversal of zonation pattern in south-west Atlantic marshes makes them a different biogeographical group. However, remote sensing showed that the inverse zonation patterns are not widespread. Indeed, south-west Atlantic saltmarshes are better characterized by the presence of the halophytic genera *Spartina* and *Sarcocornia*.

The present results support the interpretation that south-west Atlantic saltmarshes constitute a group of the temperate type (*sensu* Adam, 1990) with transitional characteristics between Australasian–South African saltmarshes (*Sarcocornia* spp. in the lower marshes and *J. kraussii* in the upper marshes; Congdon, 1981; Adam, 2002; Haacks & Thannheiser, 2003) and west Atlantic saltmarshes that extend along Atlantic coast of North America and the Gulf of Mexico (dominance of *Sp. alterniflora*; Wiegert *et al.*, 1981; Day *et al.*, 1989; Adam, 1990, 2002). Additionally, south-west Atlantic saltmarshes have as a unique characteristic the presence of extensive upper marsh areas covered by the South American cord grass *Sp. densiflora*.

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