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Tidal Suppression Negatively Affects Soil Properties and Productivity of *Spartina densiflora* Salt Marsh[☆]

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ABSTRACT

In order to intensify cattle utilization, embankments were constructed to avoid tidal ingressions in Samborombon Bay, Argentina, The objective of this study was to evaluate the effect of tidal suppression and cutting frequency of a salt marsh dominated by *Spartina densiflora Brongn*. Two paddocks of a commercial cow-calf operation farm, one prevented from tidal flooding and another exposed to overflow from natural tidal pattern (control), were the main plots of the nested design. The experiments were carried out during a dry (2008- 2009) and a wet growing season (2012-2013). Two defoliation frequencies, simulating light and moderate grazing pressure, were performed in the subplots nested within each main plot. Soil organic matter and N content were lower and soil structural instability index was much higher in the embankment than in the control treatment. Soil salinity during the dry growing season was higher in the embankment than in the control treatment. Bare soil was higher under embankment treatment and high defoliation frequency exacerbated this response. Relative contribution of *Spartina densiflora* was lower under embankment than control treatment and the changes of floristic composition depended on the growing season. Aboveground net primary production (ANPP) in the wet growing season was almost 70% higher than in the dry growing season. Embankment reduced ANPP and high defoliation increased ANPP with respect to low defoliation frequency in the control paddock, to a much higher extent in the wet season. Dry matter digestibility of *S. densiflora* was not affected by treatments. Crude protein was higher in control paddocks under high frequency. Our results showed that tidal suppression by embankment was not effective to increase productivity and forage value of *S. densiflora* saltmarsh but caused soil and structural changes that may negatively alter ecosystem processes of this vulnerable grassland of high importance for biodiversity conservation.

Introduction

Salt marshes are intertidal grasslands characterized by low species diversity but high primary and secondary production, which provide a high number of valuable benefits to humans, such as the provision of raw materials and food, coastal protection, erosion control, water purification, and carbon sequestration (Barbier et al., 2011). Both the structure and function of salt marsh plant communities are shaped by physical factors such as elevation, salinity, flooding, and nutrient availability (Mitsch and Gosselink, 2008), as well as by biotic processes, such as competition and facilitation among plants (Bertness, 1991; Hacker and Bertness, 1995) and trophic cascades driven by invertebrate grazers (Bortolus and Iribarne, 1999; Silliman and Bortolus, 2003; Silliman et al., 2005).

Salt marshes of the Northern Hemisphere have a long history of grazing by domestic animals and other management techniques (Doody, 2008). Among these techniques, the erection of embankments that completely exclude tidal flooding has been widely applied since the sixteenth century in order to extend the period of grazing all year round or for agricultural use (Dent et al., 1976; Bakker et al., 2002; Doody, 2008). It is broadly demonstrated that cattle and sheep grazing changes species composition, decreases the contribution of dominant species, and may increase bare soil at higher stocking rates (Bakker et al., 1985; Andresen et al., 1990; Bouchard et al., 2003; Kleyer et al., 2003). On the contrary, in South American salt marshes, grazing by domestic herbivores is quite recent and, consequently, the study of grazing effects is scarce and focused on native small herbivores (Jackson and Giulietti, 1988; Bortolus and Iribarne, 1999; Cardoni et al., 2007; Vila et al., 2008). Recent information about cattle grazing on *Spartina densiflora* salt marshes of Argentina

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suggests that vegetation cover decreases as grazing intensity increases (Isacch and Cardoni, 2011) and that continuous grazing reduces forage quality and increases soil salinity (Di Bella et al., 2014).

The most extended temperate salt marsh of Argentina is Samborombon Bay, which covers 244,000 hectares in the coastal plain of the Río de la Plata River and converges to the south and east by the Atlantic Ocean. Samborombon Bay represents the eastern limit of the Flooding Pampa, the main native grasslands area devoted to cow–calf operation in the humid temperate region of Argentina. The vegetation is a brackish community dominated by *S. densiflora*, which occupies the upper levels of the intertidal area and is overflowed during high tides (Isacch et al., 2006). These salt marshes have been sporadically grazed by cattle at low stocking rates (Isacch et al., 2004; Vila et al., 2008) but, over the past decade, agriculture expansion in the temperate humid region of Argentina led to a displacement of livestock to more marginal areas, such as the Samborombon Bay. Consequently, these salt marshes are currently subjected to higher grazing pressure than that historically applied. Concomitantly with the increase in grazing pressure, local embankments were constructed under the assumption that avoiding ingression of tidal flooding with saline ocean water would improve soil quality through the reduction of its salinity (Damiano, 2010). Challenging this assumption, a recent study showed that water inundating the coastal plain has low salinity levels because of the contribution of inland freshwater through artificial channels that drain into the Rio de la Plata estuary (Carol et al., 2009a).

The intensification of the use of this community, located in an area of international importance for biodiversity conservation (The Ramsar Convention on Wetlands, 1997), may be a threat to the ecological integrity of this vulnerable grassland (Bilenca and Miñarro, 2004). Therefore, the aim of this study was to evaluate the effect of tidal suppression by embankment and defoliation frequency on the main chemical and physical properties of soils, vegetation structure, forage production, and quality of an *S. densiflora* salt marsh. For this purpose, we selected paddocks on a commercial cow–calf operation farm. One of them was exposed to overflow from a natural tidal pattern, and the other received no tidal flooding due to an embankment constructed 14 years before this study. We simulated light and moderate grazing pressures through two contrasting cutting frequency treatments. We hypothesize that embankment affects soil properties, vegetation composition, primary production, and forage quality because it prevents the ingression of tidal water with low salt content. We expect that embankment increases soil salinity and reduces organic matter, total nitrogen content, and soil stability. We also expect that embankment under high defoliation frequency increases bare soil and reduces the contribution of those species less tolerant to salinity, therefore reducing aboveground net primary production (ANPP) and forage quality. This information is required to design sustainable management practices in order to simultaneously attain profitable cattle production and biodiversity conservation goals.

Methods

Study Area

The study site is located in the southern portion of Samborombon Bay (36°25′S, 56°57′W). The regional climate is subhumid, mesothermal. For the period 1994–2014, mean annual average temperature was 15°C and annual average precipitation was 883 mm. Most precipitation occurs during summer months. The regional relief is flat (0.01% slope), and average altitude is 1.6 m over sea level. A complex drainage net composed by rivers, freshwater channels, tidal channels, and temporary and permanent ponds determines water dynamic and flooding events. Tides are mixed, predominantly semidiurnal, with tidal ranges lower than 2 m. The tidal wave comes from the southern Atlantic flowing upstream the Ajó River and the numerous tidal channels distributed all over the area (Carol et al., 2009b). The Ajó River has varying salinity levels (1 345–4 345 mg·L^{-1}) due to the contributions from the main tidal channel and inland freshwater channels (Carol et al., 2009a). Floods are mainly caused by overflow of water courses due to tidal movements (Fernández et al., 2004).

Table 1
Cumulative precipitation (mm) from May to September (rest season) and from October to April (growing season) for the 1981–2013, 2008–2009, and 2012–2013 periods.

Period	Cumulative precipitation (mm) May–September (rest season)	October–April (growing season)
1981–2013	306 ± 85	653 ± 198
2008–2009	332	352
2012–2013	372	760

Monthly rainfall data from 1981 to 2013 were obtained from the General Lavalle Naval Prefecture, located 1 200 m from the farm.

The coastal plain is dominated by hydromorphic soils, belonging to the Vertisol order, most of which are Typic Natraquerts that developed in marine-estuarine sediments (Imbellone et al., 2009). The upper horizon is 0–10 cm depth, has a silty clay loam texture, neutral pH, and is well provided with organic matter. The deeper horizons have the texture of clay, strong hydromorphic features, high saline-sodium contents (electrical conductivity of soil saturation extracts > 4 dS·m^{-1} and sodium adsorption ratio > 10), and medium to low permeability rates (Damiano, 2010). The depth of the groundwater table varies throughout the year, and mean salinity of groundwater is around 16 502 mg·L^{-1} (Carol et al., 2009a).

Humid halophytes steppe community (Perelman et al., 2001) is the dominant vegetation, composed by the cordgrass *S. densiflora* associated with *Sarcocornia perennis* (Mill.) A. J. Scott and *Distichlis spicata* (L.) Greene. Other species such as *Juncus acutus* L., *Scirpus cernuus* Vahl, and *Malvella leprosa* (Ortega) Krapov are also frequent in this community (Cagnoni and Faggi, 1993). The *S. densiflora* community occupies the high, medium, and low intertidal zone and is considered a bioengineer organism, tolerant of a broad spectrum of environmental conditions (Bortolus, 2006). The *S. densiflora* community is associated with the herbivore–detritivore burrowing crab *Chasrnagnathus granulate*, and *Spartina* spp. plants are its primary food source (Iribarne et al., 1997; Bortolus and Iribarne, 1999). Crabs exert a greater consumption of *Spartina* spp. aerial biomass at the lower elevation level of salt marshes, where crab densities are higher and plants are generally most consumed (Alberti et al., 2007).

Sampling Sites

The experiments were conducted on a commercial livestock 600-ha farm located in General Lavalle (36°25′40″S, 56°57′00″W). The western limit of the farm is the Ajó River, and several tidal channels connected with it flow into the farm. We selected two paddocks of around 100 ha on the side of Ajó River, dominated by *S. densiflora* community. One paddock, which was prevented from suffering tidal flooding by means of an embankment constructed 14 years before our study, corresponded to the embankment paddock (EP) treatment. The other paddock, which was exposed to overflow derived from natural tidal pattern, corresponded to the control paddock (CP).

Both paddocks have a similar topographic pattern: the lowest elevation level (<0.4 m above mean sea level [amsl]) is near the tidal channels, and in the opposite direction the altitude increases up to the highest elevation level (0.8–1 m amsl). Along this elevation gradient, frequency and duration of tidal flooding and soil salinity increase as elevation decreases. As cattle graze mainly in the upper salt marsh

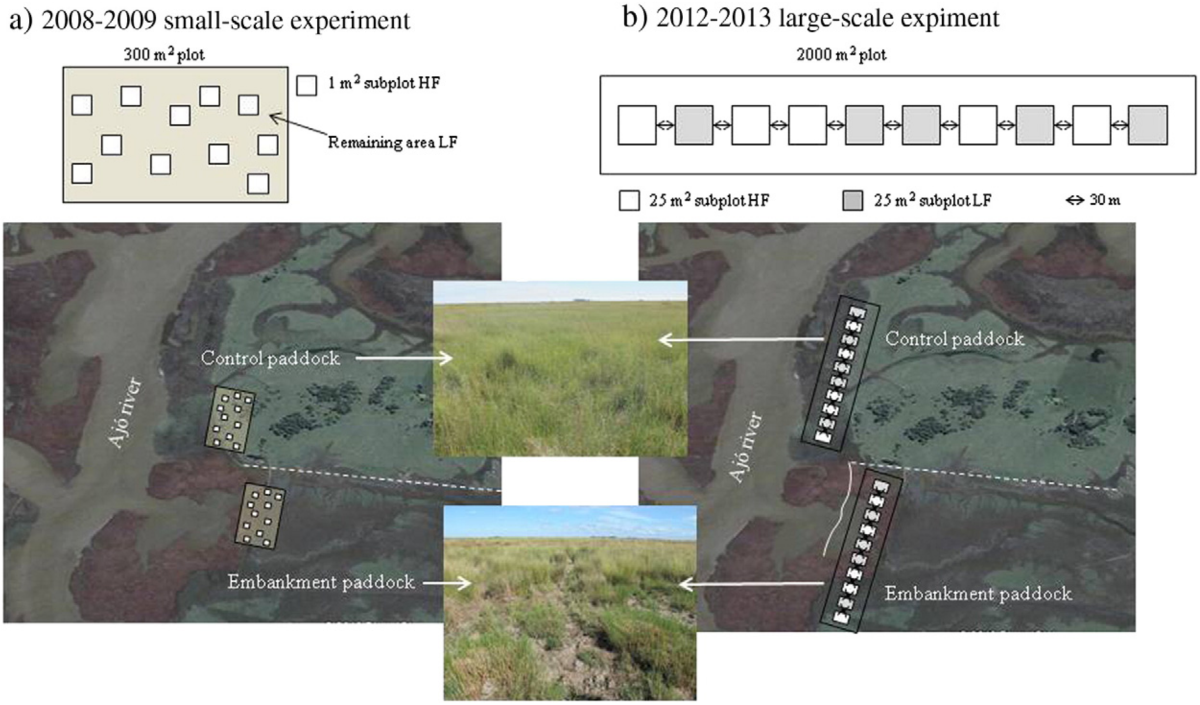

Fig. 1. Experimental design for 2008–2009 (a) and 2012–2013 (b) experiments. Insert: Photos of the embankment and control paddocks.

and grazing changes vegetation structure more intensively in this position (Di Bella et al., 2014), we selected the high elevation level of each paddock to perform the experiments. In this position, a smaller crab population is expected (Alberti et al., 2007) and therefore the confounding effect of crab herbivory on the primary production calculation (Silliman and Bortolus, 2003) was prevented.

Rainfall and Seasonal Distribution

To take into account the effect of interannual rainfall variability on vegetation structure, primary productivity, and soil salinity, the experiments were carried out during two growing seasons: 2008–2009 and 2012–2013. The cumulative precipitation of the 2008–2009 growing period was 46% lower than the average (1981–2013) of the same period, while the cumulative precipitation of the 2012–2013 growing period was 16% higher than the average (Table 1).

Experimental Design

It was difficult to locate replicates of embankment paddocks on livestock farms with similar management histories, soil properties, vegetation community condition, and age of the embankment construction. Therefore our experiments were conducted in only one plot (paddock) per embankment treatment, where a nested design was performed, assigning the experimental factor Embankment (E) to the main plot and the experimental factor Defoliation Frequency (DF) to the subplots nested within each main plot.

A small-scale experiment was conducted during the 2008–2009 growing season. A homogeneous 300 m^2-area in the high-level position of *S. densiflora* community was selected in the embankment paddock and in the control paddock. These areas, which constituted the main plots, were delimited with an electric fence to exclude cattle grazing. Biomass of each plot was mowed at 20 cm height with a manual lawn mower on 1 October 2008. Within each plot, two defoliation frequency treatments were imposed: high frequency (HF: harvests every 45 days during the complete growing season) and low frequency (LF: a single biomass harvest at the beginning of the growing period). HF treatment was assigned to ten 1-m^2 permanent subplots distributed within the plot. LF treatment was imposed in the remaining area, locating subplots randomly whenever variables were registered (Fig. 1a).

In order to increase the spatial extent and the sample size with respect to the 2008–2009 experiment, a larger-scale experiment was conducted during the 2012–2013 growing season. In the high-level position of the embankment and control paddocks, a 2 000-m^2 area (main plots) was selected and fenced to exclude cattle grazing. Inside each main plot, we established ten 25-m^2 subplots equally spaced at 30 m from each other. Biomass of each subplot was mowed at 20 cm height with a manual lawn mower on 3 October 2012, and the same defoliation treatments, HF and LF, were randomly assigned to each subplot (Fig. 1b).

Salinity, Organic Matter, N Content, and Structural Stability of Soils

Soil variables were compared only for the embankment factor because we did not expect changes due to defoliation after a single growing season.

Electrical conductivity (EC) was determined at the beginning and end of the growing seasons by collecting 5 composited samples of 10 subsamples per plot in October 2008 and May 2009 (small-scale experiment) and 5 composited samples of 20 soil subsamples per plot in October 2012 and May 2013 (large-scale experiment).

Soil organic matter content (SOM) was determined by extracting 5 composited samples of 10 subsamples per plot in March 2009 (small-scale experiment) and SOM and total nitrogen (N) content by extracting 5 composited samples of 20 soil subsamples per plot in March 2013 (large-scale experiment). Soil samples were extracted from up to 10 cm deep. EC was determined by soil saturation extracts (Rhoades, 1982), SOM by the Walkley and Black (1934) method, and N content by the Kjeldahl method (Bremner and Mulvaney, 1982).

Soil structural stability was assessed in March 2013 (large-scale experiment) by the Yoder apparatus wet-sieving method (Kemper and Chepil, 1965) by extracting twenty 15-cm-diameter and 10-cm-depth soil subsamples per plot. After air-drying, aggregates of up to 8 mm were separated by hand. These aggregates were slowly moistened up to field capacity (30% by weight) and incubated 20°C for 24 h under 98% to 100% relative humidity. The samples were wet-sieved and oven-dried, after which the mean weight diameters (MWDs) were obtained to calculate the soil structural instability index.

Basal Cover of Dominant Species, Functional Groups and Vegetation Structural Variables

At the end of the growing seasons (May 2009 and May 2013), basal cover of each plant species was registered using the phytosociological Braun-Blanquet Cover-Abundance method (Braun-Blanquet, 1932). Vegetation structural variables such as bare soil, litter, or standing dead material were recorded where no living plants were intercepted. Plant species were classified in functional groups (Jacobo et al., 2006): cool season (C$_3$) grasses, warm season (C$_4$) grasses, and dicotyledonous herbs, except the dominant species *S. densiflora* and *S. perennis*.

Aboveground Net Primary Production of S. densiflora Community

In the small-scale experiment, HF treatment was imposed by harvesting the entire 1-m^2 permanent subplot surface every 45 days. To avoid underestimating the ANPP under the LF treatment (Sala et al., 1981), biomass was harvested within ten 1-m^2 subplots (frames) randomly located every 45 days (Fig. 1a). Harvests were performed with hand scissors at 20-cm height. In the large-scale experiment, ten 1-m^2 subsamples (frames) were randomly located every 45 days within the subplots (Fig. 1b) and biomass was harvested with hand scissors at 20-cm height. Only in the HF treatment, the entire subplot surface was mowed with a manual lawn mower after harvesting subsamples.

Biomass samples were hand separated into four components: green and standing dead *S. densiflora* and green and standing dead of other species. Litter was collected by hand in each subplot. Biomass components and litter were oven dried at 70°C until constant weight and weighed.

To estimate ANPP, we applied a procedure proposed by Sala et al. (1981) that considers a standing dead biomass and litter term in order to reduce the masking effect of senescence and decay in the estimation of productivity.

ANPP during the growing period was estimated as the summation of the daily ANPP of five periods multiplied by the duration of the corresponding period. The relative contribution of *S. densiflora* to the saltmarsh community productivity was estimated as *S. densiflora* ANPP in relation to total ANPP.

Forage Quality

After samples were hand separated, oven-dried, and weighed, the green biomass components of *S. densiflora* and other species were submitted to detergent system analysis to determine neutral detergent fiber, acid detergent fiber, lignin, and ash (Van Soest et al., 1991). Crude protein (CP) was estimated by multiplying 6.25 to N obtained by Kjeldahl (AOAC, 1984). These variables were applied to estimate apparent digestibility (DMS) by the summative equation (Goering and Van Soest, 1970).

Statistical Analysis

In order to determine the effect of embankment and defoliation treatments on variables registered once during each experiment (SOM, N, SSI, Relative basal cover, and ANPP), we performed a nested analysis of variance (nested ANOVA) considering defoliation frequency (DF) as nested factor within embankment (E). When variables were collected at several sampling dates (EC, CP, and DMS), we performed the nested multivariate analysis of variance (nested MANOVA) considering dates as multiple factors. One-way ANOVA was performed for soil variables registered once in each experiment (SOM, N, SSI) and a repeated-measures ANOVA for CE, which was registered twice in each experiment. When interactions among factors were significant, we performed planned comparisons (orthogonal contrasts) to determine differences of interest. We did not perform comparisons among the small- and large-scale experiments because samples of all variables had different spatial extent and size.

Results

Embankment on Soil Properties

At the beginning of both growing seasons, EC was low and similar between embankment and control treatments (Table 2) (contrast October 2008: F = 3.74, P = 0.07; contrast October 2012 F = 0.69, P = 0.45). EC increased from October to May during the 2008–2009 growing season under both treatments, but at a higher rate in the embankment than in the control paddock. During the 2012–2013 growing season, EC increased at a similar rate in both treatments, reaching the same values in May.

Table 2
Soil properties of control and embankment paddocks in 2008–2009 and 2012–2013 growing periods. Electric conductivity (EC), soil organic matter (SOM) in both growing periods, nitrogen content (N), and soil structural instability index (SSI) are depicted in the 2012–2013 growing period.

Soil variables	Treatment	Growing Season					
		2008–2009			2012–2013		
		Oct. 2008	May 2009	*P*	Oct. 2012	May 2013	*P*
EC (ds·m^{-1})	Control	1.2 (0.63)	6.4 (0.85)	T <**0.01**	1.3 (0.49)	5.3 (0.66)	T = 0.64
	Embankment	1.8 (0.71)	8.9 (0.92)	M <**0.01**	1.6 (0.54)	5.7 (2.17)	M <**0.01**
				TxM <**0.01**			TxM = 0.90
SOM (%)	Control	7.9 (1.29)		<**0.01**	14.1 (2.63)		<**0.01**
	Embankment	5.9 (0.29)			3.3 (0.10)		
N (%)	Control				0.83 (0.03)		<**0.01**
	Embankment				0.18 (0.01)		
SSI	Control				0.88 (0.07)		0.08
	Embankment				1.53 (0.54)		

Values are the means of the embankment and control treatments. SE is shown within parentheses. For EC, *P* values of the repeated measure ANOVA. T: embankment treatment, M: moment of the growing season (beginning or end), TxM: interaction among T and M. For SOM, N, and SSI, *P* values of the one-way ANOVA for SOM, N, and SSI.

Table 3
Relative contribution (%) to basal cover of dominant species, functional groups, and structural vegetation variables under low (LF) or high (HF) defoliation frequencies in control and embankment paddocks during 2008–2009 (**a**) and 2012–2013 (**b**) growing seasons.

	CONTROL		EMBANKMENT		Factor	df	F	*P*
Species—Functional groups	LD frequency	HD frequency	LD frequency	HD frequency				
a) 2008-2009 Growing Season								
Spartina densiflora	37.4 (5.9)	35.1 (7.2)	26.7 (5.6)	20.3 (4.6)	E	1	45.29	<**0.01**
					DF (E)	2	3.36	**0.047**
Sarcocornia perennis	21.6 (13.9)	24.2 (7.8)	24.8 (8.1)	25.4 (6.4)	E	1	0.52	0.474
					DF (E)	2	0.19	0.827
Warm season grasses (C_4)	25.8 (8.6)	18.9 (8.6)	3.1 (5.8)	0.1 (0.3)	E	1	93.54	< **0.01**
					DF (E)	2	2.97	0.065
Cool season grasses (C_3)	0.6 (0.7)	0.2 (0.7)	0.0 (0.0)	0.0 (0.0)	E	1	6.26	**0.017**
					DF (E)	2	1.09	0.347
Dicotyledonous herbs	0.7 (1.0)	1.7 (1.4)	1.6 (5.5)	0.6 (1.0)	E	1	0.91	0.347
					DF (E)	2	1.11	0.340
Litter and standing dead material	2.8 (2.3)	9.0 (9.3)	23.4 (9.2)	21.4 (6.9)	E	1	45.58	< **0.01**
					DF (E)	2	1.71	0.195
Bare soil	9.6 (6.6)	12.4 (4.3)	23.4 (9.1)	32.5 (7.5)	E	1	52.13	< **0.01**
					DF (E)	2	4.32	**0.021**
b) 2012–2013 Growing Season								
Spartina densiflora	48.7 (1.5)	47.7 (5.7)	18.3 (8.4)	12.0 (6.6)	E	1	88.30	< **0.01**
					DF (E)	2	0.83	0.469
Sarcocornia perennis	12.7 (5.5)	5.0 (10.5)	20.7 (7.2)	17.3 (6.4)	E	1	8.05	**0.022**
					DF (E)	2	1.36	0.310
Warm season grasses (C_4)	1.0 (1.2)	7.0 (1.5)	7.0 (6.6)	2.0 (3.5)	E	1	0.05	0.827
					DF (E)	2	3.55	0.079
Cool season grasses (C_3)	0.7 (1.2)	7.0 (2.6)	4.3 (3.8)	3.3 (5.8)	E	1	0.00	1.000
					DF (E)	2	2.20	0.173
Dicotyledonous herbs	1.7 (2.9)	6.3 (6.1)	0.3 (0.6)	0.0 (0.0)	E	1	3.83	0.086
					DF (E)	2	1.43	0.295
Litter and standing dead material	17.3 (1.2)	21.7 (10.2)	10.7 (2.3)	19.0 (4.4)	E	1	2.01	0.194
					DF (E)	2	2.04	0.193
Bare soil	19.0 (7.9)	5.0 (7.0)	38.7 (3.5)	46.3 (3.8)	E	1	80.50	< **0.01**
					DF (E)	2	5.51	**0.031**

Values are mean (SE). Factor result from nested ANOVA, E: Embankment, DF(E): Defoliation frequency nested in embankment (LF: low defoliation frequency, HF: high defoliation frequency), degree of freedom (df), F statistics, and *P* values.

SOM was lower in the embankment than in the control paddock during both growing seasons. In the 2012–2013 growing season, N content was much lower and soil structural instability index (SSI) trended to be higher in the embankment than in the control treatment (Table 2).

Embankment and Defoliation Frequency on Vegetation Cover

Embankment dramatically increased the proportion of bare soil during both growing seasons, and high defoliation frequency exacerbated this response (contrast 2008–2009 growing season: F = 7.93, $P < 0.01$; contrast 2012–2013 growing season: F = 8.48, $P = 0.019$). Relative contribution of the dominant cordgrass *S. densiflora* was negatively affected by embankment during both growing seasons and by high defoliation frequency in the embankment paddock during the dry 2008–2009 season (contrast F = 5.99, $P = 0.019$) (Table 3a, b). The relative basal cover of the other dominant species *S. perennis* increased under embankment treatment during the wet 2012–2013 growing season (Table 3b).

The relative contribution of warm season grasses (*D. spicata, Cynodon plectostachyus* [K. Schum.] Pilg.) and cool season grasses

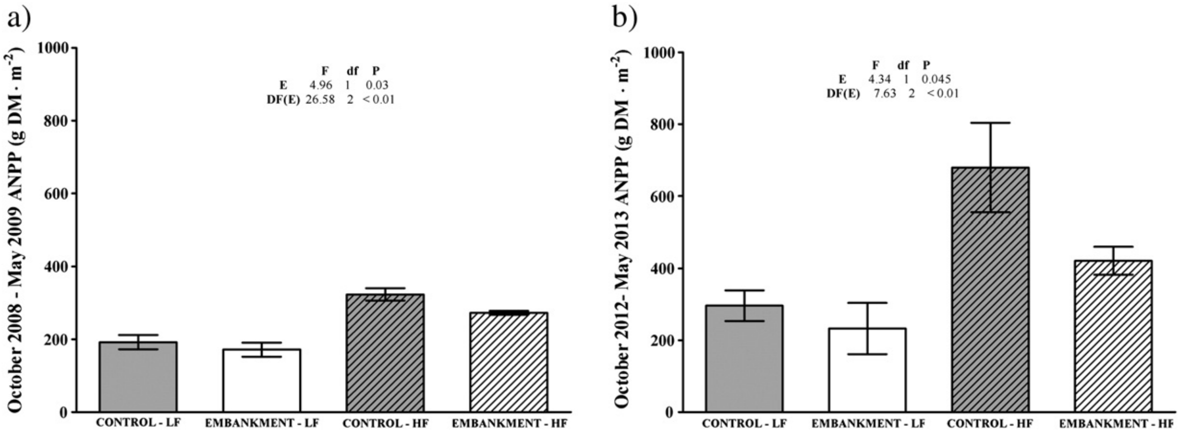

Fig. 2. Aboveground net production (ANPP) of *Spartina densiflora* community in control and embankment paddocks under low (LF) or high (HF) defoliation frequencies during the 2008–2009 (a) and 2012–2013 (b) growing seasons. Vertical bars are 1 SE. Insert: Factor resulting from the nested ANOVA. E indicates embankment treatment; DF(E), defoliation treatments nested in embankment treatment, degree of freedom; (df), F statistics and *P* values.

Table 4

a, Dry matter digestibility (DMD %) and **b,** crude protein (CP) of green leaf of *Spartina densiflora* and other species, obtained during the course of the growing season from control and embankment paddocks under different defoliation frequencies.

a) Dry matter digestibility (%)

Vegetation component	Growing season					
	Early	Middle	Late		F	*P*
Spartina densiflora	59.65 (1.36)	52.86 (7.54)	48.38 (1.27)	E	0.02	0.89
				DF (E)	0.02	0.97
				GS(E·DF)	43.62	<**0.01**
Other species	55.38 (1.43)	53.65 (9.79)	52.70 (9.48)	E	0. 28	0.59
				DF (E)	0.80	0.45
				GS(E·DF)	0.23	0.97

b) Crude protein

Vegetation component	Embankment treatment	Def. frequency	Growing season					
			Early	Medium	Late		F	*P*
Spartina densiflora	Control	Low	8.23 (1.08)	6.03 (0.92)	7.35 (0.35)	E	18.57	< **0.01**
		High	8.11 (1.36)	6.69 (0.59)	8.20 (1.06)	DF (E)	6.75	<**0.01**
	Embankment	Low	5.43 (0.87)	4.55 (0.45)	6.02 (0.77)	GS(E·DF)	2.45	**0.04**
		High	6.86 (0.71)	5.96 (0.84)	7.80 (0.75)			
Other species			10.03 (0.23)	8.57 (0.37)	6.97 (0.47)	E	1.49	0.23
						DF (E)	1.36	0.27
						GS(E·DF)	5.54	<**0.01**

As forage quality data were similar in both experiments, they were pooled for analysis. The mean of the 2008–2009 and 2012–2013 experimental periods and 1 SE in brackets are shown. Factors resulting from nested MANOVA were as follows: E indicates embankment; DF (E) indicates, defoliation frequency nested in embankment; GS(E·DF) indicates, growing season nested in embankment and defoliation frequency; F statistics; and *P* values. When the main factor embankment (E) and the nested factor defoliation frequency (DF) were not significant, dates were averaged for each stage of the growing season.

(*Lolium multiflorum* Lam., *Hordeum vulgare* L. var. Vulgare, *Poa pratensis* L. subsp. Pratensis, *Elymus ponticum* [Podp.] N. Snow) was negatively affected by embankment during the dry 2008–2009 growing season (Table 3a), while during the wet 2012–2013 growing season, embankment did not affect the relative cover of these functional groups (Table 3b). The relative contribution of the dicotyledonous herbs (*Symphyotrichum squamatum* (Spreng.) G. L. Nesom, *Bupleurum tenuissimum* L., *Baccharis pingraea* DC. Var. Pringaea, *Centaurium pulchellum* (Sw.) Druce, *Plantago myosuros* Lam., and *Sonchus asper* (L.) Hill) was not affected by embankment or defoliation frequency (Table 3a, b). The proportion of standing dead material and litter during the dry 2008–2009 growing season was higher in the embankment paddock (Table 3a).

Embankment and Defoliation Frequency on ANPP of S. densiflora Salt Marsh

Overall ANPP in the dry 2008–2009 growing season was 243.4 ± 13.1 g DM·m^{-2} and in the wet 2012–2013 growing season it was 407.5 ± 46.9 g DM·m^{-2}. The contribution of *S. densiflora* to the overall ANPP of the community was 85% ± 8% in the 2008–2009 growing season and 81% ± 2% in the 2012–2013 growing season and was not affected by embankment or defoliation frequency.

Embankment reduced ANPP during the dry 2008–2009 and the wet 2012–2013 growing seasons. High defoliation frequency increased ANPP with respect to low defoliation frequency in the control paddock, but to a much higher extent in the wet 2012–2013 (contrast $F = 12.28$, $P < 0.01$) than in the dry 2008–2009 (contrast $F = 33.5$, $P < 0.01$) growing season (Fig. 2).

Embankment and Defoliation Frequency on Forage Quality

Forage quality variables showed similar values in both experiments; therefore data were pooled for analysis and averages are shown in Table 4.

Dry matter digestibility (DMD) of *S. densiflora* tissues was affected by the course of the growing season and did not respond to embankment or defoliation treatments. The DMD of *S. densiflora* green tissues was higher at the first stage of growing, and it was gradually reduced as the growing season progressed. DMD of other components of the community, represented mainly by *S. perennis, D. spicata,* and *C. plectostachyus*, was not affected by embankment or defoliation treatments and did not change throughout the growing season (Table 4a). Crude protein (CP) of *S. densiflora* green tissues was lower in the embankment paddock and increased under high defoliation frequency. This variable showed a seasonal pattern: high CP values were registered during the early and late stages of growing, while lower values were obtained during the middle stage of growing. CP of other components of the community decreased as growing season progressed and did not respond to embankment or defoliation treatments (Table 4b).

Discussion

In Samborombon Bay, embankments were constructed to suppress tidal ingressions, in order to intensify *S. densiflora* salt marsh utilization for cattle grazing. However, our results showed that this practice was not effective to achieve this purpose because embankments deteriorated soil and community condition and reduced ANPP and forage quality.

Before salt marshes are reclaimed from the sea, their soils are often partly waterlogged, rich in organic matter and highly saline. It is expected that embankment causes desalinization of soils through percolation of salts by rainwater (French, 2006), reduces soil organic matter content due to biological decomposition, and changes soil structure (Dent et al., 1976). In *S. densiflora* salt marsh, tidal suppression by embankment drastically reduced soil organic matter content but did not reduce soil salinity.

In this low-latitude salt marsh, desalinization did not occur because the high evapotranspiration rate in summer (>100 mm·mo^{-1} Carol et al., 2009a) is not counterbalanced by rainfall. Therefore, capillary water rises from the saline groundwater (16.5 mg·L^{-1}, Carol et al., 2008) and carries soluble salts toward the topsoil (Lavado and Taboada, 1988; Alconada et al., 1993). In addition, embankment avoids the ingression of tidal water from the Ajó River, with relatively low salt content (1.3-4.3 mg·L^{-1}, Carol et al., 2008) due to the contribution of inland freshwater channels (Carol et al., 2009a). During lower precipitation periods, such as that recorded in 2008–2009 growing season, when capillary water rise is higher, this process is magnified if the ingression of fresh water is prevented by embankment, and therefore electrical conductivity increases in summer. Instead, during winter, the lower evapotranspiration rate (30 mm·mo^{-1}, Carol et al., 2009a) does not enable capillary water rise, which determines low levels of soil salinity. Therefore in this salt marsh, soil salinity shows a seasonal pattern, with low electrical conductivity values in winter (<2 dS·m^{-1}), which increase along the season in both embankment and control paddock, reaching values of saline soils in summer (>4 dS·m^{-1}). This seasonal pattern, related to the dynamics of temperature and soil water content throughout the year, occurred in the whole region (Lavado and Taboada, 1987).

The amount of soil organic matter depends on how much organic matter enters the soil and how fast this organic matter decomposes in the soil. The dramatic reduction of soil organic matter content in the embankment paddock may be explained by the lower input and the higher output with respect to the control paddock. The lower input was determined by the lack of supplies of suspended material via tidal flow for several years (Spencer and Harvey, 2012) and additionally by the reduction of litter contribution to the decomposer compartment due to the lower ANPP (Bardgett and Shine, 1999). Greater output may be expected because of the higher biological decomposition of soil organic matter, which occurs when soil regimen changes from water-saturated anaerobic to less water-saturated and more aerobic regimen (Dent et al., 1976). The lower soil organic matter in the embankment paddock may explain the higher soil structural instability index because organic matter is a main factor for the stabilization of aggregates in soils (Chaney and Swift, 1984). The low structural stability may reduce soil capacity to cope with the detrimental effects of trampling and traffic (Climo and Richardson, 1984) under embankment conditions.

Tidal suppression through embankment reduced vegetation cover and the contribution of grasses, both of the dominant *S. densiflora* and other subordinate species. The reduction of freshwater availability and the higher level of salinity in embankment paddock resulted in the exclusion of grasses less tolerant to salinity and with high forage quality, such as *L. multiflorum*, *H. vulgaris*, *P. pratensis*, and *C. plectostachyus* (Kenkel et al., 1991; Niazi et al., 1992; Sagi et al., 1997) and in the reduction of the relatively tolerant to salinity *D. spicata*. Concomitantly, species more tolerant to salinity, like *S. cernuus, S. squamatum, B. tenuissimun, C. pulchellum,* and *S. asper* (Ladero Alvarez et al., 1984; Cagnoni and Faggi, 1993; Marañon, 1998; Apóstolo, 2005), appeared or increased in the embankment paddock. The increase of this functional group did not compensate for the reduction of grass cover, resulting in the increase of bare soil. As bare soil promotes water rising by capillarity from highly saline groundwater (Lavado and Taboada, 1987), it may result in a positive feedback that enhances the halomorphic conditions promoted by embankment. These negative structural changes were overexpressed when the salt marsh was submitted to high defoliation frequency. A similar response at the ecosystem level was found in nearby inland grassland where topsoil salt content increased due to grazing, showing a close interaction among vegetation and soil conditions (Chaneton and Lavado, 1996).

Tidal suppression though embankment reduced ANPP, probably as a consequence of the lower soil water content because of the interruption of tidal contribution, the lower soil organic matter, and the higher salt content of the topsoil, which may reduce water and nutrients availability (Barber, 1995). High defoliation frequency increased ANPP with respect to low frequency, which suggests the occurrence of compensatory growth (McNaughton, 1983). Compensatory growth results from higher growth rates as a consequence of processes at plant level, mediated by environmental and physiological changes triggered by defoliation (Briske, 1991). Defoliation increases light intensity reaching basal and younger, highly active aerial tissues; reduces senescence increasing carbon gain at the whole plant level (Deregibus et al., 1985); and increases stomatal conductance and photosynthetic rate (Wallace et al., 1984). In addition, defoliation may lead to increasing the water potential of leaves (Toft et al., 1987) and nutrient uptake (McNaughton and Chapin, 1985). Although both paddocks showed compensatory growth, it occurred to a much higher extent in the control treatment and in the wet season as a consequence of the higher resource availability (Oesterheld and McNaughton, 1991).

S. densiflora community has a lower forage value than other communities not affected by tidal flooding in this region, being its digestibility and crude protein values higher than 60% and 10%, respectively (Cahuépé and Hidalgo, 1991). Tidal suppression through embankment reduced the content of crude protein of the dominant species *S. densiflora*, which may be a consequence of the lower availability of soil nitrogen under this condition. The content of crude protein was higher than that which limits animal consumption (7%) only in control paddocks under high defoliation frequency. This may be a consequence of the lower average leaves' age when defoliation is more frequent (Green and Detling, 2000; Tessema et al., 2010). DMD of *S. densiflora* was not affected by embankment treatment or defoliation frequency and decreased throughout the growing season, a general response of grasses due to the accumulation of senescent tissues and the appearance of flowering structures with higher lignin content (Demarquilly, 1978; Fick et al., 1994). The lack of response of *S. densiflora* digestibility to embankment and defoliation frequency may be related to the traits that confer adaptations to saline environments, like thick leaves, thicker cuticle, large leaf ridges that fit together as the leaf rolls during water stress, and salt-secreting glands (Maricle et al., 2009).

Implications

Embankments in Samborombon Bay were constructed to intensify the use of *S. densiflora* salt marsh for cattle grazing, under the assumption that avoiding tidal overflow would increase forage availability. However, our study showed that embankment under high defoliation frequency reduced ANPP and CP content and increased the relative proportion of lower-value forage species with respect to control paddock under high defoliation frequency. Therefore for cattle production purposes, it is more suitable to apply high defoliation frequency in paddocks under natural tidal regimens because they produce higher forage biomass with CP values that do not restrict cattle intake.

From a conservation point of view, tidal suppression caused a dramatic reduction of soil organic matter and litter cover and an increase of bare soil and topsoil salinity. These changes may alter ecosystem processes and services such as nutrient and water cycles, refugia, and genetic resources, among others. This may threaten the ecological integrity of this vulnerable grassland of high biodiversity conservation importance.

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