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Net Aboveground Primary Production and Soil Properties of Floating and Attached Freshwater Tidal Marshes in the Río de la Plata Estuary, Argentina

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ABSTRACT: In the lower delta of the Paraná River, at the head of the Río de la Plata estuary (Argentina), we compared net aboveground primary production (NAPP) and soil properties of the dominant macrophyte *Scirpus giganteus* (Kunth) in a floating and an attached marsh community. Both marshes are tidally influenced but in different ways. The floating marsh site is relatively isolated from tidal influences because its ability to float makes it resistant to overland flow and to sediment inputs from the estuary. The attached marsh lacks the capacity to float and receives sediment supplies from the estuary through overland flow. These hydrologic differences are reflected in lower mineral content in sediments of the floating marsh. Using a leaf tagging technique, estimated NAPP was 1,109 $\pm$ 206 g m^{-2} yr^{-1} for the floating marsh and 1,866 $\pm$ 258 g m^{-2} yr^{-1} for the attached marsh. We attribute the lower NAPP of the floating marsh to isolation from sediment input from overland flow.

Introduction

Hydrology is a major forcing factor in wetlands (Brinson 1993; Mitsch and Gosselink 2000). Differences in hydrologic regime are shown to influence wetland plant communities through differences in primary production, species diversity, and the distribution of species within ecosystems (Cronk and Fennessy 2001). Because water flow has the ability to transport nutrients, disperse propagules, and aerate roots, hydrological fluxes are considered an energy subsidy for wetlands (Lugo et al. 1990). In tidal wetlands, the availability of nutrients bound to particulate material is linked to current velocities and sediment sources (Gosselink and Turner 1978; Christiansen et al. 2000); this has been found to enhance primary production (Cahoon and Stevenson 1986; Mitsch et al. 1991; Carr et al. 1997).

In the upper portion of the Río de la Plata estuary, the prograding delta of the Paraná River (Argentina) is dominated by natural marshes that occupy the central depression of the developing delta islands. The dominant species, *Scirpus giganteus* (Kunth), is a robust perennial hydrophyte that forms dense networks of living rhizomes and roots (Kandus and Malvárez 2004). On some islands, plants are rooted in a predominately mineral sediment. At other sites, the root mat floats, moving vertically with fluctuating tides because it is not attached to underlying sediments. Although buoyant mats at some islands (locally called embalsados) are well known by local hunters, floating marshes in the Paraná River delta have not been previously described in the scientific literature, possibly because of their rather inaccessible location. *S. giganteus* marshes are widespread in the tidal reaches of the Lower Delta and cover an area of more than 400 km^2. At this time it is not known how many are floating, firmly attached, or a mixture of the two conditions (Pratolongo 2005).

We compared net aboveground primary production (NAPP) of *S. giganteus* and soil properties at floating and attached marsh sites that share the same tidal regime and are subjected to a similar pulsing hydrology. Due to their buoyant nature, floating marshes are less open to overland flow of sediment-rich floodwaters (Swarzenski et al. 1991), and could be relatively isolated from sediment sources normally associated with tidal inputs. We report hydrologic regime and soil mineral content as probable explanations of differences in NAPP between sites.

Materials and Methods

STUDY SITE

The Río de la Plata estuary is at the mouth of the Paraná River basin, a 2.6 $\times$ 10^6 km^2 South American

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fluvial system with a mean annual discharge of 17×10^3 m^3 s^{-1} and an annual sediment load of more than 150×10^6 tons (Orfeo and Stevaux 2002). This work was conducted in the upper portion of the estuary where a prograding delta is exposed to semidiurnal tides from the estuary. Tidal amplitudes in the Lower Delta area are typically 1 m (Vieira and Lanfredi 1996). Storm surges greater than 4 m have been reported during sudestadas (i.e., southeasters), a recurring event characterized by winds from the south-southeast (Piccolo and Perillo 1999). Salinity is lower than 0.4 psu throughout the delta area, even at the outer bars in the delta mouth, because brackish water is displaced seaward by the large freshwater discharge of the Paraná River (Framiñan and Brown 1996; Orfeo and Stevaux 2002).

At present, the Lower Delta covers an area of approximately 2,700 km^2, with an estimated rate of progradation of 70 m yr^{-1} over the past 160 years (Iriondo and Scotta 1978). The high sediment load reaching the mouth leads to the recurring formation of bars that become colonized and stabilized by *Schoenoplectus californicus*. Differential sediment accretion near distributary channels creates permanent islands that assume the form of a central depression and a surrounding levee, and constitute the basic geomorphic units of the frontal delta (Bonfils 1962). The central depression occupies about 80% of the surface of mature islands. These extensive lowlands typically become vegetated by nearly monospecific stands of *S. giganteus*, with a few associated species (Kandus and Malvárez 2004).

Hydrologic and geomorphic conditions that lead to the mat buoyancy in *S. giganteus* marshes are unknown. To explain the origins of floating marshes in the Mississippi Delta, Russell (1942) proposed that mats would spread into open water by growth along the edges. O'Neil (1949) speculated that they might originate as anchored marshes and become buoyant mats after breaking loose from a subsiding substrate. In the Paraná River delta, subsidence is not as strong as in the Mississippi Delta, and the largest floating marshes appear in the youngest islands. The presence of central lagoons in the younger islands, partially covered with marsh at their edges, suggests that a mechanism similar to that proposed by Russell (1942) is more likely.

We selected for comparison two islands with nearly homogeneous stands of *S. giganteus* (Fig. 1). At the Felipe site, only the uppermost areas on levees are altered by activities that consist of residential and small-scale farming and gardening. Although several small ditches were dug originally to drain orchards in lowlands, the activity was abandoned about 50 years ago and ditches naturally filled with sediment. The substrate at Felipe is composed of a buoyant organic layer about 25 cm thick, consisting of a dense mat of living rhizomes and roots that floats in an aqueous sludge matrix. At Barca Grande an active drainage system consists of main ditches that intersect the perimeter levee and connects the island interior with the Barca Grande River. Ditches in this area were first dug in the 1940s, but instead of being abandoned, the small-scale orchards were converted to *Salix* plantations about 40 years ago during which time the drainage ditch was deepened and widened. Ditches facilitate tidal exchange between the interior marsh and the river. On falling tides, ditches allow surface water to drain. Rising tides promote water flow up the ditches until they are at bankfull. With further rises, water begins to flow over the marsh surface. In contrast to the Felipe site, the plants at Barca Grande are rooted in a compact mineral substrate.

Sampling and Analyses

Trends in water depth were measured in the stream channel at Felipe and in the main ditch at Barca Grande. Measurements were taken hourly from September 26 to 28, 2004, during spring tide, and water depths at each sampling station were compared to tide levels at Buenos Aires Harbor gauge (Dirección Nacional de Construcciones Portuarias y Vías Navegables), located about 11 km from Felipe and 38 km from Barca Grande (Fig. 1). To establish the elevation of overbank flow initiation at each site, water depths were measured at flooded condition along a line from the channel to the study area (A–B and C–D in Fig. 1). These topographic profiles were evaluated relative to tidal records at Buenos Aires Harbor without assuming any lag time.

At Felipe, a sampling area of about 100 m^2 was established at 140 m from the levee that borders the stream, far enough toward the center of the marsh to eliminate obvious edge effects. The sampling area at Barca Grande was located 500 m from the river levee and 20 m from the upstream end of a main ditch (Fig. 1). We sampled soil at both sites at five locations during September 2004, using a 4-cm diam McCauley peat sampler. Samples were removed at 25-cm depth intervals with mid points of 12.5, 37.5, 62.5, 87.5, 112.5, 137.5, and 162.5 cm. Munsell color was recorded in the field and samples were stored in hermetic plastic bags at ca. 4°C. Soil bulk density was determined after drying samples at 80°C to constant weight. Organic matter, as loss-on-ignition (percent LOI), was determined as the ratio of weight loss (500°C, 3 h) to dry weight. To determine LOI of the surface litter, the top 5 cm of litter was collected in five 25×25 cm quadrats and processed in the same way as soil samples.

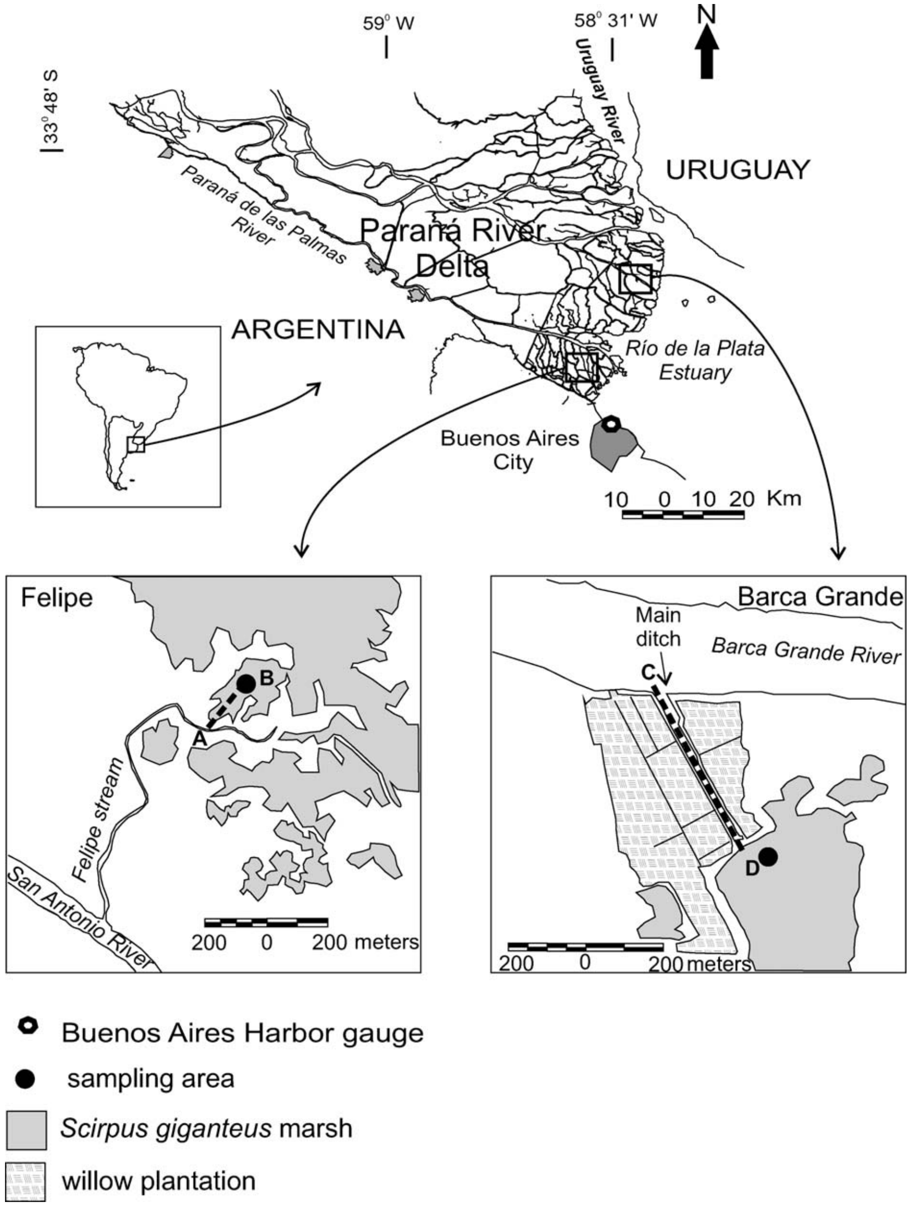

Fig. 1. Location of the study sites in the Paraná Delta, Argentina. Cross sections of A–B and C–D are shown in Fig. 3.

NAPP was obtained by a combination of tagging and harvesting plots of *S. giganteus*. Because the species grows year-round and experiences a high leaf turnover, methods based on peak standing crop or changes in living biomass are not applicable (Smalley 1959; Wiegert and Evans 1964; Milner and Hughes 1968). Phenometric techniques (Hopkinson et al. 1980) are also inadequate in this case because they involve detailed measurements on new leaves, which appear in the core of each ramet tightly enclosed within the remaining green and dead leaves.

Because of these restrictions, a tagging technique was created to estimate NAPP as reported in Pratolongo et al. (2005) and described briefly here. Ten quadrats in monospecific stands of *S. giganteus* were established for NAPP measurements over one year on September 8, 2002 (late winter) at Felipe (6 intervals) and on August 2, 2002 at Barca Grande (5 intervals). We tagged all live ramets in each quadrat (50 × 50 cm) by piercing the entire leaf cluster at the ground level with a steel needle and polyester thread, with the latter left in place. In *S. giganteus*, nodes remain below the surface so that as the leaves

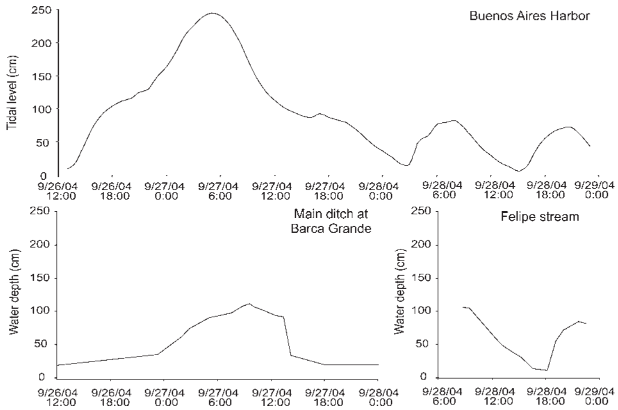

Fig. 2. Tidal level recorded at Buenos Aires Harbor gauge and water depths measured in the main ditch at Barca Grande and the stream at Felipe.

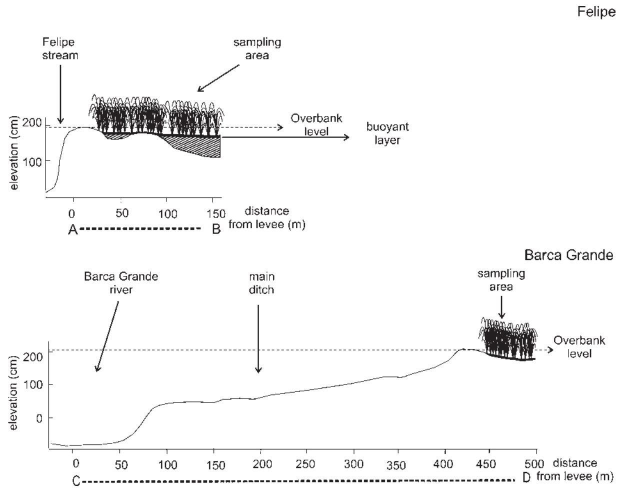

Fig. 3. Topographic profiles at Felipe and Barca Grande along transects A–B and C–D shown in Fig. 1. Elevations correspond to simultaneous records of tidal levels at Buenos Aires Harbor.

grew the threads were carried upward with the growing leaf. On the subsequent sampling date, all ramets present in previously marked quadrats were cut at ground level, 10 new quadrats were established nearby, and new ramets were tagged as before. The collected material was rinsed and each leaf was cut at the level of the thread. The portion below the thread was designated as newly produced leaf tissue, along with any new ramets that appeared inside the quadrat. The stem, involucral leaves, and spikelets were all classified as flowering structures of the flowering ramets. All collected material was dried for 72 h at 60°C and weighed.

Mean leaf production per quadrat and sampling period was estimated as the mean sum of newly produced leaf tissues of each ramet. We estimated mean annual leaf production per unit area and sampling period by adding the means obtained over the entire year. Since the means corresponding to different sampling dates were obtained from different quadrats, they were assumed to be independent measures. Annual variance was calculated as the sum of the variances for each sampling period. The tagging method does not take into account reproductive structures because they develop from nodes located in the rhizome once the ramet emerges above the ground. NAPP of reproductive structures (which accounts for approximately 3%), was estimated as the peak standing biomass per unit area during the year attained by flowering structures. We computed mean total NAPP by adding the mean annual leaf production per unit area to the peak biomass of flowering structures per unit area. Differences in total NAPP between sites were tested using the two-sample Welch's approximate *t* for the two-tailed hypothesis (Zar 1998). Results of peak standing biomass and mineral content in the top 5 cm soil layer were analyzed using one-way analysis of variance (ANOVA) tests to compare means between sites.

Results

Overbank Flow

Patterns of water depths measured both in the main ditch at Barca Grande and Felipe stream tracked tidal levels recorded at Buenos Aires Harbor gauge, but with variable lag times and different magnitudes (Fig. 2). The topographic profile and field observations at Felipe stream indicated that water overtops the levee and flows over the marsh surface when tidal levels exceed 190 cm at the Buenos Aires Harbor gauge (Fig. 3).

Comparisons of field observations at Barca Grande with tidal records indicated that once a threshold of 205 cm is exceeded at Buenos Aires Harbor, water overtops the ditch and spreads over the marsh surface (Fig. 3). During flood tide on September 27, the overland flow on the marsh surface was highly turbid, indicating a high concentration of suspended sediments. During the ebb tide, water initially receded as overland flow and, as the level fell, the flow became increasingly confined to the ditch, and the water turned clear. This suggests that either part of the sediment load was deposited over the marsh surface or a different source of water was involved. Based on field observations, the latter situation is unlikely.

Comparison of tidal records at Buenos Aires Harbor with overbank levels at Felipe and Barca Grande (Fig. 4) shows an irregular pattern at both sites. Islands in the area of Barca Grande are older and levees are about 2 m higher than those at Felipe. The presence of active ditches at Barca

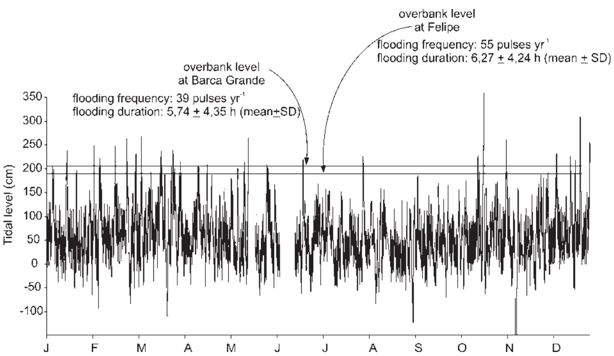

Fig. 4. Comparison of tidal records at Buenos Aires Harbor (year 2002) with overbank levels at Felipe and Barca Grande study sites. Flooding duration is expressed as mean ± standard deviation.

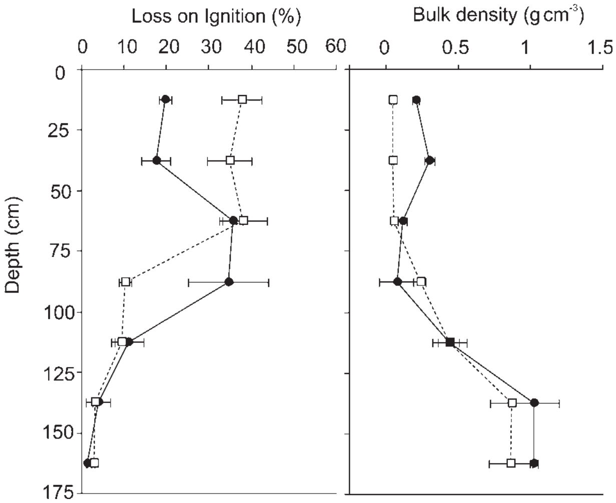

Fig. 5. Soil properties at Felipe (white squares) and Barca Grande (black circles). Values are mean ± standard deviation (n = 5).

Grande compensates by allowing water to reach the interior of the island at a tidal level estimated to be only 15 cm above that at Felipe. During five months of the study, we observed mat movement at Felipe by recording the marsh surface position on a plastic pipe driven into the marsh until it reached firm substrate. We found a maximum range of vertical movement of about 11 cm.

Soil Properties

Both sites had organic-rich soils ranging from 21.06 and 37.72 percent LOI for top layers (Fig. 5) and decreasing to between 1.45 and 2.79 percent LOI in bottom samples where sediments became more compacted and fine sand appeared (Table 1). Otherwise profiles were distinct. Surface samples at Barca Grande had bulk densities about an order of magnitude higher than those of Felipe (Fig. 5). Up to a depth of 75 cm, the Felipe profile consisted mainly of a dense mat of living rhizomes and roots floating in a matrix of water. This feature may have prevented the sampler from filling completely, resulting in underestimations of bulk density. Even so, inorganic content of the litter layer collected from the top 5 cm at Barca Grande was nearly three times that of Felipe (3,289.40 ± 100.81 versus 1,178.79 ± 226.79 g m^{-2}; ANOVA, $p < 0.001$). This is consistent with the field observations of sediment and flow dynamics described above, indicating that the marsh surface at Barca Grande is more prone to sediment deposition.

Organic content at the Barca Grande site peaked at the 50–100 cm depth interval (Fig. 5). These high LOIs can be attributed to a buried organic-rich layer of hemic texture and dark brown color that was visually distinctive (Table 1). This layer appeared consistently in every soil profile in the sampling area, with little variation in thickness and depth. On a subsequent trip to explore the interior of the island, we found firm substrate and the buried organic layer in every soil profile sampled, even as far as 1,200 m from any ditches. The presence of an organic-rich horizon throughout the island suggests an extraordinary event of sediment deposition that buried a thick layer of organic matter.

NAPP Determinations

The mean annual leaf production of *S. giganteus* estimated using the tagging technique was 1,078.21 ± 198.68 g m^{-2} yr^{-1} at Felipe and 1,819.29 ± 244.48 g m^{-2} yr^{-1} at Barca Grande. Peak biomass of flowering structures was 31.60 ± 57.21 g m^{-2} at Felipe and 46.80 ± 84.12 g m^{-2} at Barca Grande. The total annual NAPP was 1,109.81 ± 206.75 g m^{-2} yr^{-1} at Felipe and 1,866.09 ± 258.55 g m^{-2} yr^{-1} at Barca Grande (Fig. 6), and differences were significant (Welch's approximate *t*, $p < 0.001$).

Growth forms of *S. giganteus* also differed between sites. Ramets growing at Barca Grande appeared greener and more robust, while those growing at Felipe were often chlorotic, with dying leaf tips. Even though ramet densities throughout the year were very similar at the two sites (Fig. 6), peak aboveground biomass at Barca Grande was significantly higher than that at Felipe (1,267.20 ± 290.52 versus 709.28 ± 135.51 g m^{-2}, $p < 0.001$). Higher biomass at Barca Grande was not due to a greater density, but rather to a higher rate of leaf production by each ramet. We also observed that a greater proportion of dead leaves remained attached at Felipe while vegetative ramets at Barca

TABLE 1. Texture and Munsell color of soil profiles at Felipe, the floating marsh, and at Barca Grande, the attached marsh. YR = Yellow/Red.

	Texture		Munsell Soil Color	
Depth (cm)	Felipe	Barca Grande	Felipe	Barca Grande
0–25	Fibric with little silt	Silt mixed with organic matter	10 YR 3/2 Very dark grayish brown	10 YR 3/3 Dark brown
25–50	Fibric	Sapric with silt	10 YR 4/2 dark grayish brown	10 YR 2/2 Very dark brown
50–75	Fibric	Sapric, hemic	10 YR 3/2 Very dark grayish brown	10 YR 3/3 Dark brown
75–100	Fibric with silt	Hemic	10 YR 5/1 Gray	10 YR 3/3 Dark brown
100–125	Fibric with silt	Silty, hemic	10 YR 4/1 Dark gray	10 YR 3/1 Very dark gray
125–150	Silt with little fibric to fine sandy silt	Silty	10 YR 5/1 Gray	10 YR 3/1 Very dark gray
150–175	Fine sandy silt	Silty with some fine sand	10 YR 5/1 Gray	10 YR 4/1 Dark gray

Grande rarely had more than one or two dead leaves throughout the year.

Discussion

The higher NAPP of the attached marsh is partially explained by a more effective tidal connection for delivering sediments via overland flow. By comparison, the floating marsh is isolated from tidal inputs by adjusting its surface vertically, avoiding overland flow, as noted in floating marshes elsewhere (Swarzenski et al. 1991). The floating marsh is not rooted in a mineral substrate that could supply a more consistent source of nutrients. Because one marsh was floating and the other was attached, similar water level fluctuations had very different consequences for the vigor and growth of the dominant macrophyte.

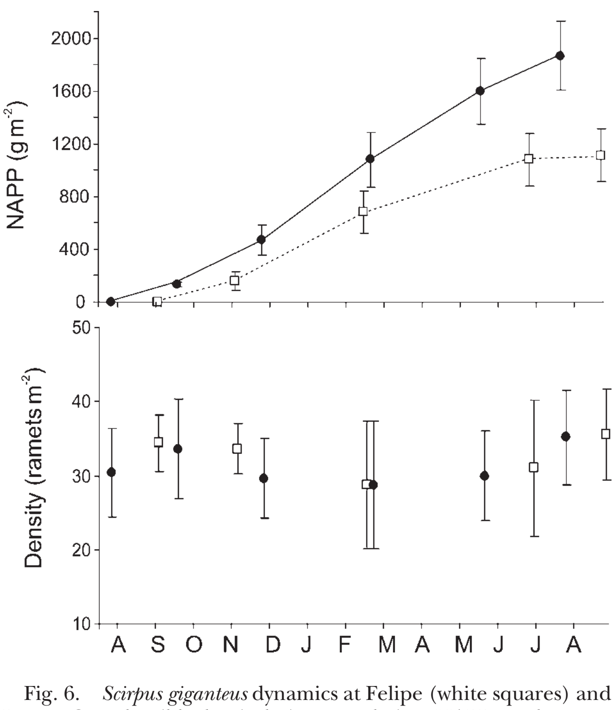

Fig. 6. *Scirpus giganteus* dynamics at Felipe (white squares) and Barca Grande (black circles): cumulative NAPP and ramet density. Values are mean ± standard deviation (n = 10).

NAPP estimates obtained at Felipe of 1,109 g m^{-2} yr^{-1} are much lower than those of 1,960 g m^{-2} yr^{-1} obtained by Sasser and Gosselink (1984) for floating freshwater marshes in Louisiana. Given the different species composition, the more temperate climate, and the methodological disparities, differences are not surprising. In the present work, different sediment regimes appear to influence NAPP. Sasser et al. (1991) argued that nutrients, such as dissolved nitrogen and phosphorus are easily exchanged between the water under mats and the adjacent source of water during overbank flow. In our study, flooding frequency and duration are quite similar between sites, and even slightly higher at Felipe. That would make both marshes comparable in their ability to exchange dissolved elements with the river. It is unlikely that differences in sediment trapping could be attributed to baffling effects of stem densities, as suggested in other tidal marshes (Christiansen et al. 2000), because stem densities were similar at both sites. Differences can be explained by the presence or absence of overland flows to deliver sediments from tidal currents. Supplementary observations support the deposition of sediments at Barca Grande where high total suspended solids (TSS) occurred at the beginning of the marsh inundation by flood tides, followed by a sharp decrease as slack tide approached, and ending with negligible TSS values during the ebb (Pratolongo 2005). In any case, further work on sediment and nutrient delivery, together with porewater salinity and sulfide concentrations, are needed to quantify the magnitude of possible differences between sites.

Studies of floating marshes elsewhere show differences and similarities with the Felipe site. Soil organic content of the floating mat at the Felipe site was only about a third of typical values reported for freshwater floating marshes in Louisiana (64–90%; Sasser et al. 1996; Holm et al. 2000). A plausible explanation for the higher mineral contents in the Lower Delta could relate to its rapidly prograding nature, and the amounts of sediments naturally delivered to the wetlands. Typical values of TSS in the Paraná River range from 49 to 302 mg l^{-1} (Depetris and Paolini 1991), which are not very different from those reported for the lower Mississippi River (Trefrey et al. 1994). The heavily modified Mississippi River Delta has extensive containment levees that impede exchange between the channel and wetlands. Hydrology of the Paraná River delta has not been extensively altered by comparison. Overbank flow is a recurrent and important source of sediment delivery to wetlands in the Lower Delta, delivering sediments not only during tidal events, but also from floods of much longer duration and depth from the Paraná River itself (Framiñan et al. 1999).

Attempts to identify single factors, such as nutrient supply, stressors, or sediments, miss the larger point that similar tidal regimes can lead to different effects depending on ecosystem structure. For the attached marsh at Barca Grande, suspended sediments can easily reach the marsh surface through tidal flows because the surface elevation of the marsh is fixed, allowing overland flow to import suspended sediments. The substrate at Felipe consisted of a buoyant organic layer that floats in a water matrix; mineral content of the soil surface revealed that the marsh at this site was less prone to sediment deposition. The floating marsh site is isolated from sediment inputs even though tides are effective in causing water level fluctuations similar to those of the attached marsh site. Due to the floating property, hydrologic fluctuations and sediment delivery become decoupled in a way that influences primary production of the plant community.

The proportion of floating and attached marshes is not known for the Paraná River delta. Even the islands with floating marshes have portions that are attached around the perimeters near the natural levees. Moreover, active drainage ditches are likely to enhance sediment supply and deposition, increasing the extent of attached marshes at the expense of floating ones.

For islands like Barca Grande, a firm substrate extends throughout the interior marsh, far from the influence of ditches. It is reasonable to assume that attached marshes were once the floating type and have progressively filled in with sediments delivered by tidal flows. The lack of floating marshes toward the delta interior suggests that they have become attached over time as the delta progrades. Whether the transition from floating to attached is the result of progressive sediment infilling from island edges or by some other mechanism is not known. The buried organic-rich layer observed at the Barca Grande site is more consistent with an extreme event in which the marsh was completely buried by a flood of long duration and depth from upstream rather than from tidal flows. As the percent LOI of the buried layer was similar to that of the floating marsh surface at Felipe, it is possible that Barca Grande once supported a floating marsh that became buried by sediment deposition. This burying may have occurred during a combination of high sediment input from the Paraná River and sustained south-southeast winds, which is a common situation during El Niño periods (Framiñan et al. 1999), and might have a greater effect on those islands close to major channels like Barca Grande River. A much broader series of sampling sites would be needed to link El Niño flows with the possibility that floating marshes become attached during such events.

The floating characteristic has implications for other ecosystem properties besides primary production. The endangered and endemic marsh deer, *Blastocerus dichotomus*, is known to avoid deep flooding from extreme tides and high river stages by seeking refuge in floating marshes as reported in local technical reports (D'Alessio et al. 2001, 2002). These studies focused mostly on a single marsh about 1 km^2 in area, located in a very young island about 1,200 m from the delta mouth. Vertical movements of this marsh were greater than 50 cm during a major storm surge (D'Alessio et al. 2006), far larger than the 11 cm range that we observed at Felipe under normal tidal fluctuations.

The pattern and distribution of anchored and floating marshes in this area may be an important variable in the vegetation dynamics of the delta islands. As part of a larger study, Pratolongo (2005) used spectral analysis from remote sensing, coupled with leaf tagging production estimates, to demonstrate differences between the two sites. The same spectral analysis from satellite imagery showed that marsh edges close to levees, as well as sites prone to flooding during El Niño (i.e., sites close to main channels with potential for high sediment supplies), have higher photosynthetic activity (Pratolongo 2005). Further work is needed to explain the connection between lower primary production and floating marshes. The present study is a first step toward providing insight into the potential of high flows during El Niño to deliver sediments, and the role of drainage ditches on the distribution and properties of floating marshes.

Acknowledgments

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