DARWINIANA 46(2): 258-269. 2008 ISSN 0011-6793

NET ABOVEGROUND PRIMARY PRODUCTION AND BIOMASS DYNAMICS OF *SCHOENOPLECTUS CALIFORNICUS* (CYPERACEAE) MARSHES GROWING UNDER DIFFERENT HYDROLOGICAL CONDITIONS

Paula Pratolongo[1,2], Patricia Kandus[3] & Mark M. Brinson[4]

[1]*Instituto Argentino de Oceanografía (CONICET), Florida 8000, 8000 Bahía Blanca, Argentina; paulapra@criba.edu.ar* (autor corresponsal).
[2]*Departamento de Biología, Farmacia y Bioquímica, Universidad Nacional del Sur, Colón 80, 8000 Bahía Blanca, Argentina.*
[3]*Departamento de Ecología Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, 1428 Ciudad Autónoma de Buenos Aires, Argentina.*
[4]*Biology Department, Howell Science Complex, N-108 East Carolina University, Greenville, North Carolina 27858-4353, USA.*

Abstract. Pratolongo, P.; P. Kandus & M. M. Brinson. 2008. Net aboveground primary production and biomass dynamics of *Schoenoplectus californicus* (Cyperaceae) marshes growing under different hydrological conditions. *Darwiniana* 46(2): 258-269.

We studied different functional attributes on two *Schoenoplectus californicus* (C. A. Mey) Sójak marshes that appear as very similar communities in terms of structure and dominant species, although they are settled on opposite ends along a fluvial-tidal gradient in the Lower Delta of the Paraná River. Obtained results showed a significantly higher net aboveground primary production (NAPP) in the marsh directly affected by tides (1999.41 ± 211.97 g m^{-2} $year^{-1}$). In the upstream site, less prone to tidal flooding, *S. californicus* had a lower NAPP (1299.17 ± 179.48 g m^{-2} $year^{-1}$) and the system showed a higher ability to keep the produced biomass within the marsh, with significantly higher amounts of standing dead biomass (1316.00 ± 336.01 vs. 112.40 ± 55.05 g m^{-2}), as well as higher organic contents in soils (16.20 ± 0.12 % vs. 0.70 ± 0.08 %). Results of the present study suggest that high energy overland flows may change the marsh functioning from a stable system accumulating organic matter to an aggressively growing marsh with higher rates of mineral accumulation.

Keywords. Net primary production, Paraná River Delta, *Schoenoplectus*, tidal freshwater wetlands.

Resumen. Pratolongo, P.; P. Kandus & M. M. Brinson. 2008. Productividad primaria neta aérea y dinámica de la biomasa de juncales de *Schoenoplectus californicus* (Cyperaceae) bajo diferentes condiciones hidrológicas. *Darwiniana* 46(2): 258-269.

Se estudiaron diferentes atributos funcionales de 2 pajonales de *Schoenoplectus californicus* (C. A. Mey) Sójak que son muy similares en su estructura y especie dominante, pero aparecen en los extremos opuestos a lo largo de un gradiente de influencia fluvial-mareal en el Bajo Delta del río Paraná. Los resultados mostraron una productividad primaria neta aérea (PPNA) significativamente más alta en el pajonal afectado directamente por la marea (1999.41 ± 211.97 g m^{-2} $año^{-1}$). En el sitio aguas arriba, menos proclive a la inundación por mareas, *S. californicus* tuvo una menor PPNA (1299.17 ± 179.48 g m^{-2} $año^{-1}$) y el sistema mostró una mayor capacidad para retener la biomasa producida dentro del pajonal, con cantidades significativamente mayores de biomasa muerta en pie (1316.00 ± 336.01 vs. 112.40 ± 55.05 g m^{-2}) y mayores contenidos de materia orgánica en el suelo (16.20 ± 0.12 % vs. 0.70 ± 0.08 %). Los resultados obtenidos en este trabajo sugieren que los flujos superficiales de alta energía pueden cambiar el funcionamiento de estos pajonales, de un sistema estable acumulador de materia orgánica a un pajonal de rápido crecimiento, con altas tasas de acumulación de sedimentos minerales.

Palabras clave. Delta del río Paraná, humedales mareales de agua dulce, productividad primaria neta, *Schoenoplectus*.

Original recibido el 18 de marzo de 2008; aceptado el 20 de agosto de 2008

INTRODUCTION

Hydrological characteristics are often considered to be critical variables in the structure and functioning of wetland ecosystem types (Brinson, 1993; Mitsch & Gosselink, 2000). Hydrology controls water chemistry, soil characteristics, deposition of sediments, and nutrient availability (Cronk & Fennessy, 2001) and wetland hydrophytes can even be classified according to their tolerance to saturation and inundation (Tiner, 1999). Perennial species, however, may persist at a site, once established, in spite of changes in hydrologic conditions. For a dominant species to be replaced, physical disturbance (Pickett & White, 1985), increasingly eutrophic conditions, or changes in salinity (Galatowitsch, 1999) may be associated with changes in hydrology.

In Argentina, the progradation of the Paraná River Delta sets up a large sequence of change from sediment bars, continuously depositing at the shoreline, to mature islands located upstream, formed 700-900 years ago (Iriondo & Scota, 1979). As islands develop, deep changes in geomorphologic and hydrological settings of marshes occur. The low elevation of new emergent bars allows relatively unimpeded tidal flow to reach the marsh surface. In contrast, mature islands develop an elevated levee surrounding the interior marsh, which get largely isolated from tidal inputs.

In this sequence, *Schoenoplectus californicus* (C. A. Mey.) Sójak ("California bulrush") forms monospecific marshes at both ends of the gradient. In new islands, *S. californicus* is the only colonizer of bare sediments, and the same species forms monospecific marshes on the inner lowlands of mature islands, located as far as 70 km upstream from the delta shoreline. In the newly emergent marshes, tidal inundation follows a regular semidiurnal pattern. In contrast, mature marshes upstream undergo periods of drawdown of the water table, with less frequent episodes of flooding from tides, but long periods of flooding from the Paraná River, which may be persistent for several months under extreme climatic conditions, as those observed during "El Niño" periods (Kandus, 1997).

One indicator of a species range of tolerance is its response to different hydrologic conditions. Species that have wide ranges of distribution across environmental gradients may be among the ones best adapted to take advantage of disturbances and changes in state, favouring invasions where hydrological shifts occur (Newman et al., 1996; Kercher & Zedler, 2004). *Schoenoplectus californicus* is indigenous to coastal regions of the southern North America (Mason, 1957), south to Chile and Argentina (Wagner et al., 1990). In Australia, *S. californicus* is considered as a potential environmental weed species, which was first found in 1995 (Csurhes & Edwards, 1998), and in the early 1990's specimens of this species were also collected in New Zealand (Lange et al., 1998). Given the very different hydrological settings under which *S. californicus* marshes develop, we followed net aboveground primary production (NAPP) and net biomass accumulation to compare the species response and the marsh functions in a newly emergent and a mature island in the Paraná Delta.

METHODS

Study area

The Paraná River basin is a 2.6 x 10^6 km^2 fluvial system with a mean annual discharge of 17.0 x 103 m^3 s^{-1} and an annual sediment load of more than 150 x 10^6 Mg (Orfeo & Stevaux, 2002). Located at the mouth of this basin, the Paraná Delta is a 2.700 km^2 freshwater tidal system, which is aggrading into Rio de la Plata Estuary at an estimated rate of 70 m $year^{-1}$ through development of bars that lead to the establishment of new islands (Iriondo & Scotta, 1979; Parker & Marcolini, 1992).

In the frontal zone of the delta, semidiurnal tides from the Río de la Plata Estuary are typically about 1 m amplitude (Vieira & Lanfredi, 1996). However, high tides greater than 4 m (Piccolo & Perillo, 1999) have been reported during sudestadas (southeasters). Upstream, the Paraná River seasonally raises its level and occasionally floods lowlands in mature islands, but extraordinary floods occur during "El Niño" at grater intervals. "El Niño" phenomenon has been shown to have a significant effect on flow patterns and sediment accumulation on islands towards the upstream portion of the delta (Karszenbaum et al., 1999). However, flooding patterns downstream seem to be little affected by the increase in Paraná River discharge (Kandus & Malvarez, 2004).

Schoenoplectus californicus is a perennial reed, with culms developing at nodes located on creeping rhizomes and with leaves reduced to bladeless sheaths at the base of culms. *Schoenoplectus californicus* marshes are the most widespread natural community upstream, covering extended areas in the inner lowlands of mature islands. In the frontal zone, these communities settle on narrow strips a few hundred meters. In the latter case, *S. californicus* colonizes emergent bars of bare sediments, and the establishment of these monospecific marshes sets the environmental condition for further development of islands and species replacement (Kandus & Malvárez, 2004).

Selected sites were "Bajos del Temor" and "Los Milagros" and located, respectively, in a recently deposited bar in the frontal zone, and in the inner lowland of a mature island upstream (Fig. 1). In both cases, study sites were established in nearly monospecific stands of *S. californicus*, with a few associated species present in very low abundances.

Hydrological settings

In order to asses the hydrological parameters at both study sites, for the specific time frame considered for field work, we used water levels registered at Paraná de las Palmas River station, near Zárate city, and Río de la Plata station, near Buenos Aires city (Fig. 1), during the years 2002 and 2003 (Dirección Nacional de Construcciones Portuarias y Vías Navegables). We used both mean hourly levels and mean monthly levels to describe daily and seasonal variations respectively at both sites. As additional information, we also used mean monthly levels during the years 1982 and 1983, coincident with a Paraná River extraordinary flooding, associated with "El Niño" (Schnack, 2002). We determined overbank levels at both sites using a time series of Landsat ETM+ satellite images, acquired over the same time period, by relating water level at the corresponding station at the acquisition time of those scenes showing standing water over the study sites.

NAPP and standing biomass

Field measures were made nearly bimonthly at both sites between July 2002 and August 2003, with higher sampling frequencies (nearly monthly) during the growing season. NAPP estimates were obtained using a technique that combines tagging and harvesting of individual culms (Pratolongo et al., 2005). The tagging technique used here has been initially developed for estimating NAPP of *Scirpus giganteus* in the same area (Pratolongo et al., 2005) but further works demonstrated that the technique is widely applicable to other wetland plants, including *S. californicus* (Pratolongo, 2005; Pratolongo & Kandus, 2005).

On the first sampling date, we established 10 quadrats on each site in monospecific stands of S. californicus. All live culms in each quadrat (50 x 50 cm) were tagged by piercing them at the ground level with a steel needle followed by polyester thread. In this species, nodes remain below the surface so, as each culm grows the thread rises above the substrate. On subsequent sampling dates, all culms present in previously marked quadrats were cut at ground level, 10 new quadrats were established, and new plants were tagged. The collected material was rinsed and each culm was cut at the level of the thread. The portion below the thread was classified as newly produced tissue, as well as any new plant that appeared inside the quadrat. In order to assess the aboveground standing biomass dynamics, the remaining green and dead biomass were also separated, and in flowering culms, we classified the spikelets as flowering structures. Classified material was oven dried for 72 h at 60 ºC and weighed.

Mean biomass production per quadrat and sampling period was estimated as the mean sum of newly produced tissues of every stem in each quadrat. Mean annual production per unit area was calculated by adding the means obtained on every sampling period over the entire year. Since the means corresponding to different sampling dates were obtained from different quadrats, they were assumed to be independent measures, and then the annual variance was calculated as the sum of the variances for each sampling period. We tested differences in total NAPP between sites using the two-sample Welch's approximate t for the two-tailed hypothesis (Zar, 1998). We also evaluated dif-

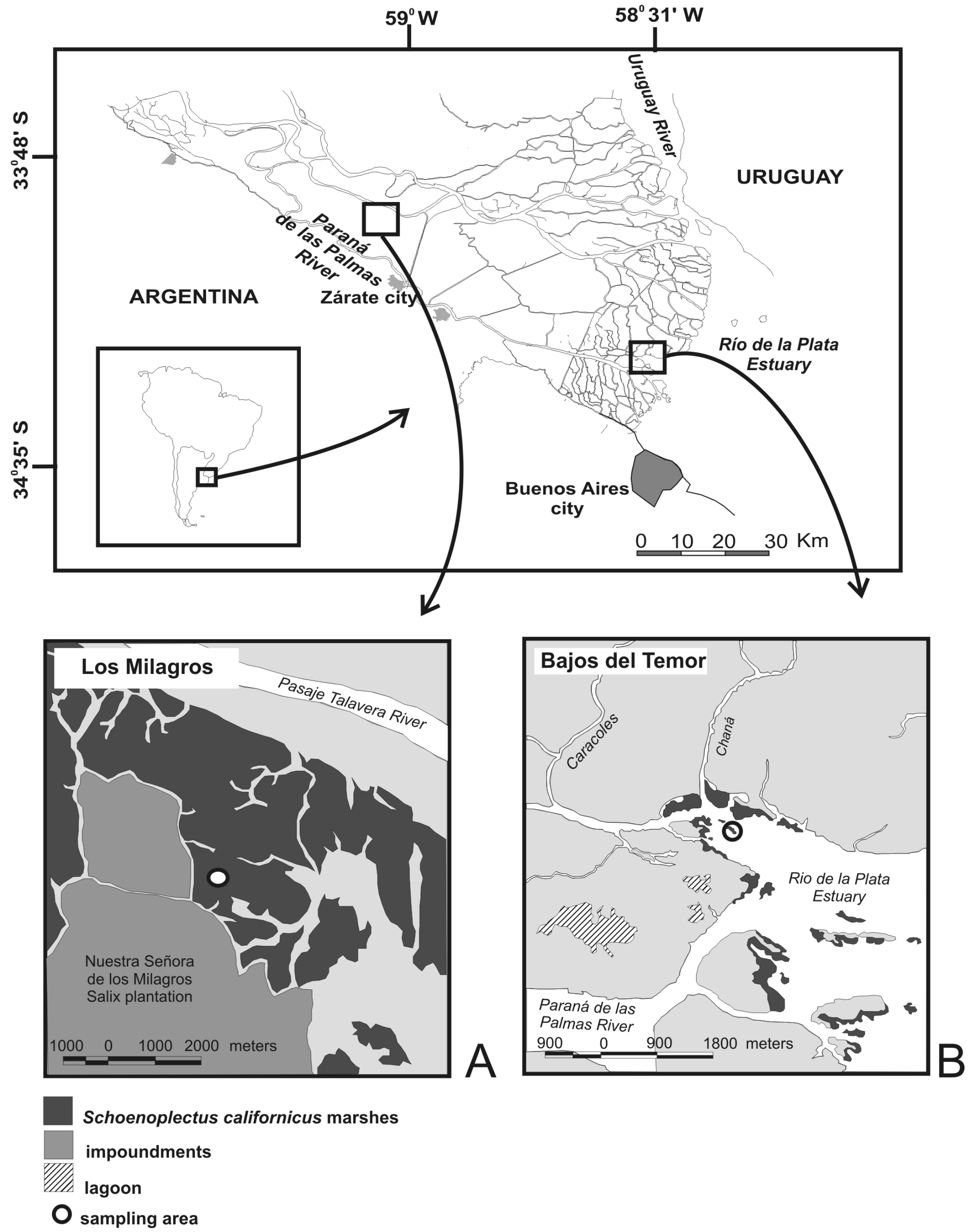


Fig. 1. Location of the study sites in the Lower Delta of the Paraná River, Argentina. **A,** "Los Milagros". **B,** "Bajos del Temor"

ferences between sites in the maximum values obtained for aboveground live, standing dead, and flowering structures biomass through Kruskal-Wallis (non-parametric ANOVA) tests.

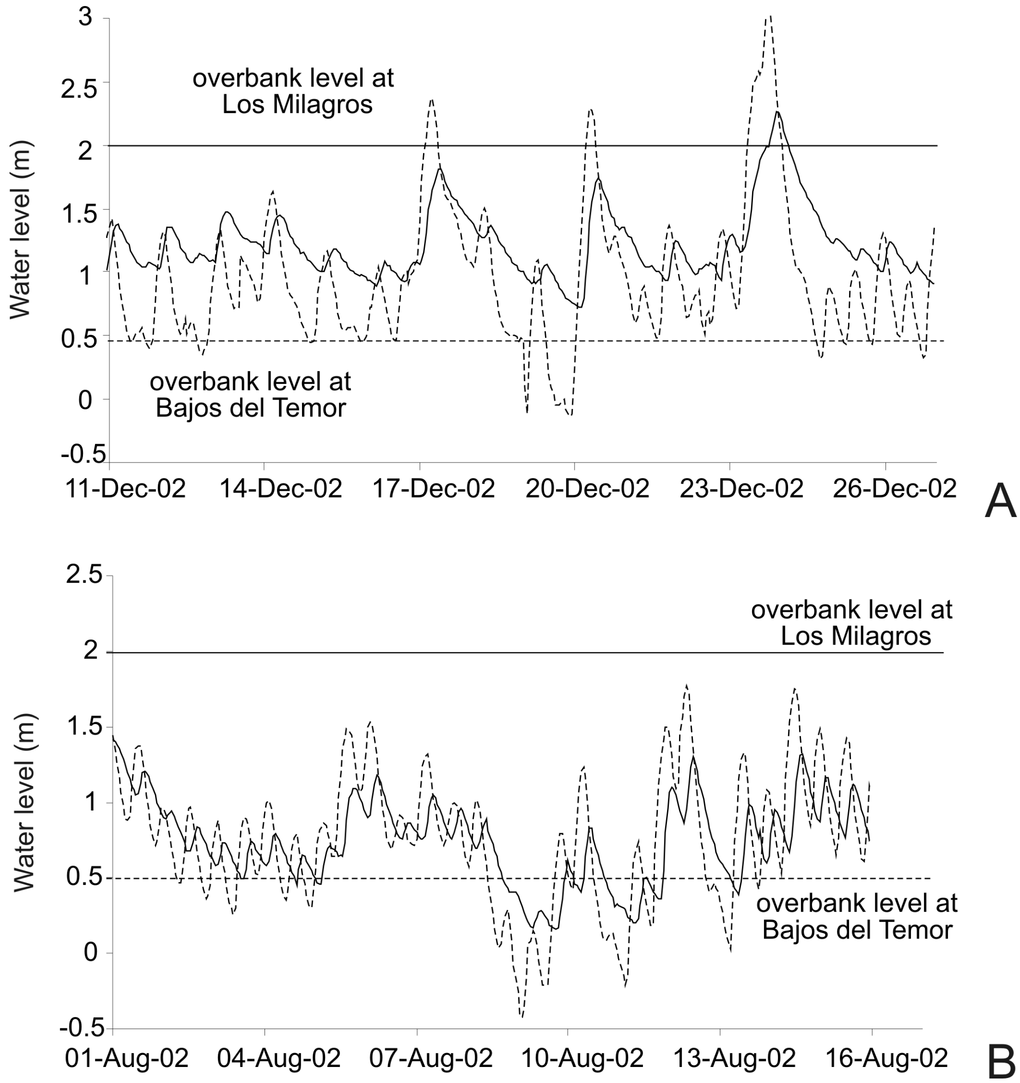
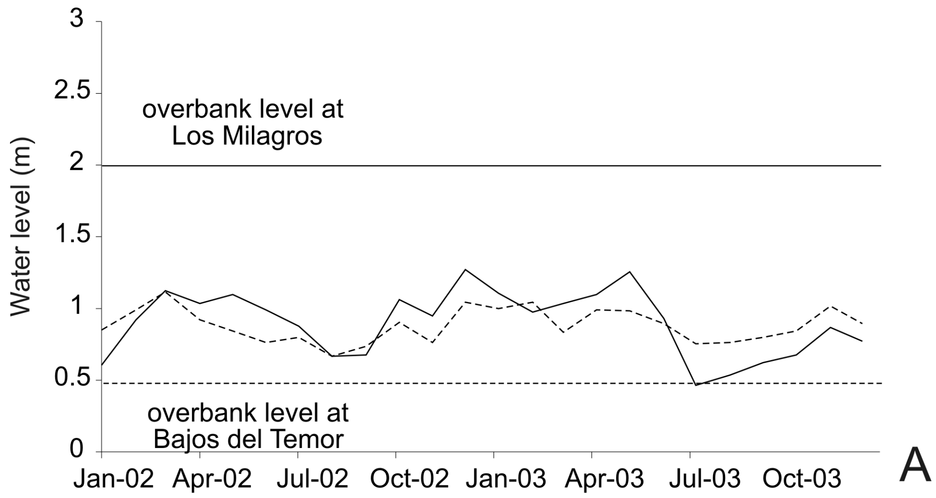


Fig. 2. Mean hourly hydrometric levels registered in Paraná de las Palmas River (——) and Buenos Aires Harbor (----) for a period of **A,** relatively high and **B,** relatively low river discharge. Overbank levels at "Los Milagros" (——) and "Bajos del Temor" (----) are also indicated. Note the damping of tidal amplitudes and the lower occurrence of tidal flooding at "Los Milagros".

Soil sampling and biomass decay

Soil sampling in both sites was performed during December 2002 using a McCauley peat sampler. In the surroundings of the area considered for NAPP determination, a soil sampling area of about 100 m2 was established and 5 soil profiles were built from 25 cm deep and 4 cm diameter sections, centered at increasing depths. The maximum depth was determined by the McCauley sampler characteristics, which preclude taking samples on predominantly mineral soils. At "Los Milagros" the high organic content allowed the use of the McCauley sampler up to 75 cm depth (3 sections). At "Bajos del Temor", however, just one section (25 cm depth) could be taken on each profile. Samples were stored in hermetic plastic bags at 4°C. Back at the laboratory, samples were oven



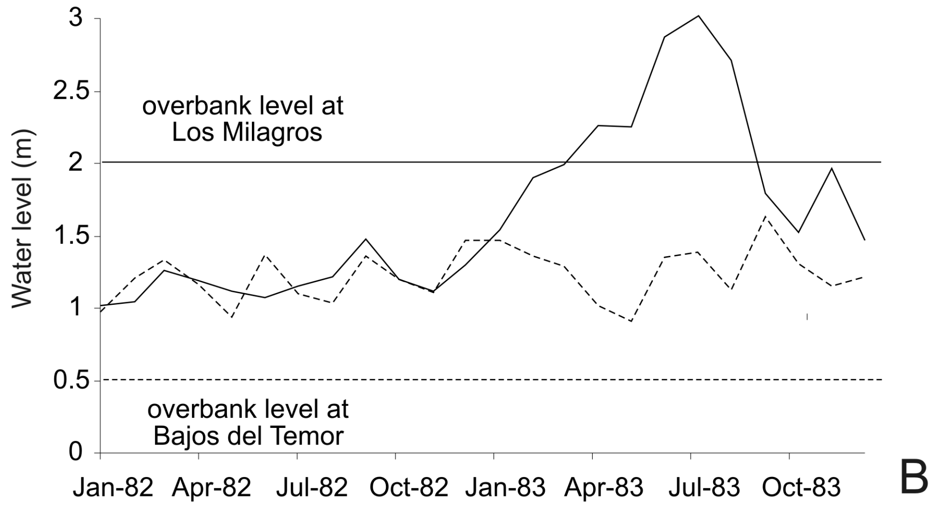


Fig. 3. Mean monthly hydrometric levels registered in Paraná de las Palmas River (—) and Buenos Aires Harbor (----) for **A,** years 2002-2003 (normal levels) and **B,** years1982-1983 (during "El Niño" flooding). Overbank levels at "Los Milagros" (—) and "Bajos del Temor" (----) are also indicated.

dried (80°C, to constant weight) and organic matter as percent Lost On Ignition (LOI) was determined as the ratio of weight loss (500°C, 3 h) compared to the dry weight.

The annual decay rate was assessed only at "Los Milagros". In outlet bars of the frontal zone, the strong daily influence of high energy tidal flows preclude deposition of detritus over the sediment surface. In these high energy environments, dead biomass is promptly exported from the system, in such a way that the decomposition process cannot take place over the marsh surface. To determine decay rate of *S. californicus* biomass at "Los Milagros", 30 litter bags were constructed from *S. californicus* dead biomass, previously oven dried for 72 h at 60 ºC and weighed, and were placed on the marsh surface. The first 5 bags were withdrawn immediately after placing them in the field, in order to determine the amount of material lost by handling. Remaining bags were

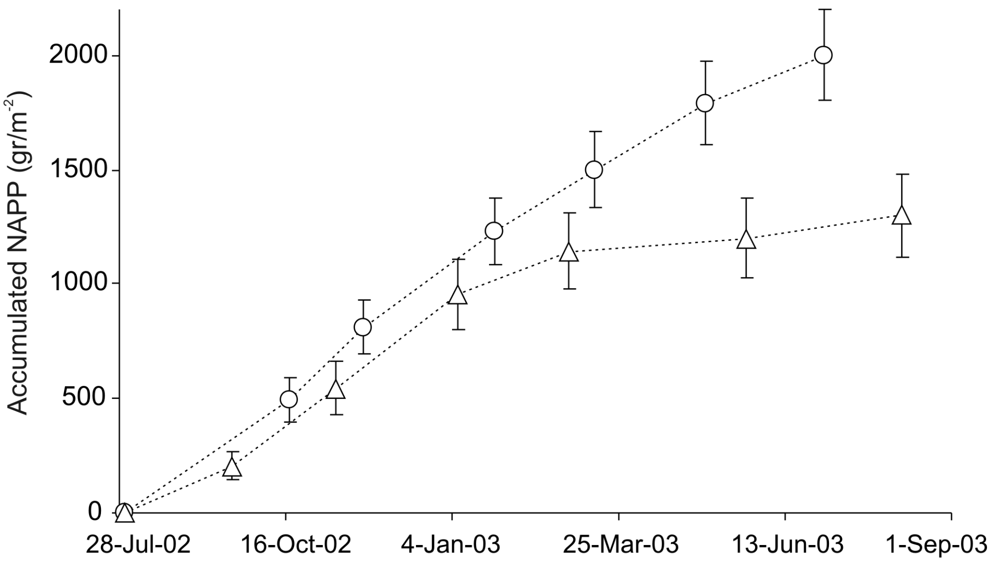


Fig.4. Accumulated values of NAPP (g m^{-2}) for *S. californicus* growing at the upstream site "Los Milagros" (Δ) and the tidal site "Bajos del Temor" (O). Values are mean ± std. error.

withdrawn at 20, 80, 192, 305, and 396 days after deployment. The material retrieved from bags was gently rinsed, and any observable macroinvertebrates and living roots growing inside the bags were removed. The remaining biomass was then oven dried and weighed. Finally, mass loss from each litter bag was estimated as the change in dry mass plus the estimated mean mass lost by handling, and we fitted the percent remaining biomass through time to an exponential function.

RESULTS

Hydrological settings

Mean hourly hydrometric levels registered in Paraná de las Palmas River and Buenos Aires Harbour are shown in Fig. 2. Graphs compare hydrological behaviour in both stations for a period of relatively high and relatively low discharge of the Paraná River (Figs. 2A and 2B, respectively) and they clearly show that semidiurnal tidal oscillations, although delayed and damped still affect water levels upstream, even during high discharge periods. However, if we observe the site specific hydrological traits, the overbank level at "Los Milagros" indicates that, although tidal oscillations are conspicuous in the river, overland flows trough the marsh surface only occur during extraordinary high tides. Considering the hydrological series for years 2002-2003, only on 13 dates was water level in the Paraná de las Palmas River high enough to exceed overbank threshold, and to allow overland flow at "Los Milagros". At "Bajos del Temor", in contrast, the lower elevation allowed marsh inundation and superficial flows at least once a day. Mean monthly levels for years 2002-2003 show that, even though there is a very slight trend to the occurrence of higher values in fall (March to June) for Paraná de las Palmas records, there is not a clear seasonal pattern neither upstream nor at Río de la Plata station (Fig. 3A). However, monthly levels during "El Niño" events show extremely different responses in both sites (Fig. 3B). During years 1982-1983, mean water levels at Río de la Plata suggested that the frontal zone of the Lower Delta was little influenced by the extraordinary flooding of the Paraná River. Upstream records, on the other hand, showed that "Los Milagros" marsh must have been dramatically affected, since mean water levels were persistently above overbank threshold for more than 6 months.

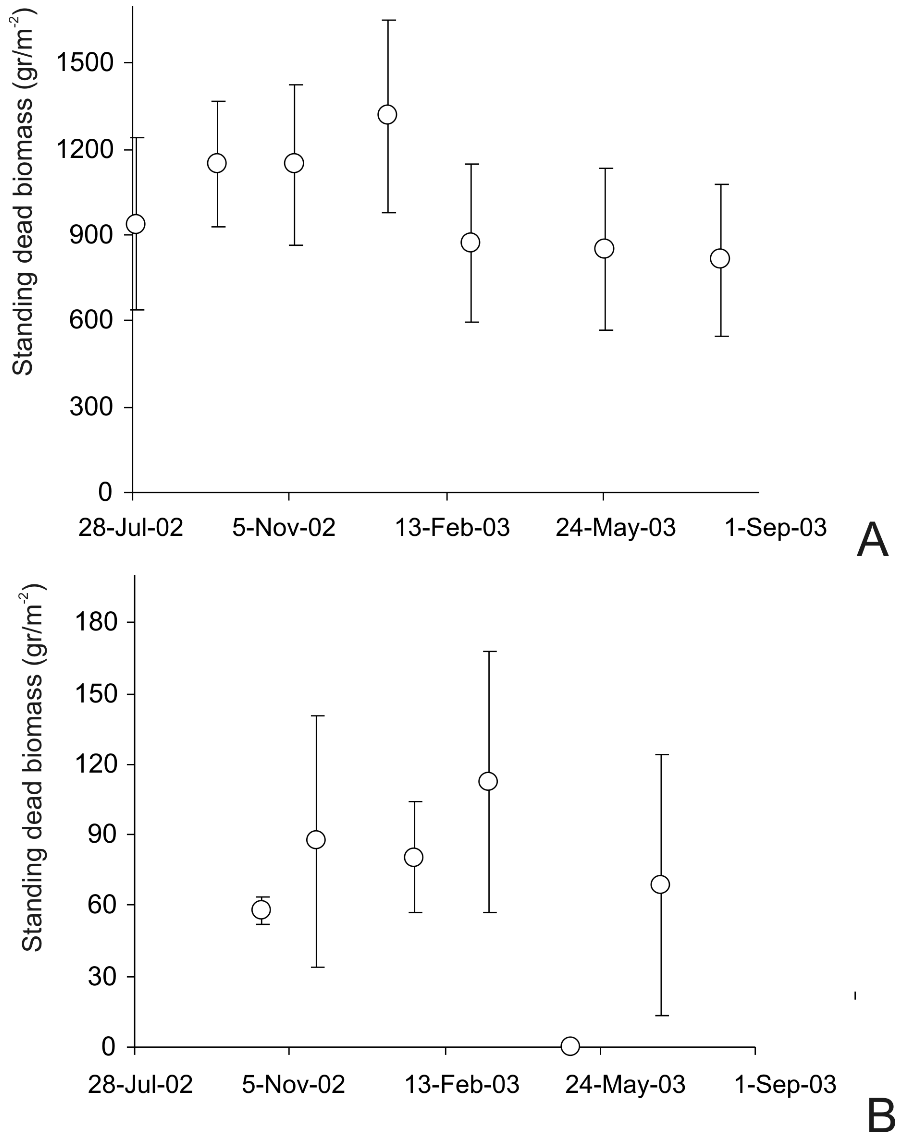


Fig. 5. Standing dead biomass (g m^{-2}) of *S. californicus* at **A,** the upstream site "Los Milagros" and **B,** the tidal site "Bajos del Temor". Values are mean ± std. error. Note that scales were changed to allow visualization.

NAPP and standing biomass

Net aboveground primary production (NAPP) of *S. californicus* estimated at "Bajos del Temor" was significantly higher than the value obtained at "Los Milagros" (1999.41 ± 211.97 and 1299.17 ± 179.48 g m^{-2} $year^{-1}$, t =7.8, respectively, gl=7, p<0.01). Accumulated values of NAPP (Fig. 4) show a higher slope between September and January at "Los Milagros" indicating that, even though growth occurred during the whole year, daily increments in biomass were higher during spring and early summer, and growth rate was slower during the rest of the year. The growth rate at "Bajos del Temor" was high and steady through the year, leading to higher values of total biomass

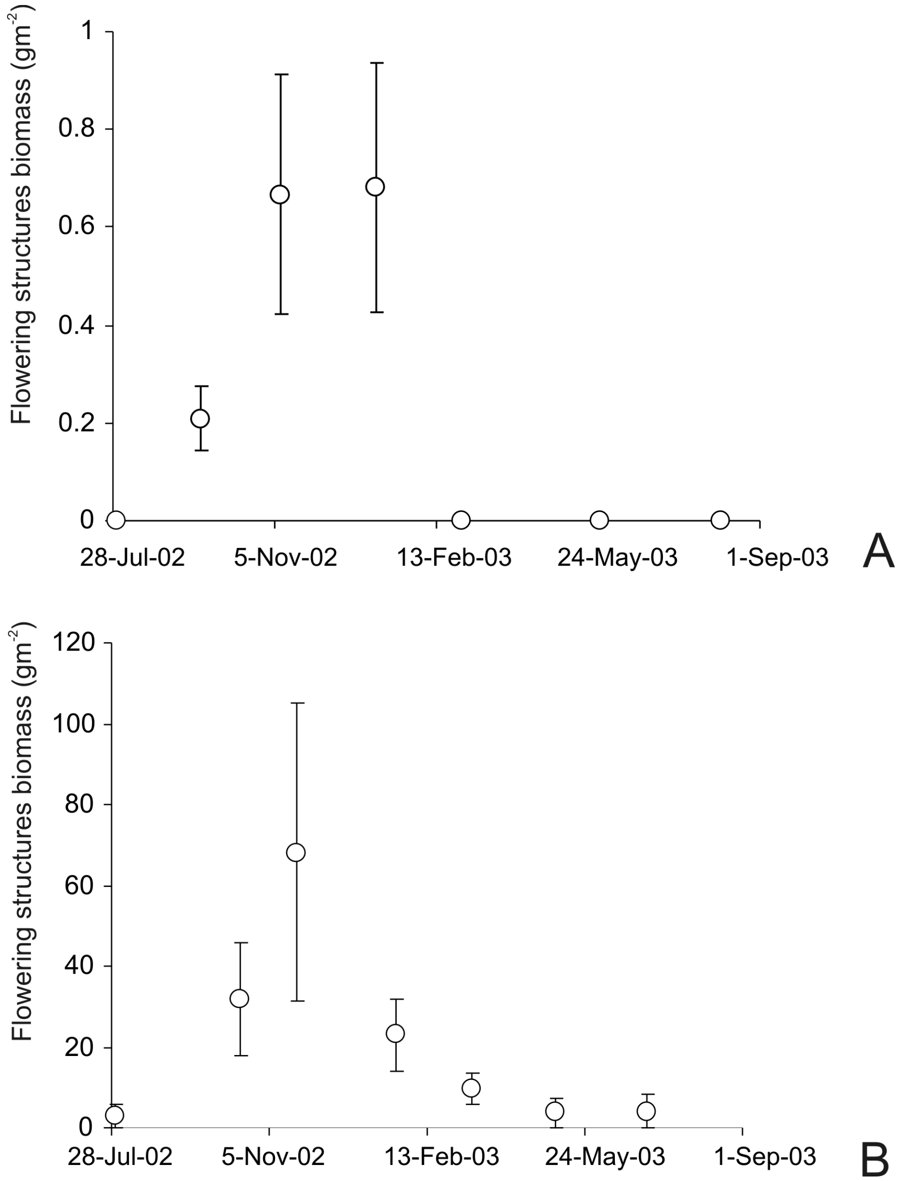


Fig. 6. Biomass of flowering structures (g m^{-2}) of *S. californicus* at the upstream site **A,** "Los Milagros" and the tidal site **B,** "Bajos del Temor". Values are mean + std. error. Note that scales were changed to allow visualization.

production. Besides the higher values of NAPP at "Bajos del Temor", the maximum registered value for standing live biomass (used as a proxy for peak standing biomass) was significantly lower in this site (661.80 ± 195.62 and 1009.91 ± 265.64 g m^{-2}, respectively, Kruskal-Wallis H=6.64, n=20, p<0.01), indicating a higher turnover rate.

The maximum standing dead biomass was an order of magnitude higher at "Los Milagros" (112.40 ± 55.05 and 1316.00 ± 336.01 g m^{-2}, respectively, Kruskal-Wallis H=12.64, n=20, p<0.01). Standing dead biomass at this site showed little differences through the year, but was slightly higher at the end of the period of maximum growth (early summer). At "Bajos del Temor", standing dead biomass did not show any seasonal pattern (Fig. 5), and dead biomass did not appear at all in samples collected on May (fall).

At "Los Milagros", spikelets begun to appear in September (early spring) and the maximum biomass of flowering structures (0.68 ± 0.25 g m^{-2}) was attained in January (early summer), after that, all flowering structures fell off. By blossoming time, less than 10 % of the living culms developed spikelets. At "Bajos del Temor", in contrast, spikelets were harvested in every sampling date through the year and the maximum biomass of flowering structures was 68.04 ± 36.89 g m^{-2} (Fig. 6), an order of magnitude higher than the peak attained at "Los Milagros" (Kruskal-Wallis H=12.76, n=20, $p<0.01$), and 100% of the harvested culms showed spikelets.

Soil properties and biomass decay

Soil organic contents were 16.20 ± 0.12 % and 0.70 ± 0.08 % at "Los Milagros" and "Bajos del Temor", respectively, and field observations indicated a persistent presence of a 10 cm thick layer of litter at "Los Milagros", while organic detritus were never observed on the marsh surface at "Bajos del Temor". Moreover, soils at "Los Milagros" showed organic contents higher than 1 % up to a depth of 75 cm, and traces of sand appeared only at depths higher than 50 cm. At "Bajos del Temor", in contrast, soils have lower organic contents and presence of sand in the surface.

Biomass loss from litter bags at "Los Milagros" was relatively fast during the first 2 months, but the overall decay constant was fairly low (0.0017 $days^{-1}$, R^2=0.97), with 52.80 ± 5.09% of initial dry weight remaining by the end of the sampling year. Considering results obtained in the previous section, NAPP of *S. californicus* incorporated a mean amount of 1299.17 g m^{-2} of biomass to the system. Taking the mean amounts of standing dead biomass at the beginning and the end of the sampling (937.00 and 811.20 g m^{-2}, respectively) an estimated mean amount of 1424.97 g m^{-2} of litter collapsed to the marsh surface through the year. Applying the obtained decay rate, and in the absence of any removal processes, 752.38 g m^{-2} of non-decomposed litter would still remain on the surface at the end of the sampling period.

DISCUSSION

There is a large amount of published work, especially in salt marshes, on the factors limiting wetland plants production. In *Spartina alterniflora*, Turner (1976) has earlier demonstrated that primary production is mainly limited, on a regional scale, by climate and by the length of the growing season. Beyond latitudinal differences, tidal amplitude is considered a major factor controlling plant growth (Mitsch and Gosselink, 2000). Under the "tidal subsidy" hypothesis (Odum et al., 1979), tides may enhance marsh growth by flushing salts and bringing nutrients into salt marshes. In tidal freshwater marshes, however, where salt stress is not important, the role of tidal flushing has not been as intensively studied.

In studies performed by different authors, and on different locations both phenology and aboveground biomass dynamics of *S. californicus* showed a wide range of variations. Reported values for maximum amount of standing live biomass can vary from less than 700 g m^{-2} in one of our study sites to more than 5 kg m^{-2} under high nutrient conditions in constructed wetlands (Lange et al., 1998). In some locations, growth did not show any seasonal pattern (Lange et al., 1998) but partial diebacks in winter and constricted flowering and fruiting seasons were described in other areas (Ramirez & Anazco, 1982; Pastore, 1991). Besides differences throughout the wide geographical extent of this species, results obtained in this work indicate that *S. californicus* marshes established at both edges within a fluvial-tidal gradient in the Paraná River delta showed significant differences in key aspects of the ecosystems functioning, expressed as biomass production and storage, and the differences were closely related to inundation period and frequency. At the tidal end, marshes in new islands showed higher growth rates and flowering, but lower organic matter accumulation. At the fluvial edge, *S. californicus* marshes occupy a lower energy environment in the protected inner lowlands of islands. At these sites, less productive marshes develop on largely organic soils.

In terms of ecosystem functioning, Odum et al. (1983) stated that water flows are energy inputs into a wetland, and may act as an energy stress, as well as a subsidy. In this case, similar to what those authors found when comparing *Zizaniopsis* *miliacea* in tidal and impounded marshes, under the more dynamic conditions at the open tidal site marshes a greater net primary production and a lower organic matter accumulation were shown. In that case, water flow was proposed to be acting as an energy subsidy by performing mechanical work such as removing dead matter and toxins and recycling or importing oxygen and nutrients.

Observing the species performance, the higher production and flowering at "Bajos del Temor" may suggest that *S. californicus* would have a niche that is more directed to the dynamic conditions. Under this assumption, conditions at "Los Milagros" would be far from optimal, and it could be expected that *S. californicus* would be soon overgrown by another species from the succession scheme. However, even after large scale fires and the massive floods during "El Niño" periods (Karszenbaum et al., 2003) the large areas covered by monotypic stands of *S. californicus* were observed to recover the original structure in a few years, suggesting that these marshes constitute a fairly steady state in terms of permanence and resilience.

Under the more favorable and highly dynamic conditions in the frontal zone, marshes cause deep changes in topography through suspended sediment trapping and mineral accumulation. Colonization of bare sediments triggers a sequence of state changes in which *S. californicus* is replaced by different plant communities, and leads to the formation of mature islands in the frontal zone, where the species is almost completely displaced (Kandus and Malvárez, 2004). Whether the large marshes of *S. californicus* dominating the landscape upstream are relicts of the pioneer marshes colonizing the area 800 years ago, at the beginnings of the delta progradation, and why they haven't been replaced is an open question that remains still unresolved.

ACKNOWLEDGMENTS

This research was supported by UNESCO-MAB under a MAB Young Scientists Award and by ANPCyT under project PICT 4503, "Relaciones entre la heterogeneidad ambiental y las comunidades naturales en la porción inferior del Delta del Río Paraná". Partial support was provided by a Buenos Aires University Fellowship. We especially thank Dr. James Perry and an anonymous reviewer for their helpful comments that greatly improved the manuscript. We also thank Julieta Bono, Mariela Biondini, Mariana Burghi, and Santiago Arias for help with fieldwork and sample processing.

REFERENCES

Brinson, M. M. 1993. Changes in the functioning of wetlands along environmental gradients. *Wetlands* (Wilmington) 13: 65-74.

Cronk, J. K. & M. S. Fennesy. 2001. *Wetland Plants: Biology and Ecology*. Boca Raton: CRC Press LLC.

Csurhes, S & R. Edwards. 1998. *Potential Environmental Weeds in Australia. Candidate Species for preventative control*. Canberra: Queensland Department of Natural Resources.

Galatowitsch, S. M.; N. O. Anderson & P. D. Ascher. 1999. Invasiveness in wetland plants in temperate North America. *Wetlands* (Wilmington) 19: 733-755.

Iriondo, M. & E. Scotta. 1979. The evolution of the Paraná River Delta. *Proceedings of the 1978 International Symposium on Coastal Evolution in the Quaternary*, fecha, Sao Paulo: pp?.

Kandus, P. & A. I. Malvárez. 2004. Vegetation patterns and change analysis in the Lower Delta islands of the Paraná River (Argentina). *Wetlands* (Wilmington) 24: 620-32.

Kandus, P. 1997. *Análisis de patrones de vegetación a escala regional en el Bajo Delta bonaerense del río Paraná (Argentina)*. Tesis doctoral, Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales.

Karszenbaum, H.; P. Kandus; G. Parmuchi & J. Bava. 1999. Evaluation of the effects of El Niño '98 in the Lower Delta of Paraná River using RADARSAT images and GIS. *Proceedings of the "Simposio Final GlobeSAR2 Aplicaciones de RADARSAT en América Latina*", mes-año, Buenos Aires: 17-20.

Karszenbaum, H.; J. Tiffenberg; F. Grings; J. M. Martinez; P. Kandus & P. Pratolongo. 2003. A SAR time series analysis toolbox for extracting fire affected areas in wetlands. *IEEE International Proceedings*, mes-año, lugar: 4107-4109.

Kercher, S. M. & J. B. Zedler. 2004. Flood tolerance in wetland angiosperms: a comparison of invasive and noninvasive species. *Aquatic Bot.* 80: 89-102.

Lange, P. J.; R. O. Gardner, P. D. Champion & C. C. Tanner. 1998. *Schoenoplectus californicus* (Cyperaceae) in New Zealand. *New Zealand J. Bot.* 36: 319-27.

Mitsch, W. J. & J. G. Gosselink . 2000. *Wetlands*, 3rd. ed. New York: John Willey & Sons.

Newman, S.; J. B. Grace & J. W. Koebel. 1996. Effects of nutrients and hydroperiod on Typha, Cladium and Eleocharis: implications for everglades restoration. *Ecol. Appl.* 6: 774-783.

Odum, E. P.; J. T. Finn & E. H. Franz. 1979. Perturbation theory and the subsidy-stress gradient. *Bioscience* 29:349-352.

Odum, E. P.; J. B. Birch & J. L. Cooley. 1983. Comparison of Giant Cutgrass Productivity in Tidal and Impounded Marshes with Special Reference to Tidal Subsidy and Waste Assimilation. *Estuaries*. 6: 88-94.

Orfeo, O. & J. Stevaux . 2002. Hydraulic and morphological characteristics of middle and upper reaches of the Paraná River (Argentina and Brazil). *Geomorphology* 44: 309-22.

Parker, G. & S. Marcolini. 1992. Geomorfología del Delta del Paraná y su extensión hacia el Río de la Plata. *Revista Asoc. Geol. Argent.* 47: 243-49.

Pastore, P. M. 1991. Productvidad aérea y subterránea de *Schoenoplectus californicus* en dos arroyos de la Provincia de Buenos Aires. *Biol. Acuática* 15: 154-5.

Piccolo, M. C. & G. M. E. Perillo . 1999. Estuaries of Argentina: a review, in G. M. E. Perillo, M. C. Piccolo & M. Pino Quivira (eds.), *Estuaries of South America: their geomorphology and dynamics*, pp. XXX-XXX. Berlín: Springer.

Pickett S. T. A. & P. S. White. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. New York: Academic Press.

Pratolongo, P. & P. Kandus. 2005. Dinámica de la biomasa aérea en pajonales de *Scirpus giganteus* y juncales de *Schoenoplectus californicus* en la zona frontal del Bajo Delta del río Paraná (Argentina). *Ecotrópicos* 18: 30-37.

Pratolongo, P.; R. Vicari; P. Kandus & A. I. Malvárez. 2005. A new method for evaluating net aboveground primary production (NAPP) of *Scirpus giganteus* (Kunth). *Wetlands* (Wilmington) 25: 228-32.

Pratolongo, P. 2005. *Dinámica de comunidades herbáceas del Bajo Delta del Río Paraná sujetas a diferentes regimenes hidrológicos y su monitoreo mediante sensores remotos*. Tesis doctoral. Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales.

Ramirez, C. G. & R. Anazco. 1982. Seasonal variations in the development of *Scirpus californicus*, *Typha angustifolia* and *Phragmites communis* in Valdivian swamps, Chile. *Agro Sur* 10: 111-23.

Schnack, E. J. 2002. *Contribuciones del Taller "El Niño: sus impactos en el Plata y en la región pampeana"*. La Plata: CIC-ABC-Facultad de Ciencias Naturales y Museo de la Universidad Nacional de La Plata.

Tiner, R. W.1999. *Wetland indicators: a guide to wetland identification, delineation, classification and mapping*. Boca Raton: CRC Press.

Turner, R. 1976. Geographic variations in salt marsh macrophyte production: a review. Contr. *Mar. Sci.* 20: 47-68.

Vieira, J. R. & N. W. Lanfredi. 1996. A hydrodynamic model for the Río de la Plata, Argentina. *J. Coastal Res.* 12: 430-446.

Wagner, W. L.; D. R. Herbst & S. H. Sohmer. 1990. *Manual of the flowering plants of Hawaii*. Vol 2 . Bishop Museum special publication 83. Honolulu: University of Hawaii and Bishop Museum Press.

Zar, J. H. 1998. *Biostatistical Analysis*. Englewood Cliffs: Prentice-Hall Inc.