Estuaries Vol. 25, No. 3, p. 309–324 June 2002

# Net Primary Production and Decomposition of Salt Marshes of the Ebre Delta (Catalonia, Spain)

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**ABSTRACT: Net primary production was measured in three characteristic salt marshes of the Ebre delta: an *Arthrocnemum macrostachyum* salt marsh, *A. macrostachyum-Sarcocornia fruticosa* mixed salt marsh and *S. fruticosa* salt marsh. Aboveground and belowground biomass were harvested every 3 mo for 1 yr. Surface litter was also collected from each plot. Aboveground biomass was estimated from an indirect non-destructive method based on the relationship between standing biomass and height of the vegetation. Decomposition of aboveground and belowground components was studied by the disappearance of plant material from litter bags in the *S. fruticosa* plot. Net primary production (aboveground and belowground) was calculated using the Smalley method. Standing biomass, litter, and primary production increased as soil salinity decreased. The annual average total aboveground plus belowground biomass was 872 g m$^{-2}$ in the *A. macrostachyum* marsh, 1,198 g m$^{-2}$ in the *A. macrostachyum-S. fruticosa* mixed marsh, and 3,766 g m$^{-2}$ in the *S. fruticosa* marsh. The aboveground to belowground live biomass ratio was 3.8, 2.6, and 2.1, respectively, in the three plots. Litter biomass (aboveground plus belowground) was 226, 445, and 1,094 g m$^{-2}$, respectively. Total aboveground plus belowground net primary production was 240, 1,172, and 1,531 g m$^{-2}$ yr$^{-1}$. There was an exponential loss of weight during decomposition. Woody stems and roots, the most recalcitrant material, had 70% and 83% of the original material remaining after one year. Only 20–22% of leafy stem weight remained after one year. When results from the Mediterranean are compared to other salt marshes dominated by shrubby *Chenopodiaceae* in Mediterranean-type climates, a number of similarities emerge. There are similar zonation patterns with elevation and maximum aboveground biomass and primary production occurring in the middle marsh. This is probably because of stress produced by waterlogging in the low marsh and by hypersalinity in the upper marsh.**

## Introduction

There is an extensive literature concerning net primary production and decomposition in tidal marshes of temperate Atlantic coasts of North America and Europe, particularly for *Spartina* spp. (Linthurst and Reimold 1978; Gallagher and Plumley 1979; Hackney and de la Cruz 1980; White and Trapani 1982; Groenendijk 1984; Buth and Wolf 1985; Groenendijk and Vink-Lievaart 1987; Day et al. 1989). There are relatively few studies of production and decomposition in Mediterranean-climate marshes (Mahall and Park 1976; Berger et al. 1978; Zedler et al. 1980; Ibàñez et al. 1999), where environmental conditions and the structure of shrub-dominated salt marsh communities are distinctly different from the grass-dominated marshes. Decomposition studies are scarce in the Mediterranean coastal marshes and we know of only two references on decomposition in Mediterranean salt marshes (Ibàñez et al. 1999; Scarton et al. 2002).

The vegetation of macrotidal and mesotidal coasts with Mediterranean climates (south California, southwest Iberian Peninsula, South Africa, Pacific Coast of central South America, southwest and south Australia) has a zonation pattern where the intertidal low marsh subzone is dominated by *Spartina* marshes and most of the higher zones by succulent shrubby species of the *Chenopodiaceae* (*Sarcocornia, Arthrocnemum, Suaeda*; West 1977; Rivas-Martínez et al. 1980; Adam 1990; Zedler et al. 1992; Peinado et al. 1994). In Mediterranean climates, salt marsh soils that are not flushed by daily tides are hypersaline in summer, when high temperatures coincide with low rainfall, producing an highly negative evapotranspiration balance (Heurteaux 1970; Cameron 1972; Berger et al. 1978; Callaway et al. 1990). Under these conditions, annual and perennial succulent halophytic plants adapted to hypersalinity are dominant in many salt marshes of different regions of the world (Clarke and Han-

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non 1967; Chapman 1977; Peinado et al. 1995). Vegetation structure and ecomorphological adaptations of dominant plants have a pronounced similarity with those of saline semi-deserts and steppes (Adam 1990).

In microtidal areas (e.g., most of the Mediterranean coast), hypersaline soils extend to the lowest zone of the salt marsh, and shrubby *Chenopodiaceae* can dominate throughout the entire elevation gradient. In the Ebre delta, like other regions of the northern Mediterranean coast, two species are widespread and often form pure stands: *Sarcocornia fruticosa* and *Arthrocnemum macrostachyum. S. fruticosa* is characteristic of coastal lagoon and bay edges, where soils have a moderate variation of moisture and salinity during the year, whereas *A. macrostachyum* colonizes higher levels of seasonally flooded salt marshes (normally during sea storms and heavy rains) with a strong hypersaline period during summer. In this paper we present the results of studies concerning aboveground and belowground primary production and decomposition carried out in two stands dominated by each species. We also studied an additional mixed stand (where *S. fruticosa* is more abundant) in a transition salt marsh area.

## Study Location

The study was carried out in the Ebre delta, one of the largest (330 km$^2$) deltas in the northwestern Mediterranean (Fig. 1). The majority of the delta plain is devoted to rice agriculture (65% of the total surface) and natural areas cover only about 80 km$^2$ (25%). These areas include salt marshes, reed-type marshes, sand dunes, coastal lagoons, natural springs, and bays.

The area has a coastal Mediterranean-type climate (Fig. 2) with winter temperatures largely moderated by the sea; mean monthly temperature range from 9.1°C in January to 25.6°C in August. The average annual rainfall of 548 mm is mainly concentrated in the fall (238 mm between September and December), though interannual variability is very high (e.g., during the last 30 yr rainfall has ranged between 251 and 1,054 mm). A sub-arid period extends through the summer months as a result of high temperatures and low rainfall. The dominant winds are strong northwesterlies (often with speeds greater than 100 km h$^{-1}$), which usually occur from November to April. Easterly winds occur mainly in spring and fall; the latter are associated with marine storms and maximum rainfall events (Jiménez 1996).

The Ebre delta, like most of the Mediterranean coast, is microtidal with a maximum astronomical tidal range of about 0.25 m. Meteorological tides associated with atmospheric pressure changes and winds can result in water level changes greater than 1 m (Jiménez 1996). High water levels occur during offshore passages of low-pressure systems and strong easterly winds (normally in February–May and September–December), often producing flooding in lower elevations of the delta. Low sea levels occur during periods of high atmospheric pressure, generally in January–February and July–August.

The salt marsh study site was located in a marine influenced area in the extreme eastern part of the delta known as Buda Island (40°42′N, 00°51′E). Three major types of salt marshes dominated by succulent shrubby species of *Chenopodiaceae* occur between the Calaixos de Buda lagoon and the shoreline (Fig. 1). These salt marsh types are associated with differences in microtopography, soil texture, soil salinity, and frequency and duration of marine inundation. The first type (site 1), dominated by *A. macrostachyum,* occurs just behind the beach dune at an elevation of about 40 cm (in relation to the sea level recorded during the topographic survey), and it is a nearly pure stand with a cover of 60–70% and a vegetation height of 20 cm. Other species in this site are *S. fruticosa, Cakile maritima, Limonium girardianum,* and *Limonium virgatum.* In the second marsh type near the Calaixos de Buda lagoon (site 3), *S. fruticosa* is the dominant species, where vegetation cover is nearly 100%, vegetation height is about 60 cm, and elevation is 20 cm. Other species occur rarely in this site: *Limonium bellidifolium* and *Scirpus maritimus.* Calaixos de Buda is a brackish lagoon with strong seasonal variations in water salinity. In spring and summer, water conductivity drops to 3 mS cm$^{-1}$ in some parts as a result of rice field drainage. Conductivity can reach 25 mS cm$^{-1}$ during periods of maximum marine intrusion (Comín et al. 1987). An intermediate structural type (site 2), where both *A. macrostachyum* and *S. fruticosa* form a mixed assemblage, occurs between the two other marsh types. It has a vegetation cover of 70–80%, a vegetation height of 24 cm, and an elevation of 30 cm.

## Materials and Methods

At the end of 1994, the three sampling sites were selected based on the representativeness of the different marsh types, homogeneity of the vegetation structure and species composition, low influence of human activities affecting plant biomass and vegetation structure, and ease of access. Two paired plots of 10 × 10 m were randomly chosen in each marsh type, one to carry out direct biomass measurements and the other for indirect biomass measurements.

Water level and conductivity were measured monthly in three grooved PVC wells screened from

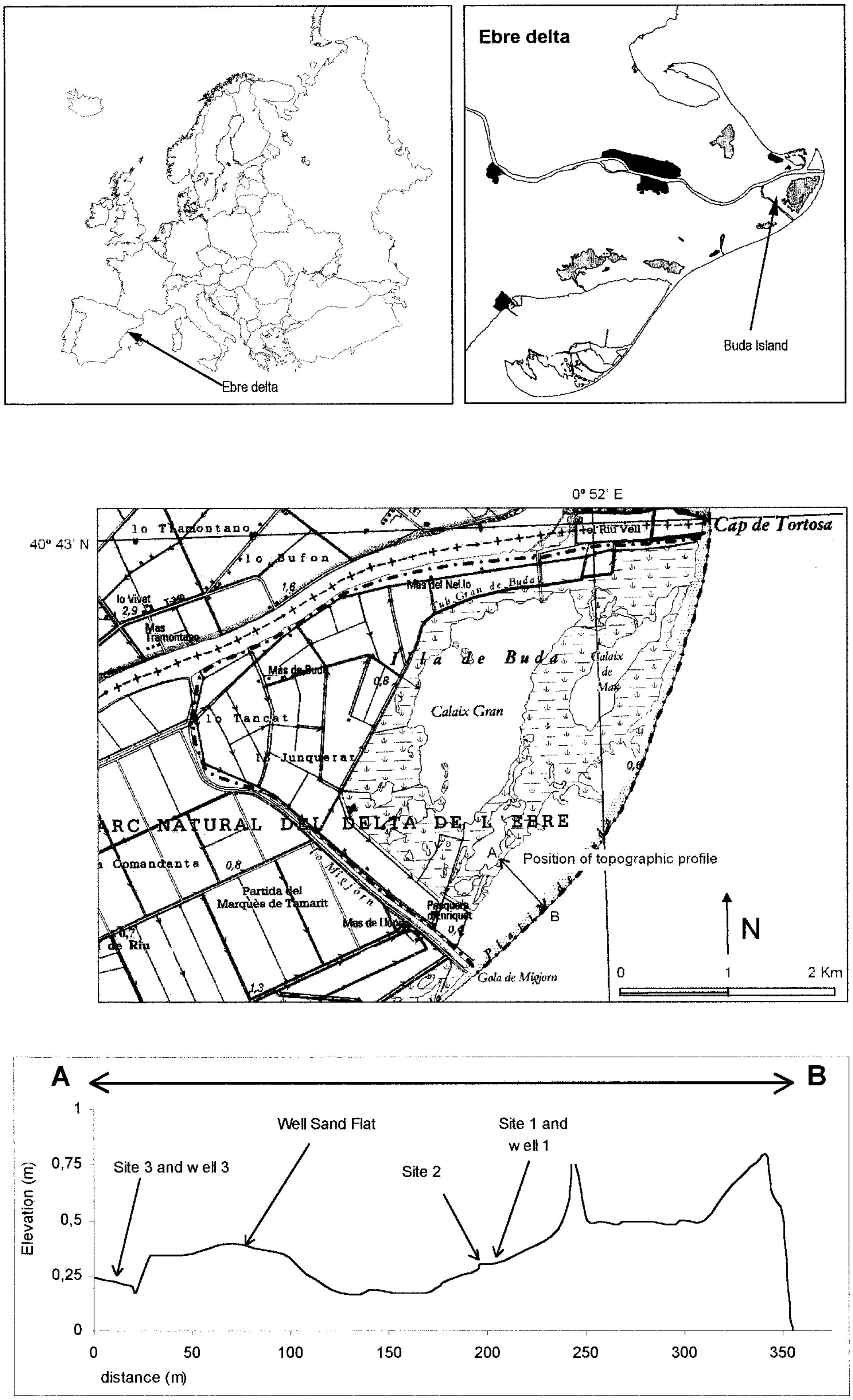


Fig. 1. Location of the study area and sampling sites, as well as topographic profile (Sánchez-Arcilla, Jiménez, and Gracia unpublished data). Elevations are related to the sea level recorded during the topographic survey. Site 1: *Arthrocnemum macrostachyum* plot, Site 2: *Sarcocornia fruticosa-Arthrocnemum macrostachyum* mixed plot, Site 3: *Sarcocornia fruticosa.*

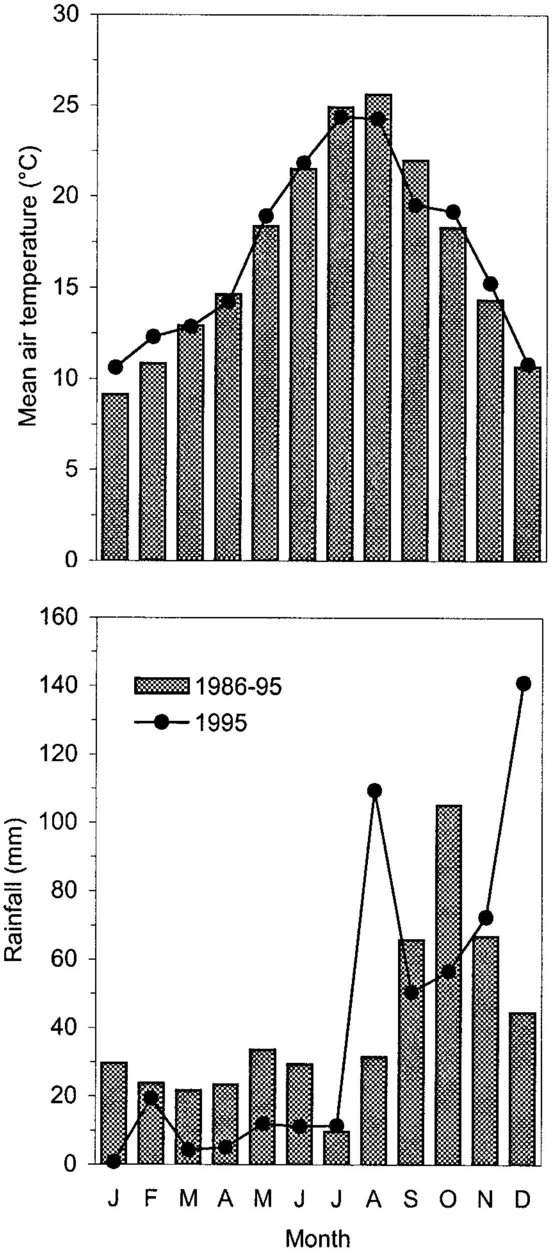


Fig. 2. Climate data from the Deltebre meteorological station (located 10 km from the sampling sites). Average for the study period (1995) and 10-year average (1986–1995).

the ground level to the bottom placed in the *S. fruticosa* (site 3) and *A. macrostachyum* (site 1) plots to a depth of 60–70 cm, as well as in a sand flat without vegetation located between them (Fig. 1). Ground or surface water level was measured to the nearest 0.5 cm in relation to the ground surface. Conductivity of the top of the underground or surface water (depending on water level) was determined in the field with an INSTRAN portable conductivimeter to the nearest 0.1 mS $cm^{-1}$. Differences between annual averages of environmental variables for wells were tested using the non-parametric test of Kruskall-Wallis (Sokal and Rohlf 1995).

A 20-cm deep soil core was collected from the *S. fruticosa* plot with a 11.5 cm (internal diameter) PVC corer. The core was extruded in the field, sliced in 2 cm layers, sealed in labelled plastic bags, weighed the same day, and dried to constant weight at 60°C. Soil bulk density was calculated from these layers. Samples were washed by hand through a 2-mm sieve and homogenized with an automatic rotation shaker for 8 h. Soil texture was determined using the Robinson method (Page et al. 1982), except for sandy layers where the method described by Dupuis (1969) was used. The following particle size classes were measured: sand (diameter between 2 and 0.05 mm), silt (0.05 mm $< d <$ 0.002 mm), and clay ($d <$ 0.002 mm). Total carbon and nitrogen content were determined using the procedures described in Page et al. (1982), using a Carlo Erba NA 1500 analyser, and organic matter content was determined by loss on ignition at 500°C for 12 h.

Aboveground vegetation biomass was measured seasonally (January—winter, April—spring, July—summer, and October—fall) at the three stations using the harvest method. This method has been widely used for herbaceous marsh species (Gabriel and de la Cruz 1974; Hopkinson et al. 1978; Linthurst and Reimold 1978) and for low stature perennial woody salt marsh species (Mahall and Park 1976; Berger et al. 1978; Hussey and Long 1982; Scarton et al. 1998). Seven randomly chosen 0.25-$m^2$ quadrates were harvested from each site. Superficial litter present in each quadrate was also collected. The two species studied, like other perennial *Chenopodiaceae,* are dwarf shrubs with very reduced scale-like leaves. Photosynthesis takes place in herbaceous stems at the end of the main woody branches. These photosynthetic stems are articulated, green and fleshy, and several segments can be carriers of inflorescence. Reflecting this structure, harvested plant material was separated into these categories: woody live stems, herbaceous live stems, and dead stems. The sorted material was dried to constant weight at 60°C and weighed. Differences in plant biomass among plots and sampling periods were analyzed using ANOVA tests. To estimate ash content, three replicates of about 1 g dry weight (for each species and each plant component) were weighed to the nearest 0.001 g, ignited at 550°C for 4 h in a muffle furnace, and reweighed.

Aboveground biomass was also estimated using an indirect non-destructive method based on the relationship between standing biomass and vege-

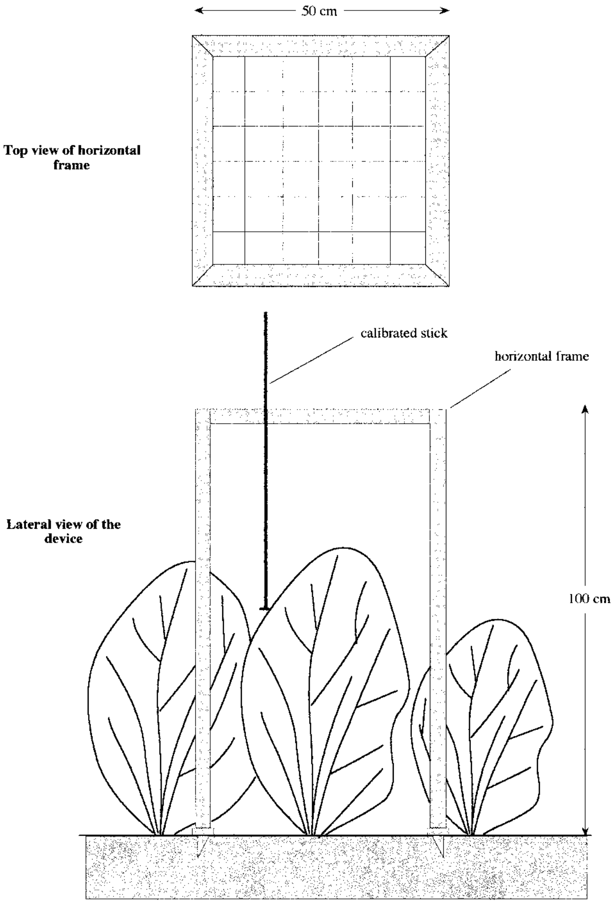


Fig. 3. Drawing of the device used to measure vegetation height.

tation height. This was done using 1 m high aluminium frame with a 50 × 50 cm top containing a wire grid of 25 points (Fig. 3). Each frame foot was inserted at the ground level into an aluminium quadrate, which avoided the sinking of the feet and ensured the same frame height in relation to ground surface at each sampling time. The height of the vegetation was measured at each of the 25 points by vertically lowering a 3.8 cm diameter metal disk fitted with a calibrated rod until it touched the top of the vegetation. An additional 10 × 10 m plot for each of the three study sites was selected to survey the vegetation height. In each of additional plots, ten 50 × 50 cm permanent quadrates were randomly placed, and vegetation height was measured monthly for 1 yr. Pipes were placed in the ground of each quadrate (in the four corners) in order to fit the feet of the frame to ensure that we measured the same location each interval. Differences in vegetation height between plots and sampling periods were analyzed using ANOVA.

Height-biomass regression equations were obtained using harvested biomass samples in which the height was measured before clipping. The regression between ln (height) and ln (weight) was obtained from height-biomass measurements for 28 samples in the *A. macrostachyum* salt marsh, 28 in the *A. macrostachyum-S. fruticosa* mixed salt marsh, and 48 in *S. fruticosa* salt marshes (28 samples from the *S. fruticosa* plot and 20 additional samples in a salt marsh nearby). These measurements were made in January, April, July, and October (7 samples × 4 months). A *t*-test for significance of regression was performed.

Belowground biomass was sampled every 3 mo in each study site during one growing season (January 1995–December 1995) by collecting five soil cores (50 cm long, 11.8 cm internal diameter) from the center of the areas clipped for aboveground biomass. To improve the efficiency of core extraction, the top was sealed with a screw-top before extracting the core from the sediment (Schuurman and Goedewaagen 1971). Preliminary samples were taken to assess the root distribution with depth, in order to determine the depth in which about 95% of root biomass occurred.

Each soil core was sectioned and washed in tap water through a 1-mm mesh sieve to remove inorganic sediments. The plant material was then sealed into labelled plastic bags and stored at 2–5°C. Each sample was placed in a receptacle of water and sorted into live and dead roots and litter. When a core contained a high biomass of small plant debris and small roots, a sub-sample of about 1 g dry weight was taken to assess the proportion between them. All samples and sub-samples were dried to constant weight at 60°C. Differences in plant biomass between plots and sampling periods were analyzed with ANOVA tests. Ash content was estimated using the same methods as for the aboveground plant biomass.

Net primary production of emergent wetland vegetation has been measured in many studies (e.g., Hopkinson et al. 1978; Linthurst and Reimold 1978; Day et al. 1989). We used the Smalley method (described in Linthurst and Reimold 1978) to calculate aboveground and belowground production. The Smalley method takes into consideration changes in live and dead material during the growing season and accounts for some plant mortality between sampling periods. It is inadequate for species in which growth, mortality, and dead plant disappearance occur at a relatively constant rate throughout the year (Hopkinson et al. 1978). The Smalley method does not consider grazing and export/import of plant matter by the tide, but our observations indicate that these were not important in the studied sites.

Decomposition of aboveground and belowground biomass was determined from the disappearance of materials from litter bags (Newell et al. 1989; Van der Valk et al. 1991). In February 1995, 18 litter bags (6 times × 3 replicates) were placed in the *S. fruticosa* plot used for primary production measurements. The litter bags were 40 × 10 cm with a mesh size of 1.6 mm. Each litter bag had 3 compartments: one for herbaceous stems, one for woody stems (both placed on the ground surface), and one for roots (placed 10 cm under the ground surface at the level of maximum root biomass). Twelve additional aerial litter bags (6 × 2 replicates) containing two compartments (herbaceous and woody stems) were placed 20–40 cm above the ground by tying them to plants in order to see if decomposition rates were different from the material on the ground. The samples of each bag compartment contained dry biomass (5 g of woody stems or 3 g of roots), except for herbaceous stems, where fresh material (about 5 g) was used and the relation between fresh and dry weight was experimentally calculated. This procedure was used because herbaceous stems crack when dried. All material for these experiments was collected from site 3. Three replicates (or 2 in the case of aerial bags) were removed after approximately 1, 4, 8, 17, 32, and 54 wk. The samples were carefully rinsed, invertebrates removed and the remaining biomass was dried at 60°C until constant weight. The material removed in the final litter bag sampling was used to determine the ash content.

The decomposition data (remaining dry weight) were fitted to an exponential decay model (first order decay function): $W_t = W_0e^{-kt}$, where $W_t$ is the weight of litter left from the initial weight, $W_0$, after time t, and k is the decay constant (Wieder and Lang 1982). The decay constants were calculated by fitting a linear regression between ln $(W_t/W_0)$ and time by the least-squares method, and the coefficients of determination ($r^2$) were estimated for each plant component and location. A *t*-test for significance of regression was also performed. Differences between k constants were tested by an analysis of covariance (test of parallelism between the regression lines).

Plant nomenclature is that of Tutin et al. (1964–1980) for European species and Kartesz (1994) for North American species. However, the taxonomy of *Salicorniaceae* follows Scott (1977).

## Results

Air temperatures during the study period were near the long-term average, ranging from a mean of 11°C in January to 24°C in July and August. Total rainfall during the study period was 494 mm and showed a strong seasonal pattern. The highest precipitation occurred in August (109 mm) and December (141 mm) in contrast with the long-term pattern where the highest month is October. Another important difference on precipitation was also recorded in spring, since it was about 21 mm in 1995 while long-term mean is about 80 mm.

The annual average water level in relation to the soil surface was −12 ± 4.5 cm (mean ± SE) in the *S. fruticosa* plot (site 3), −14 ± 6 cm in the *A. macrostachyum* plot (site 1), and −43 ± 4 cm in the non-vegetated sand flat. Mean annual soil water conductivity was 59 ± 6, 74 ± 10, and 126 ± 13 mS $cm^{-1}$, respectively. Differences in annual mean of soil conductivity and water level were highly significant between wells (Kruskall-Wallis test; $p = 0.0006$ for water level and $p = 0.0026$ for soil water conductivity). There was a similar seasonal pattern for all three sites, but the range of values differed among sites. High meteorological tides and periods of heavy rainfall resulted in high groundwater levels and lowered conductivity during several periods; March, July–August, and November–January (Fig. 4). There was flooding in the two vegetated plots but not in the non-vegetated sand flat. Periods of hypersalinity were observed in both vegetated plots, but the values were higher in the *A. macrostachyum* plot. The non-vegetated sand flat, which is located at a higher elevation, had lower moisture and higher soil salinity (the maximum conductivity was 174 mS $cm^{-1}$), which probably prevented the establishment of vegetation (Fig. 4). High rainfall and marsh flooding are rare in summer, although rainfall in August 1995 was 110 mm compared to the long-term average of about 30 mm. Environmental conditions were probably less stressful in 1995 due to lowered salinity.

The *S. fruticosa* plot soil had two well defined layers (Table 1). The upper one (0–10 cm) had relatively low values of sand (12.7–23%) and bulk density (0.87–1.32 g $cm^{-3}$), while the lower layer (10–20 cm) was dominated by sand (73.9–94.9%) and had higher bulk density values (1.17–1.55 g $cm^{-3}$). Organic matter and total nitrogen and carbon contents decreased more gradually with depth. Organic matter decreased from 9.81% to 2.49%, total nitrogen content from 0.09% to 0.03%, and carbon content from 6.05% to 4.16%.

### ABOVEGROUND BIOMASS

The annual average aboveground standing biomass was 732 g $m^{-2}$ in the *A. macrostachyum* plot (site 1) and 2,824 g $m^{-2}$ in the *S. fruticosa* plot (site 3). The *A. macrostachyum-S. fruticosa* mixed plot (site 2) had an intermediate biomass of about 950 g $m^{-2}$, with about 60% of the total standing biomass due to *S. fruticosa* (Table 2). Differences in mean biomass were highly significant among plots for all plant components: total standing biomass (F

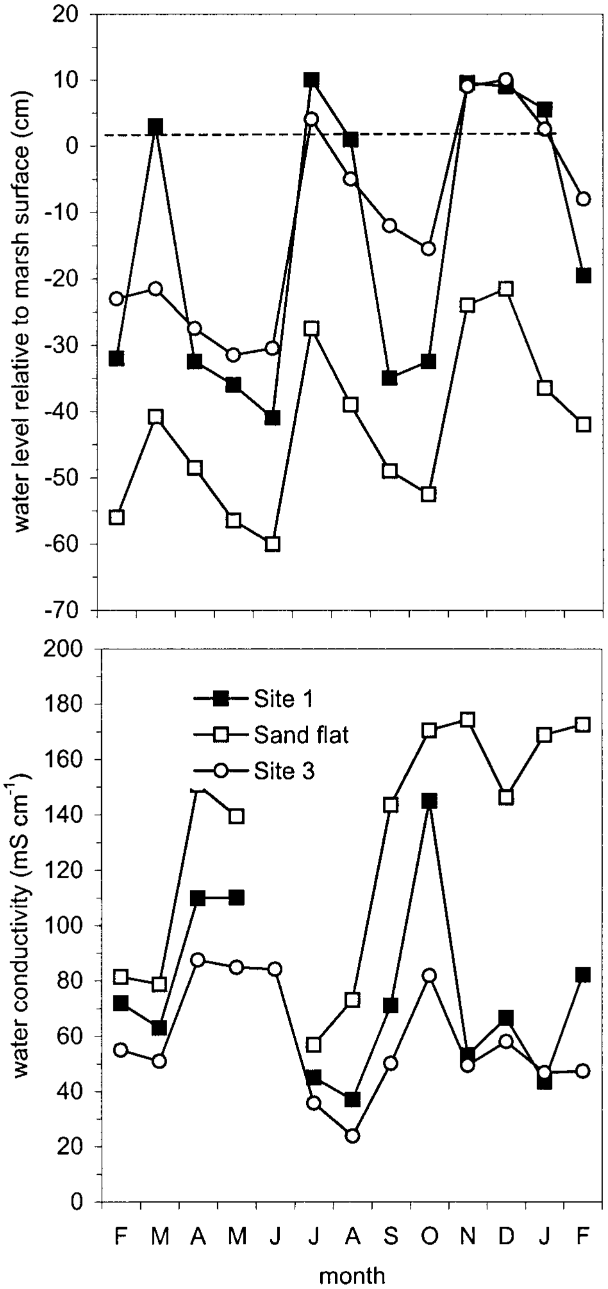


Fig. 4. Water level and conductivity of the studied plots during 1995. Site 1: *Arthrocnemum macrostachyum* salt marsh, Site 3: *Sarcocornia fruticosa* salt marsh.

TABLE 1. Soil features of the *Sarcocornia fruticosa* salt marsh (Site 3). N = total nitrogen content, C = total carbon content, and OM = organic matter.

| Layer (cm) | Bulk Density ($g\ cm^{-3}$) | N (%) | C (%) | OM (%) | Sand (%) | Silt (%) | Clay (%) |
|---|---|---|---|---|---|---|---|
| 0–2 | 0.91 | 0.09 | 6.05 | 9.81 | 19.8 | 48.8 | 32.8 |
| 2–4 | 1.13 | 0.08 | 5.79 | 8.70 | 16.5 | 51.7 | 33.2 |
| 4–6 | 0.87 | 0.07 | 5.66 | 7.89 | 12.7 | 52.7 | 36.8 |
| 6–8 | 1.32 | 0.06 | 5.24 | 6.73 | 16.0 | 60.5 | 24.9 |
| 8–10 | 1.18 | 0.07 | 4.96 | 6.07 | 23.6 | 53.1 | 24.2 |
| 10–12 | 1.17 | 0.07 | 4.73 | 4.53 | 73.9 | 16.6 | 8.0 |
| 12–14 | 1.24 | 0.07 | 4.69 | 3.81 | 64.6 | 27.3 | 9.6 |
| 14–16 | 1.33 | 0.04 | 4.39 | 3.11 | 79.1 | 13.5 | 8.3 |
| 16–18 | 1.55 | 0.04 | 4.39 | 2.56 | 88.1 | 8.0 | 4.7 |
| 18–20 | 1.32 | 0.03 | 4.16 | 2.49 | 94.9 | 2.0 | 4.0 |

= 65.18; $p < 0.0001$), woody live stems ($F = 61.96$; $p < 0.0001$), herbaceous live stems ($F = 40.12$; $p < 0.0001$)) , dead stems ($F = 23.81$; $p < 0.0001$), and litter ($F = 34.40$; $p < 0.0001$).

In relative terms, live biomass (woody plus herbaceous stems) was higher in the pure stands (about 60% of total standing biomass) than in the mixed one (about 45%). A similar pattern existed for the woody live stems; about 40% in pure stands compared to 34% in the mixed stand. The percentage of total standing biomass as green herbaceous stems was 21% in the *A. macrostachyum* plot, 12% in the mixed plot, and 17% in the *S. fruticosa* plot. Total standing biomass in the mixed plot was higher than in the *A. macrostachyum* plot due to the dead component (Table 2). The percent dead material for each species considered separately was higher in the mixed plot than in the pure plot: 41% for *S. fruticosa* in the pure plot and 47% in the mixed plot, and 37% and 66%, respectively, for *A. macrostachyum.*

Maximum litter biomass occurred in the *S. fruticosa* plot (site 3; 761 g $m^{-2}$), compared to the *A. macrostachyum* (site 1) and mixed plot (site 2; 270 and 350 g $m^{-2}$, respectively). The ratio of litter biomass to standing biomass was similar to the dead component; it was quite similar in *A. macrostachyum* and *S. fruticosa* plots (21% and 27%, respectively) and higher in the mixed plot (about 37%).

The maximum standing aboveground biomass in the *A. macrostachyum* plot was in July, while maximum live biomass was in April (Fig. 5). The *S. fruticosa* salt marsh had a different seasonal pattern, since the standing biomass was relatively low during spring and summer and high in autumn and winter, and the variation of live material was not pronounced. The mixed plot showed two peaks of standing biomass corresponding to the different peaks of the two species (Fig. 5). The first and lesser peak occurred in April due to *A. macrostachyum,* and the second biomass peak took place in October due to *S. fruticosa.* Differences in biomass among sampling periods for each plot considered separately were significant only for herbaceous live stems in the *A. macrostachyum* plot ($F = 2.892$; $p = 0.0562$) and for litter in the *S. fruticosa* plot ($F = 3.874$; $p = 0.0216$).

All plant components had high ash contents (Table 2), especially the herbaceous stems, which

TABLE 2. Mean dry weight biomass (g $m^{-2}$) and ash content (%) from the studied salt marshes in the Ebre delta. Site 1: *Arthrocnemum macrostachyum* salt marsh, Site 2: mixed salt marsh, Site 3: *Sarcocornia fruticosa* salt marsh.

| | Dry Weight Biomass | | | Ash Content | | |
|---|---|---|---|---|---|---|
| | Site 1 | Site 2 | Site 3 | Site 1 | Site 2 | Site 3 |
| Aboveground biomass | | | | | | |
| *Sarcocornia fruticosa* | | | | | | |
| Live | 5.1 | 313.5 | 1,658.1 | — | — | — |
| Herbaceous stems | 1.9 | 80.9 | 482.1 | — | 39.6 | 40.1 |
| Woody stems | 3.1 | 232.6 | 1,176.0 | — | 8.4 | 3.7 |
| Dead | 0.6 | 275.9 | 1,165.7 | — | 10.4 | 5.9 |
| *Arthrocnemum macrostachyum* | | | | | | |
| Live | 461.9 | 124.2 | 0 | — | — | — |
| Herbaceous stems | 151.0 | 33.4 | 0 | 37.8 | 4.5 | — |
| Wood stems | 310.9 | 90.8 | 0 | 1.1 | 11.4 | — |
| Dead | 264.8 | 238.9 | 0 | 11.8 | 16.3 | — |
| Total standing biomass | 732.4 | 952.5 | 2,823.9 | — | — | — |
| Litter | 155.5 | 349.7 | 761.2 | 32.1 | 13.3 | 18.5 |
| Belowground biomass | | | | | | |
| Roots | 139.3 | 245.7 | 941.8 | — | — | — |
| Live | 122.7 | 168.6 | 793.2 | 11.1 | 8.6 | 10.5 |
| Dead | 16.6 | 77.1 | 148.6 | 2.4 | 7.6 | 7.7 |
| Litter | 70.6 | 95.3 | 333.1 | 10.5 | 10.3 | 8.3 |

ranged between 38% and 40% of dry weight for all plots and species. Herbaceous stems of *A. macrostachyum* in the mixed stand, had a very low ash content (4.5%), in contrast to a much higher value in the pure stand (38%). The ash content of woody live stems of *A. macrostachyum* was considerably higher in the mixed plot (11%) than in the pure plot (1%).

### RELATIONSHIP BETWEEN VEGETATION HEIGHT AND ABOVEGROUND BIOMASS

There was a significant relationship between vegetation height and standing aboveground biomass for the three study plots (Fig. 6), indicating that height can be used to estimate biomass. The maximum mean annual height and predicted biomass was in the *S. fruticosa* plot (57.4 cm and 3,367 g $m^{-2}$, respectively), compared to 23.9 cm and 1,083 g $m^{-2}$ in the mixed plot and 19.3 cm and 929 g $m^{-2}$ in the *A. macrostachyum* plot. Vegetation was highest in spring and early summer months for both pure stands, but the *S. fruticosa* plot had a much broader peak. In the mixed plot, there were two peaks of height, occurring in June (24.7 cm corresponding to a biomass of 1,118 g $m^{-2}$) and October–November (24.3 cm corresponding to a biomass of 1,099 g $m^{-2}$). Differences in mean height among permanent plots were significant ($F = 902.50$; $p = 0.0001$). Differences in mean height among months were not significant for any plot: site 1 ($F = 0.144$; $p = 0.994$), site 2 ($F = 0.018$; $p = 1$), and site 3 ($F = 1.10$; $p = 0.367$).

The mean height of the plots used for indirect measurements of biomass was significantly higher than in the plots used for direct measurements for sites 1 (19.5 and 14.7 cm, respectively; $F = 6.1$; $p < 0.05$) and 3 (58.1 and 47.6 cm, respectively; $F = 23.3$, $p < 0.05$), but it was not significant for site 2 (24.1 and 21.9 cm, respectively; $F = 0.54$; $p = 0.59$). None of the harvest plots showed significant differences in vegetation height among sampling months (April, July, and October), as in the case of non-harvest plots. These results indicate that this method is valid for estimating standing biomass, but not for detecting temporal changes in biomass, either because real changes were actually small or because variance of replicates was too high. In the latter case, the variance could be reduced by increasing the sampling size or by tracking height changes for individually tagged plants at least monthly and applying biomass conversion (Morris and Haskin 1990).

### BELOWGROUND BIOMASS

The mean annual belowground biomass was 942 g $m^{-2}$ in the *S. fruticosa* plot (site 3), 246 g $m^{-2}$ the mixed plot (site 2), and 140 g $m^{-2}$ in the *A. macrostachyum* plot (site 1; Table 2). Live roots were the main component in all three plots, especially in both pure plots (where live roots were 84% and 88%, respectively, of the total). In the mixed plot, live roots represented 68% of the total. The litter component also differed greatly among marshes, and values were 70.6 g $m^{-2}$ for the *A. macrostachyum* salt marsh, 95 g $m^{-2}$ for the mixed plot, and 333 g $m^{-2}$ for the *S. fruticosa* plot. In relative terms, litter was similar in the mixed and *S. fruticosa* salt marshes (39% and 35% of belowground biomass, respectively), whereas it was higher in the *A. macrostachyum* salt marsh (51%). Differences in mean

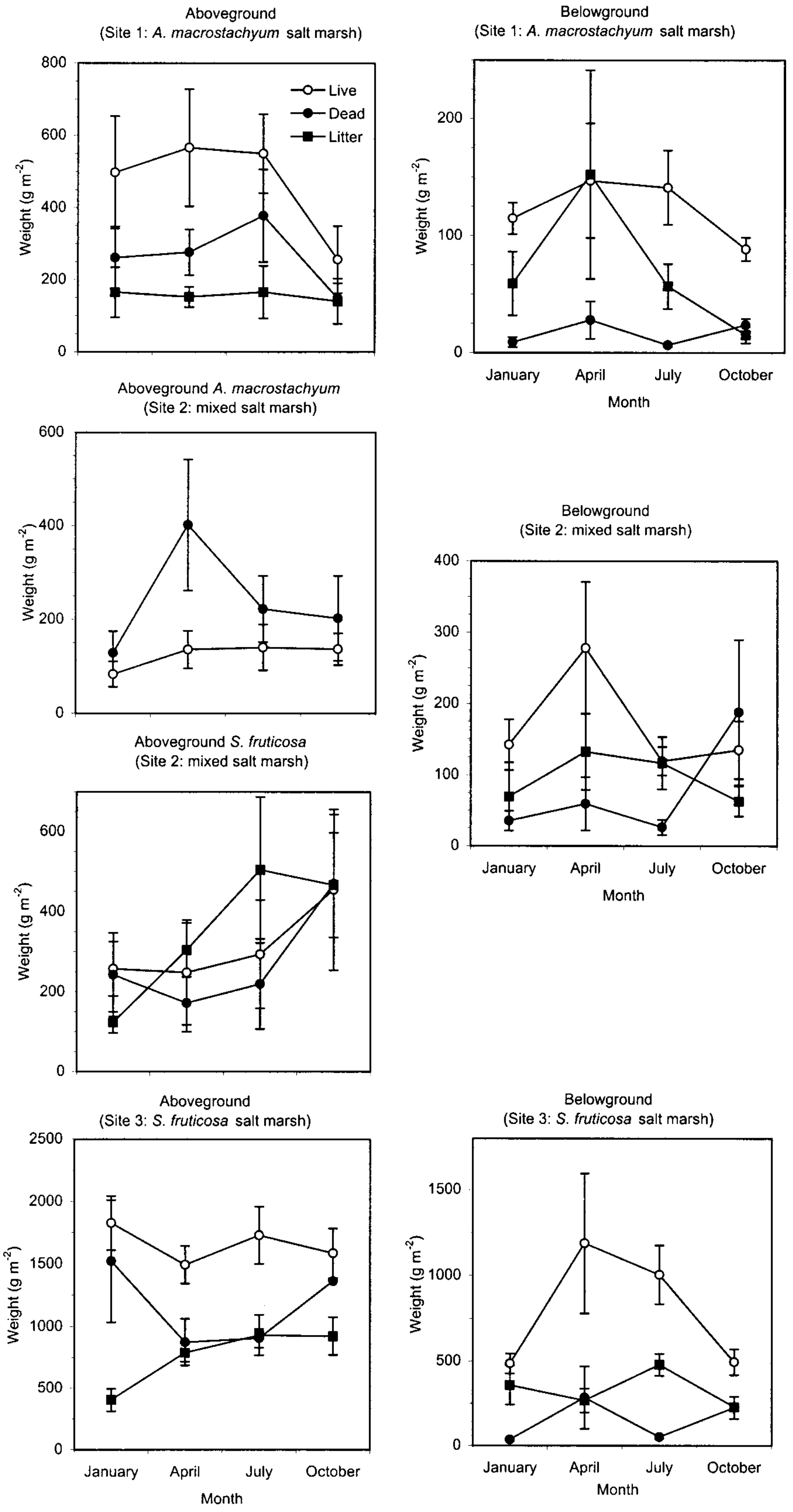


Fig. 5. Seasonal changes of aboveground and belowground biomass in the *Arthrocnemum macrostachyum* (site 1), *Sarcocornia fruticosa-Arthrocnemum macrostachyum* mixed (site 2) and *Sarcocornia fruticosa* (site 3) plots.

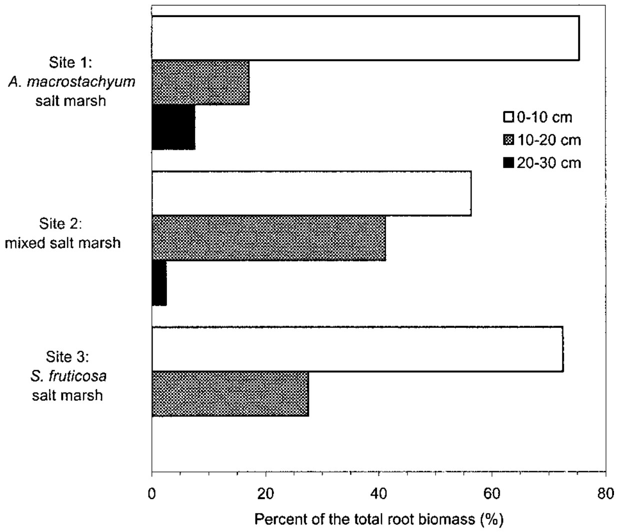
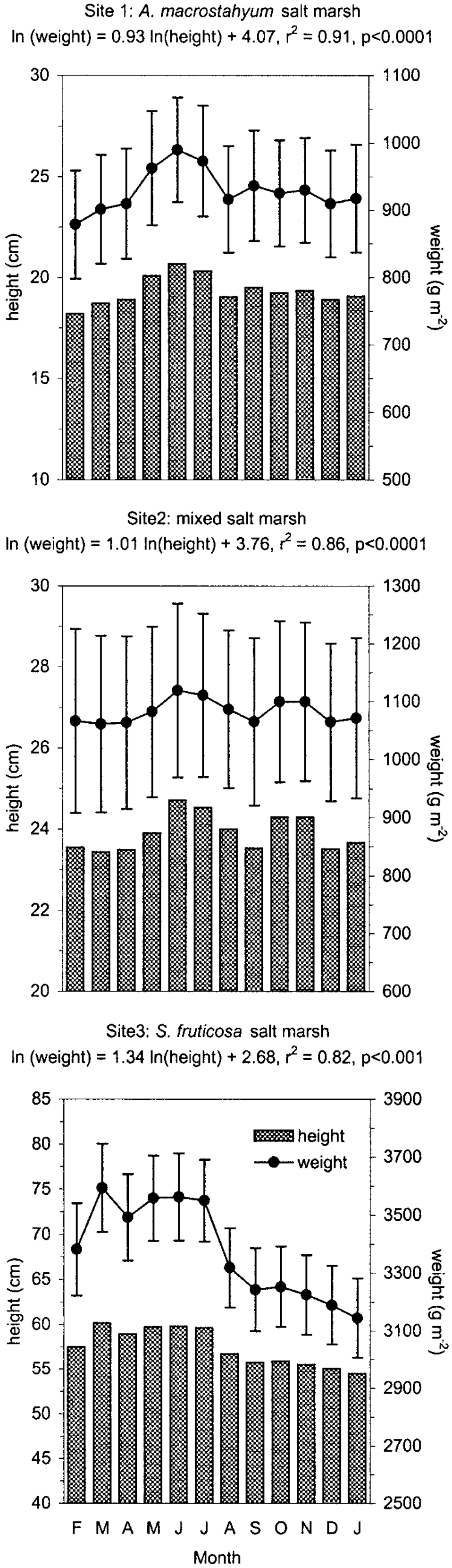


Fig. 7. Vertical distribution of belowground biomass in the studied plots. Site 1: *Arthrocnemum macrostachyum* plot, Site 2: *Sarcocornia fruticosa-Arthrocnemum macrostachyum* mixed plot, Site 3: *Sarcocornia fruticosa.*

biomass were highly significant among plots for all plant components: total biomass ($F = 38.32$; $p < 0.0001$), live roots ($F = 30.58$; $p < 0.0001$), dead roots ($F = 4.09$; $p < 0.0229$), and litter ($F = 26.94$; $p < 0.0001$).

Seasonal changes in belowground biomass in the three plots were quite similar with a peak in April for most of the underground components (Figs. 5 and 6). Live roots were the main component in all the plots with maximum values of 1,187 g $m^{-2}$ in the *S. fruticosa* plot, 280 g $m^{-2}$ in the mixed plot, and 150 g $m^{-2}$ in the *A. macrostachyum* plot. There was no clear seasonal pattern for dead roots, except for the mixed plot which had a maximum in October. Differences in biomass among sampling periods for each plot were not significant for all plant components. Ash contents were similar in all three plots for each component: live roots (9–11%), dead roots (2–7%), and litter (8–10%; Table 2).

Total belowground biomass decreased rapidly with depth for all three plots (Fig. 7). Biomass below 20 cm accounted for less than 2% of the total root biomass and for the *S. fruticosa* plot, it was zero. In this latter plot, 72% of roots occurred in the upper 10 cm, where there were the highest


Site 1: *A. macrostahyum* salt marsh
$\ln(\text{weight}) = 0.93 \ln(\text{height}) + 4.07$, $r^2 = 0.91$, $p<0.0001$

Site2: mixed salt marsh
$\ln(\text{weight}) = 1.01 \ln(\text{height}) + 3.76$, $r^2 = 0.86$, $p<0.0001$

Site3: *S. fruticosa* salt marsh
$\ln(\text{weight}) = 1.34 \ln(\text{height}) + 2.68$, $r^2 = 0.82$, $p<0.001$

←

Fig. 6. Monthly variation of the vegetation height in the permanent plots and estimated monthly standing biomass. Site 1: *Arthrocnemum macrostachyum* plot, Site 2: *Sarcocornia fruticosa-Arthrocnemum macrostachyum* mixed plot, Site 3: *Sarcocornia fruticosa.*

TABLE 3. Aboveground and belowground production, turnover rates (ratio between primary production and mean live biomass), and aboveground to belowground ratios of the studied plots. Site 1: *Arthrocnemum macrostachyum* salt marsh, Site 2: *Arthrocnemum macrostachyum-Sarcocornia fruticosa* mixed salt marsh, Site 3: *Sarcocornia fruticosa* salt marsh.

| Plot | Site 1 | Site 2 | Site 3 |
|---|---|---|---|
| Primary production (g $m^{-2}$ $yr^{-1}$) | | | |
| Aboveground | 189 | 835 | 581 |
| Belowground | 51 | 337 | 950 |
| Turnover ($yr^{-1}$) | | | |
| Aboveground live | 0.41 | 1.90 | 0.35 |
| Belowground | | | |
| Aboveground to belowground | 0.41 | 1.99 | 1.20 |
| biomass ratios | | | |
| Mean live biomass | 3.80 | 3.00 | 2.09 |
| Mean total biomass | 5.26 | 3.88 | 3.00 |
| Litter | 2.20 | 3.67 | 2.28 |
| Production | 3.71 | 2.48 | 0.61 |

values for clay, silt, nutrients, and organic matter (Table 1).

### NET PRIMARY PRODUCTION

Total aboveground plus belowground primary production increased from the *A. macrostachyum* plot (240 g $m^{-2}$ $yr^{-1}$) to the mixed plot (1,172 g $m^{-2}$ $yr^{-1}$) and to the *S. fruticosa* plot (1,531 g $m^{-2}$ $yr^{-1}$; Table 3). Aboveground primary production increased from the *A. macrostachyum* (189 g $m^{-2}$ $yr^{-1}$) to the *S. fruticosa* plot (581 g $m^{-2}$ $yr^{-1}$) and to the mixed plot (835 g $m^{-2}$ $yr^{-1}$), in which *S. fruticosa* accounted for 60% of total aboveground production. Belowground primary production increased from the *A. macrostachyum* plot (51 g $m^{-2}$ $yr^{-1}$) to the mixed plot (337 g $m^{-2}$ $yr^{-1}$) and to the *S. fruticosa* plot (950 g $m^{-2}$ $yr^{-1}$).

The turnover of the aboveground live biomass (the ratio between primary production and mean live biomass), was lower than 1 in the pure stands and higher for both species in the mixed plot (Table 3). On the other hand, in the case of belowground live biomass, turnovers were higher than 1 in the *S. fruticosa* plot and lower in the *A. macrostachyum* and mixed plots. Aboveground and belowground turnovers were similar, except for the *S. fruticosa* plot, where belowground turnover was considerably higher than the aboveground.

The mean biomass of the different aboveground components was higher than the respective belowground components (Table 3). Most of the ratios of aboveground to belowground components decreased from the *A. macrostachyum* to the mixed plot and to the *S. fruticosa* plot. Aboveground was higher than belowground production in the *A. macrostachyum* and the mixed plots, but belowground production was higher in the *S. fruticosa* plot (Table 3).

TABLE 4. Values of remaining dry weight in the litter bags after one year ($w_t$) and $k_{days}$, $r^2$, and t values corresponding to a first-order decay fitting of weight loss in the *Sarcocornia fruticosa* salt marsh (Site 3). Ash content in the last sampling time (about 48 wk) is also shown. All t values are highly significant ($p < 0.0001$).

| Plant Component and Position | $w_t$ (%) | $k_{days}$ | $r^2$ | t | Ash (%) |
|---|---|---|---|---|---|
| Herbaceous stems (aerial) | 20.3 | 0.00389 | 0.921 | 14.93 | 10.6 |
| Herbaceous stems (ground) | 22.7 | 0.00389 | 0.898 | 12.90 | 16.9 |
| Woody stems (aerial) | 83.0 | 0.00047 | 0.908 | 10.90 | 4.9 |
| Woody stems (ground) | 74.5 | 0.00075 | 0.936 | 16.55 | 9.6 |
| Roots (belowground) | 70.0 | 0.00079 | 0.826 | 9.23 | 12.6 |

### DECOMPOSITION

The main parameters of the first-order decay model from litter weight loss and the relative changes in remaining dry weight are shown in Table 4 and Fig. 8, respectively. The high values of correlation coefficients and the highly significant values of the *t*-test indicate that the negative exponential model is satisfactory to describe decomposition kinetics in all five cases (plant component and location).

Herbaceous stems had the highest decomposition rates with a mean k value of 0.00389 $d^{-1}$ and approximately 20% of the initial weight remaining after 1 yr. For this plant component, decomposition was not significantly different between ground and aerial litter bags. Lignified plant parts had low decomposition rates, especially woody stems. This plant part had k values of 0.00047 and 0.00075 $d^{-1}$, with 83% and 75%, of the material remaining after 1 yr for aerial and ground litter bags. Nevertheless, differences among both bag locations were significant and aerial woody stems decomposed more slowly. Roots decomposed at a similar rate to woody stems placed on the ground ($k = 0.00079$ $d^{-1}$ and 70% of the material remaining after 1 yr), though the difference was significant. The herbaceous stems decomposed much more rapidly than other plant components of *S. fruticosa* due the lack of lignification and to its high mineral content, mainly soluble salts (Table 2), which are quickly leached by the water during the early stages of decomposition.

## Discussion

The values for aboveground biomass and net primary production in the Ebre delta are within the range of other salt marshes dominated by shrubby *Chenopodiaceae* in other Mediterranean areas. For *S. fruticosa,* reported total biomass ranges between 600 and 3,500 g $m^{-2}$ and primary production between 950 and 1,000 g $m^{-2}$ $yr^{-1}$ in the Rhône Delta (Eckardt 1972; Berger et al. 1978; Rioual et al. 1996; Ibàñez et al. 1999), and 750–3,500 g $m^{-2}$ and 350–700 g $m^{-2}$ $yr^{-1}$ in Venice Lagoon (Caniglia et

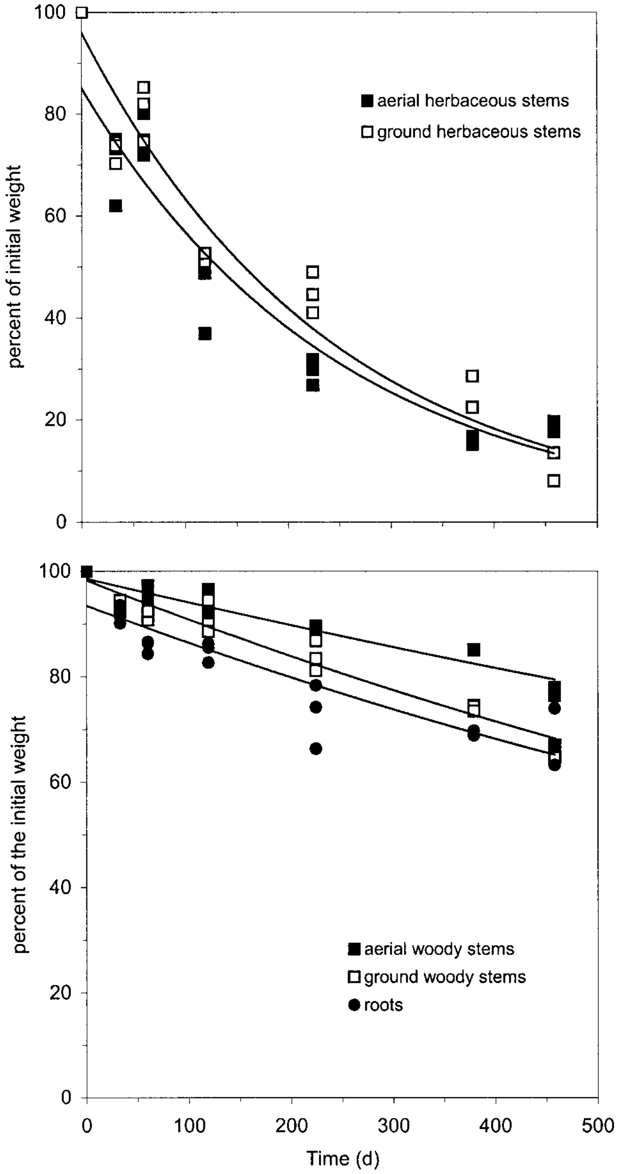


Fig. 8. Remaining dry weight in the litter bag experiment carried out in the *Sarcocornia fruticosa* plot.

al. 1976, 1978; Scarton et al. 1998). Studies carried out in the Rhône Delta on *A. macrostachyum* salt marshes gave lower values than at our *A. macrostachyum* site: about 300 g $m^{-2}$ and 90–300 g $m^{-2}$ $yr^{-1}$ (Berger et al. 1978; Rioual et al. 1996; Ibàñez et al. 1999). There are few studies of belowground biomass and productivity in Mediterranean salt marshes, and our data are within the wide range reported: 340–3,400 g $m^{-2}$ and 65–1,260 g $m^{-2}$ $yr^{-1}$ for *S. fruticosa* (Caniglia et al. 1976; Rioual et al. 1996; Scarton et al. 1998).

The total primary production estimated in 1995 was likely high in relation to the long-term average, since the unusually high rainfall in summer 1995 reduced soil salinity (Fig. 4). In these conditions, as other authors have suggested (Berger et al. 1978; Zedler et al. 1980; Zedler 1983), primary production in Mediterranean-type salt marshes can be relatively high due to a decrease in salinity stress. Differences in seasonal growth were observed in both species between pure and mixed plots. The maximum standing aboveground biomass of *A. macrostachyum* in the pure stand occurred in July, whereas in the mixed stand took place in April. In the case of *S. fruticosa,* standing aboveground biomass of the mixed plot was quite constant throughout the year, except a maximum in October, whereas in the pure plot it was relatively high in January and October and showed a strong minimum in April. These differences would be related to different tolerance to soil salinity and flooding conditions between both species. *A. macrostachyum* is more tolerant to high salinity, but more sensitive to flooding, and maximum standing biomass occurs normally in summer. *S. fruticosa* grows better than *A. macrostachyum* in anaerobic soils, but is more sensitive to extreme salinity, so maximum growth takes place in fall. In 1995, unusual summer floods due to rainfall and sea storms strongly affected the mixed plot, located in a lower elevation, and perhaps suppressed the *A. macrostachyum* growth in the mixed plot during this season. The soil salinity drop induced by summer floods possibly enhanced the *S. fruticosa* growth in the mixed plot.

There are difficulties in measuring net primary productivity in Mediterranean salt marshes dominated by shrubby species, especially in comparison to those dominated by grass and rush species (*Spartina, Distichlis, Juncus*). In areas like the Ebre delta where the salt marsh vegetation is evergreen most of the years, primary production may take place throughout the year, and seasonal changes in biomass are not pronounced. The errors in biomass measurements due to a high variability in the spatial distribution can be greater than temporal changes. In the salt marsh study sites of the Ebre delta, biomass was not statistically different over time. Our results suggest that studies of net primary production in shrubby salt marshes should increase biomass measurement precision in order to detect more accurately biomass changes. One study carried out in southern California, based on marking and tracking the demography of *Sarcocornia pacifica* branches, showed that production calculations based on the harvest method can be gross underestimates, because such species have high loss rates between sampling dates, high spatial heterogeneity, and year-round growth (Onuf et al. 1978). These data affirm the importance of long-

TABLE 5. Aboveground biomass (g m$^{-2}$) and net aboveground primary production (NAP; g m$^{-2}$ yr$^{-1}$) of Mediterranean salt marshes dominated by shrubby *Chenopodiaceae.* AM: *Arthrocnemum macrostachyum,* AS: *Arthrocnemum subterminale,* SF: *Sarcocornia fruticosa,* SPa: *Sarcocornia pacifica,* and SPe: *Sarcocornia perennis.*

| Species | Site | Total | Live | Dead | Live Woody | Total Woody | Herbaceous Stems | Litter | NAP | Source |
|---|---|---|---|---|---|---|---|---|---|---|
| AM | Camargue, France | 311 | 222 | 89 | — | — | — | — | 294 | Ibàñez et al. 1999 |
| AM | Ebre delta, Spain | 732 | 467 | 265 | 314 | 579 | 153 | 155 | 190 | This study |
| AM | Camargue, France | 400 | — | — | — | 250 | 150 | — | — | Berger et al. 1978 |
| AM | Camargue, France | 329 | 227 | 102 | — | — | — | — | 187 | Ibàñez et al. 1999 |
| AM | Camargue, France | 309 | 280 | 29 | 151 | 180 | 139 | — | 94 | Rioual et al. 1996 |
| AS | Carpinteria, California | 1,700 | — | — | — | — | — | — | — | Pennings and Callaway 1992 |
| AS | Carpinteria, California | 200 | — | — | — | — | — | — | — | Pennings and Callaway 1992 |
| SF | Venice Lagoon, Italy | 760 | 678 | 86 | 486 | 570 | 182 | — | 683 | Scarton et al. 1998 |
| SF | Venice Lagoon, Italy | 588 | — | — | — | 427 | 161 | — | 347 | Caniglia et al. 1976 |
| SF | Venice Lagoon, Italy | 3,448 | — | — | — | — | — | — | — | Caniglia et al. 1978 |
| SF | Camargue, France | 2,748 | 1,990 | 758 | 1,676 | 2,434 | 577 | — | 773 | Rioual et al. 1996 |
| SF | Camargue, France | 2,481 | 1,963 | 518 | 1,489 | 2,007 | 397 | — | 102 | Rioual et al. 1996 |
| SF | Camargue, France | 2,400 | — | — | — | 2,200 | 200 | — | — | Berger et al. 1978 |
| SF | Camargue, France | 3,515 | — | — | — | 3,050 | 465 | 692 | 997 | Berger et al. 1978 |
| SF | Camargue, France | 2,340 | — | — | — | 2,310 | 210 | — | — | Berger et al. 1978 |
| SF | Camargue, France | 2,275 | — | — | — | 1,955 | 320 | 383 | 948 | Berger et al. 1978 |
| SF | Camargue, France | 1,357 | — | — | — | 1,020 | 337 | — | — | Eckardt 1972 |
| SF | Camargue, France | 1,362 | — | — | — | 1,192 | 170 | — | — | Eckardt 1972 |
| SF | Camargue, France | 1,900 | 1,560 | 340 | — | — | — | — | 1,262 | Ibàñez et al. 1999 |
| SF | Camargue, France | 2,897 | 2,310 | 587 | — | — | — | — | 1,123 | Ibàñez et al. 1999 |
| SF | Ebre delta, Spain | 2,824 | 1,658 | 1,166 | 1,176 | 2,342 | 482 | 761 | 580 | This study |
| SF & AM | Ebre delta, Spain | 952 | 438 | 515 | 323 | 838 | 114 | 350 | 835 | This study |
| SPa | Sonoma, California | 595 | — | — | — | — | — | 550 | 1,185 | Cameron 1972 |
| SPa | San Diego, California | 1,477 | 970 | 507 | — | — | — | 254 | — | Zedler 1983 |
| SPa | Mare Island, California | 1,315 | — | — | — | 904 | 411 | — | 818 | Mahall and Park 1976 |
| SPa | Mare Island, California | 1,864 | — | — | — | 1,438 | 426 | — | 850 | Mahall and Park 1976 |
| SPa | Mare Island, California | 2,304 | — | — | — | 1,824 | 480 | — | 959 | Mahall and Park 1976 |
| SPa | Petaluma, California | 798 | — | — | — | 587 | 211 | — | 210 | Mahall and Park 1976 |
| SPa | Petaluma, California | 1,772 | — | — | — | 1,494 | 278 | — | 553 | Mahall and Park 1976 |
| SPa | Carpinteria, California | 1,500 | — | — | — | — | — | — | — | Pennings and Callaway 1992 |
| SPa | Capinteria, California | 2,000 | — | — | — | — | — | — | — | Pennings and Callaway 1992 |
| SPa | Tijuana estuary, California | 966 | 926 | 40 | — | — | — | 76 | 632 | Zedler et al. 1980 |
| SPa | Tijuana estuary, California | 1,053 | 1,019 | 34 | — | — | — | 197 | 729 | Zedler et al. 1980 |
| SPa | San Diego R. channel, California | 1,391 | 884 | 507 | — | — | — | 254 | 599 | Zedler et al. 1980 |
| SPa | Peñasquitos Lagoon, California | 3,543 | 3,491 | 52 | — | — | — | 483 | 2,858 | Zedler et al. 1980 |
| SPa | Suisin marsh, California | — | — | — | — | — | — | — | 650 | Mall 1969 in MacDonald 1977 |
| SPa | San Diego Bay, California | — | — | — | — | — | — | — | 1,500–2,000 | Mudie 1970 in MacDonald 1977 |
| SPe | Odiel, Spain | 600 | — | — | — | — | — | — | — | Castellanos et al. 1994 |
| SPe | Odiel, Spain | 550 | — | — | — | — | — | — | — | Castellanos et al. 1994 |
| SPe | Odiel, Spain | 450 | — | — | — | — | — | — | — | Castellanos et al. 1994 |

TABLE 6. Belowground biomass (g $m^{-2}$) and net belowground primary production (NBP) (in g $m^{-2}$ $yr^{-1}$) of Mediterranean salt marshes dominated by shrubby *Chenopodiaceae*. AM: *Arthrocnemum macrostachyum,* SF: *Sarcocornia fruticosa,* SPa: *Sarcocornia pacifica,* and SPe: *Sarcocornia perennis.* Sampling depth is also indicated (cm).

| Species | Site | Depth | Total | Live | Dead | Litter | NBP | Source |
|---|---|---|---|---|---|---|---|---|
| AF | Camargue, France | 40 | 1,419 | 1,148 | 271 | — | 65 | Rioual et al. 1996 |
| AF | Camargue, France | 40 | 1,375 | 1,160 | 215 | — | 174 | Rioual et al. 1996 |
| AF | Venice Lagoon, Italy | 35–40 | 3,368 | 2,829 | 539 | — | 1,260 | Scarton et al. 1998 |
| AF | Venice Lagoon, Italy | 20 | 340 | — | — | — | 500 | Caniglia et al. 1976 |
| AF | Ebre delta, Spain | 30 | 941 | 793 | 148 | 333 | 581 | This study |
| AF-AM | Ebre delta, Spain | 30 | 245 | 168 | 77 | 95 | 835 | This study |
| AM | Camargue, France | 40 | 1,107 | 908 | 199 | — | — | Rioual et al. 1996 |
| AM | Ebre delta, Spain | 30 | 138 | 122 | 16 | 70 | 189 | This study |
| SPa | Mare Island, California | 25 | 1,960 | 259 | — | — | — | Mahall and Park 1976 |
| SPa | Mare Island, California | 25 | 1,020 | 405 | — | — | — | Mahall and Park 1976 |
| SPa | Mare Island, California | 25 | 620 | 1,033 | — | — | — | Mahall and Park 1976 |
| SPa | Petaluma, California | 25 | 910 | 185 | — | — | — | Mahall and Park 1976 |
| SPa | Petaluma, California | 25 | 490 | 299 | — | — | — | Mahall and Park 1976 |
| SPe | Odiel, Spain | 30 | 1,665 | — | — | — | — | Castellanos et al. 1994 |

term monitoring studies on primary production in permanent plots and particularly the effects of meteorological variability, interspecific competition (especially in ecotones), and biotic-abiotic feedbacks.

The decomposition rates of *S. fruticosa* from the Ebre delta were quite similar to those estimated in the Rhône Delta (0.0046, 0.00052, and 0.00066 $d^{-1}$ for herbaceous stems, woody stems, and roots, respectively; Rioual et al. 1996), but considerably higher than those estimated for Venice Lagoon (0.0020, 0.00027, and 0.00027 $d^{-1}$, respectively; Scarton and Rismondo 1996). In all these areas there is a large difference in the decomposition rates between herbaceous and lignified parts (woody stems and roots). Normally, marsh grasses decompose more slowly than succulents (Zedler et al. 1980), though the decomposition of the herbaceous stems of *S. fruticosa* was similar to the *Spartina* leaves in some studies of low marshes of the United States (Long and Mason 1983). Woody stems located on the ground and roots of *S. fruticosa* decomposed at rates similar to *Spartina* leaves in high marshes and slower than in low marshes. Woody stems located in aerial bags decomposed very slowly, due to both the high content in lignin and the low moisture of the microhabitat, and the loss of material was similar to several high marsh species (*Spartina, Elytrigia, Halimione*) of northwestern Europe (Buth and Wolf 1985).

In Mediterranean-type climate salt marshes, maximum aboveground biomass and net primary production occurs in the middle marsh (Table 5), where the stress produced by waterlogging in the low marsh, and by hypersalinity in the upper marsh, were relatively moderate. This pattern has also been reported by Pennings and Callaway (1992) and Adams and Bate (1994) in other Mediterranean-type climate regions. The *A. macrostachyum* upper salt marsh in the Mediterranean had aboveground biomass values between 300 and 700 g $m^{-2}$ and primary production between 90 and 300 g $m^{-2}$ $yr^{-1}$. *Arthrocnemum subterminale* is the vicariant species in the southern California salt marshes (Pennings and Callaway 1992). At its lower distribution limit, *A. subterminale* is tall and has aboveground biomass up to 1,200 g $m^{-2}$, whereas at higher elevations biomass is only about 200 g $m^{-2}$, a value similar to the Mediterranean *A. macrostachyum* upper salt marsh. For the Mediterranean *S. fruticosa* middle salt marsh, aboveground biomass ranges between 1,350 and 3,350 g $m^{-2}$ and primary production between 102 and 1,260 g $m^{-2}$ $yr^{-1}$, though an important part of this high variability may be due to the different methods used. A fairly erect and highly herbaceous form of *S. fruticosa,* studied in a marsh in Venice Lagoon (Caniglia et al. 1976; Scarton et al. 1998), had lower values of aboveground biomass and primary production (600–760 g $m^{-2}$ and 350–680 g $m^{-2}$ $yr^{-1}$, respectively) likely due to a higher tidal range. For *S. pacifica* in California, values range between 595 and 3,543 g $m^{-2}$ for aboveground biomass and between 210 and 2,858 g $m^{-2}$ $yr^{-1}$ for aboveground primary production. There are no data concerning Mediterranean *Sarcocornia perennis* low marsh, and the only measurement carried out in an Atlantic salt marsh in the southwestern Iberian Peninsula reports an aboveground biomass between 450 and 600 g $m^{-2}$ (Castellanos et al. 1994).

Total belowground biomass in Mediterranean salt marshes dominated by shrubby *Chenopodiaceae* ranges between 138 and 3,468 g $m^{-2}$ (Table 6), lower than most of the temperate salt marshes (Gallagher and Plumley 1979; Hussey and Long 1982; Groenendijk and Vink-Lievaart 1987), where much of the belowground biomass is formed by rhizomes. The belowground biomass in Mediterranean salt marshes ranges between 138 g m$^{-2}$ in the Ebre delta and 1,107 g m$^{-2}$ in the Rhône Delta for *A. macrostachyum*; from 941 g m$^{-2}$ in the Ebre delta to 1,375–1,419 g m$^{-2}$ in the Rhône Delta, and to 340–3,368 g m$^{-2}$ in the Venice Lagoon for *S. fruticosa*. Net belowground production ranges between 65 and 1,260 g m$^{-2}$ yr$^{-1}$, but an important part of the this high variability is probably due to the different methods used. In any case, these values are much lower than the belowground primary production values measured in temperate salt marshes (Gallagher and Plumley 1979; Groenendijk and Vink-Lievaart 1987).

## ACKNOWLEDGMENTS

This research was supported by the Environment Program (Directorate General for Science, Research and Development) of the European Communities (MedDelt Project, Impact of the Climate Change on North-western Mediterranean Deltas), contract no. EV5V-CT94–0465, Climatology and Natural Hazards. We thank C. Bladé, A. Canicio, I. Fabra, M. A. López, X. Riera, A. Vendrell, and M. van Elk for field and laboratory assistance.

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## SOURCE OF UNPUBLISHED MATERIALS

SÁNCHEX-ARCILLA, A., J. A. JIMÉNEZ, AND V. GRACIA. unpublished data. Laboratori d'Enginyeria Marítima, Universitat Politècnica de Barcelona, Gran Capità s/n 08034 Barcelona, Spain

*Received for consideration, January 23, 2001*
*Accepted for publication, July 6, 2001*