

# Primary Production and Decomposition of Wetlands of the Rhône Delta, France: Interactive Impacts of Human Modifications and Relative Sea Level Rise

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## ABSTRACT

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Above ground primary production and above ground and below ground decomposition of several wetland species were studied in seven wetland sites in the Rhône delta from October 1992 to October 1993. The sites were located in three characteristic zones of the delta: a low salinity area close to the river mouth, a marine site near the Mediterranean Sea and managed, impounded areas. These areas are vegetated by helophytes and glassworts (family Chenopodiaceae). Wetland production was affected by salinity, cattle and horse grazing and water levels. In a grazed freshwater wetland dominated by *Scirpus maritimus*, production was  $452 \text{ g m}^{-2} \text{ yr}^{-1}$ , while in an adjacent ungrazed site dominated by *Typha angustifolia* production was  $2989 \text{ g m}^{-2} \text{ yr}^{-1}$ . The most productive glasswort marshes were dominated by *Arthrocnemum fruticosum*, one near the river mouth ( $1123 \text{ g m}^{-2} \text{ yr}^{-1}$ ), and a second with a free connection to the sea ( $1262 \text{ g m}^{-2} \text{ yr}^{-1}$ ). The least productive glasswort marshes were dominated by *Arthrocnemum glaucum*. The lowest production ( $244 \text{ g m}^{-2} \text{ yr}^{-1}$ ) was in a grazed, semi-impounded marsh with high soil salinity and high ground water levels, while a second area in the central part of the delta with high soil salinity and grazing had a production of  $294 \text{ g m}^{-2} \text{ yr}^{-1}$ . In the non-grazed brackish *Phragmites australis-Scirpus maritimus* marsh at the river mouth, production was  $824 \text{ g m}^{-2} \text{ yr}^{-1}$ , whereas in an unprotected site nearby, grazing was so intense that above ground vegetation was eliminated. Decomposition rates were significantly different among species and plant parts but not among sites when the same species were used. Root decomposition was not significantly different with depth. Shoots had the highest decomposition rates with mean K values of  $0.033 \text{ wk}^{-1}$  for *Arthrocnemum fruticosum*,  $0.024 \text{ wk}^{-1}$  for *Phragmites australis* and  $0.019 \text{ wk}^{-1}$  for *Typha angustifolia*. Root decomposition had mean K values of  $0.0042 \text{ wk}^{-1}$  for *Arthrocnemum fruticosum*,  $0.021 \text{ wk}^{-1}$  for *Phragmites australis* and  $0.038 \text{ wk}^{-1}$  for *Typha angustifolia*. The decomposition rate of woody stems of *Arthrocnemum glaucum* had a mean K value of  $0.0037 \text{ wk}^{-1}$ . The main factors affecting primary production are grazing, soil salinity, waterlogging and nutrients. Human impacts such river and sea dikes, impoundments, and introduction of large grazers have altered productivity, diversity and successional patterns of the vegetation communities. Increases in sea level will exacerbate these impacts because of increased waterlogging and salt stress. These impacts are presently leading to wetland loss and this will likely accelerate unless conditions are changed.

**ADDITIONAL INDEX WORDS:** Wetlands, waterlogging, grazing, sea level rise, hypersalinity, Mediterranean.

## INTRODUCTION

Intertidal wetlands make up a significant proportion of many coastal systems. This is especially true in deltaic areas where there are often large expanses of near sea level wetlands. These wetlands are ecologically and economically important in terms of nutrient cycling, sediment dynamics, trophic interactions, habitat for many species of nekton and wildlife, and fisheries (DAY *et al.*, 1989; MITSCH and GOSSELINK, 1986). The biomass and productivity of coastal wetlands are good indicators of vegetation health and of the importance of

wetlands to ecosystem functioning (DAY *et al.*, 1989). Factors such as competition, salinity, degree of waterlogging, and nutrient status play important roles in regulating productivity (PENNINGS and CALLAWAY, 1992; COOPER, 1982; CALLAWAY *et al.*, 1990; MAHALL and PARK, 1976 a, b, c).

One of the most critical problems facing many deltaic wetlands is a high rate of relative sea level rise (RSLR) due to a combination of eustatic sea level rise and subsidence. The current rate of eustatic rise is  $1-2 \text{ mm yr}^{-1}$  (GORNITZ *et al.*, 1982). Subsidence in the Rhône Delta ranges from 0.5 to 4.5 mm/yr (L'HOMER, 1992), thus, RSLR in the delta is between 1.5 and 6.5 mm/yr, whereas accretion rates have been drastically re-

duced in the deltaic plain by the construction of dams, river dikes and impoundments (DAY *et al.*, 1995; HENSEL *et al.*, 1998). Vertical accretion must lead to a marsh surface elevation gain which keeps pace with RSLR to avoid increased flooding stress. It is also predicted that there will be an acceleration of eustatic sea level rise of about 50 cm over the next 100 years due to global warming (IPCC, 1996). If vertical accretion rates in the deltaic plain do not keep pace with present and future RSLR rates, wetlands will likely undergo reduced primary production due to salt stress and waterlogging, and they may ultimately disappear. Current evidence indicates that high RSLR is leading to wetland loss, coastal erosion and salt water intrusion in a number of coastal areas (GORNITZ *et al.*, 1982; CLARK, 1986; HACKNEY and CLEARY, 1987; KANA *et al.*, 1986; CONNER and DAY, 1989; DAY and TEMPLET, 1989; SESTINI, 1992 a,b; STANLEY, 1988, 1990).

In order to investigate spatial patterns of productivity and the factors affecting wetland health and survival in the Rhône Delta under RSLR conditions, as well as to propose management practices to prevent wetland deterioration, we began a research program in 1992, called "Impacts of sea level rise on the Rhône Delta." In this program, a number of environmental and biological factors related to the consequences of RSLR were studied, including the subsidence rate, wetland production and decomposition, vertical accretion and wetland surface elevation change, organic and inorganic matter accumulation, spatial and temporal patterns of soil salinity and water levels, and sediment characteristics. In this paper we present results of studies of above ground primary production as well as above ground and below ground decomposition in several different types of wetlands in the Rhône delta. Previous literature concerning primary production and decomposition of wetlands is very extensive, especially for helophytic species (MASON and BRYANT, 1975; WHITE *et al.*, 1978; HOPKINSON *et al.*, 1978, 1980; HACKNEY and DE LA CRUZ, 1980; BRINSON *et al.*, 1981; WHITE and TRAPANI, 1982; SCHUBAUER and HOPKINSON, 1984; BUTH and DE WOLF, 1985; WEBSTER and BENFIELD, 1986; GRONENDIJK and VINK-LIEVAART, 1987; HIETZ, 1992; MITSCH and GOSSELINK, 1986). However, there has been little research concerning primary production and decomposition of coastal shrub species of the family Chenopodiaceae (often referred to as *Salicornia* type species) such as *Arthrocnemum glaucum* (more recently named *Arthrocnemum macrostachyum*) and *Arthrocnemum fruticosum* (more recently named *Sarcocornia fruticosa*) and other similar species, which are very extensive in coastal wetlands with Mediterranean climates (MAHALL and PARK, 1976 a; BERGER *et al.*, 1978; REY *et al.*, 1990; PENNINGS and CALLAWAY, 1992).

The specific objectives of the study were:

1. To measure seasonal changes in above ground biomass of a number of characteristic wetland species in three different areas of the Rhône delta and to calculate above ground productivity for these sites.
2. To measure the decomposition of above ground and below ground plant parts in the different study sites.
3. To measure several environmental variables including, ground water and surface water salinity, water levels, and

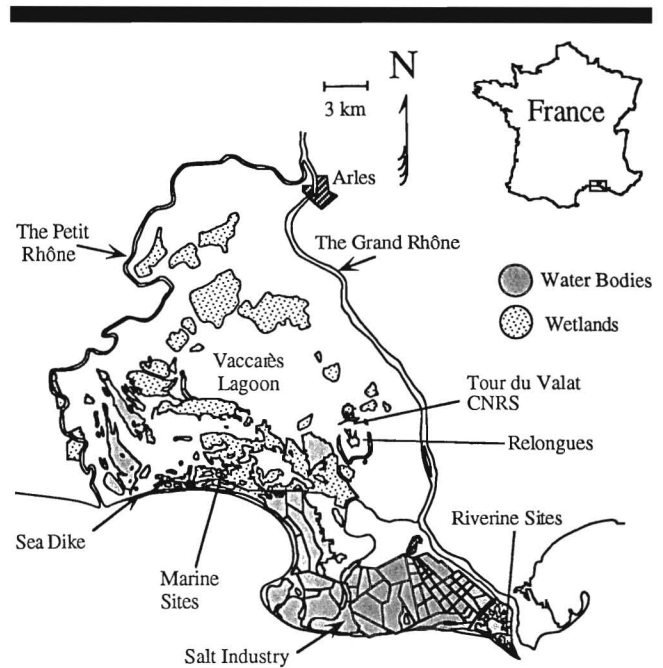


Figure 1. The central Rhône Delta, known as the Camargue. The three types of study sites are indicated on the map. Marine sites: Digue North and Digue South; Riverine sites: Palissade Exclosure and Palissade Impoundment. Managed sites: Relongues In, Relongues Out and Tour du Valat CNRS.

soil surface elevation and to relate these to productivity and decomposition patterns.

4. To consider the role of human modifications and sea level rise on the vegetation communities of the Rhône delta.

#### AREA AND SITE DESCRIPTION

The delta of the Rhône River is one of the largest Mediterranean deltas. It has a surface area of 1750 Km<sup>2</sup>, and its central part, the Camargue (750 Km<sup>2</sup>), is a protected area located between the two main distributaries, the Petit Rhône and the Grand Rhône (Figure 1). The Camargue contains large areas of wetlands that are ecologically important as wildlife habitat and for fisheries (TAMISIER, 1990), but the natural system has been greatly altered by human activities such as agriculture (mainly rice and orchards), grazing by cattle and horses, and salinas (areas of salt production) (TAMISIER and GRILLAS, 1994). The upper Camargue and the areas close to the river channels are mainly devoted to agriculture, whereas the lower Camargue is largely occupied by shallow lagoons, salt marshes and salinas (Figure 1), due to the low land elevation (<0.5 m above msl).

Seven sampling sites were established in three different areas of the Camargue (Figure 1): a low-salinity area close to the mouth of the Grand Rhône (La Palissade), a high salinity marine area located adjacent to the Mediterranean in the south-central Camargue (Digue a la Mer), and two managed fresh to saline areas located in the east-central Camargue (Tour du Valat and Relongues). Elevations of the different sites above mean sea level (msl) were determined from 1:

25,000 topographic maps. The sites are characterized by differences in riverine and marine influence, salinity, water depth, grazing by cattle and horses, and degree of impoundment, which are described below.

(1) Palissade Enclosure is located in a microtidal area bordering a canal connecting the Rhône River (near the mouth) with a shallow lagoon. The area is a brackish marsh with a vegetation coverage >90% which is protected from grazing by a fenced enclosure. The dominant species are *Phragmites australis*, *Scirpus maritimus* and *Scirpus lacustris*. The zone adjacent to the enclosure is heavily grazed and marsh vegetation is very sparse or absent. Within this grazed zone, there were two small 4 × 4 m enclosures constructed for sedimentation studies which we monitored for vegetation growth. The tide range at this site is about 25 cm and there is regular flooding by river and low-salinity near-shore water. The elevation is 5–10 cm msl.

(2) Palissade Impoundment is located in an impounded salt marsh about one km north of the first site where vegetation cover is greater than 90%. The dominant species is *Arthrocnemum fruticosum*, accompanied by *Juncus maritimus*, *Salicornia gr.europaea* and *Halimione portulacoides*. This area is surrounded by low dikes with one water control structure which greatly reduce water exchange. The elevation is about 10 cm above msl.

(3) Digue a la Mer South (referred to as Digue South) was located on the south side of Digue a la Mer, a sea dike constructed during the last century to restrict movement of sea water into the lower Camargue. The site is adjacent to a shallow lagoon which has a free connection with the sea about 0.5 km away. The area has a vegetation cover >90% and high biomass. The most abundant species is *Arthrocnemum fruticosum*, accompanied by *Halimione portulacoides*, *Suaeda fruticosa* and *Limonium vulgare* in the highest elevation. Elevation is 20–30 above msl.

(4) Digue a la Mer North (referred to as Digue North) was located on the north side of Digue a la Mer, about 100 m from the Digue South site. It is thus isolated from normal marine flooding. Vegetation cover is less than 50% and biomass is low. The most abundant species is *Arthrocnemum glaucum*, with lesser occurrence of *Arthrocnemum perennis* and *Arthrocnemum fruticosum*. Both Digue sites are subject to grazing. Elevation is about 10 cm above msl.

(5) Relongues Out was in a grazed fresh-marsh located in an abandoned arm of the Rhône River within Tour du Valat, a private nature reserve in the east-central Camargue. The marsh is dominated by *Scirpus maritimus* with lesser occurrence of *Scirpus lacustris* and vegetation cover is about 70%.

(6) Relongues In was located adjacent to the Relongues Out site in a 5 × 5 m enclosure which protected the site from grazing. The dominant species is *Typha angustifolia* but *Scirpus maritimus* was also present. Vegetation cover was 100%. Elevation for both Relongues sites is 10–20 cm above msl.

(7) Tour du Valat CNRS was located on the flank of a relic natural levee of the Rhône River in the Tour du Valat reserve about two km north of the Relongues site. The area is a grazed salt marsh with vegetation cover of about 50%. The most abundant species is *Arthrocnemum glaucum*, with some

patches of *Arthrocnemum fruticosum* in the highest elevations. Other species present are *Suaeda fruticosa*, *Halimione portulacoides*, and *Limonium vulgare*. Elevation is about 50 cm above msl.

## MATERIALS AND METHODS

Estimates of above ground primary production were calculated from periodic harvest of above ground biomass. In each study site, a 40 × 40 m plot was randomly established near the middle of the area. At each sampling period, sampling locations within the plot were randomly selected taking care not to resample previously-harvested locations. For helophytic species (*Phragmites australis*, *Scirpus lacustris*, *Scirpus maritimus* and *Typha angustifolia*), all above ground biomass was harvested from 5 quadrats of 0.1 m<sup>2</sup> at approximately 40 day intervals from October 1992 until October 1993 for a total of nine sampling events. For *Arthrocnemum glaucum* and *Arthrocnemum fruticosum*, 10 replicates of 0.25 m<sup>2</sup> were harvested from each site in October 1992 (end of the growing season). From this sampling, we determined that seven replicates were sufficient. After, 7 replicates were harvested from each site in March (beginning of the growing season), May, and August 1993 (peak biomass). Differences in biomass among locations and sampling periods were tested using a 2-way ANOVA test (see SOKAL and ROHLF, 1995). At the beginning of the study, ground water wells were established at each site. At each sampling interval, water level (either surface or ground water) was measured with a staff gauge and conductivity and temperature (of the surface or ground water) were measured with a Merck CM85T field conductivity meter. In the absence of surface water, conductivity and temperature were measured in the root zone (–30 cm), or in the top of the water column when the level was lower than 30 cm. Differences between means of environmental variables were tested using a Kruskal-Wallis test (see SOKAL and ROHLF, 1995).

The biomass samples were separated into live and dead material for each species and then dried at 70 °C to constant weight. The glassworts were further separated into leafy stems, senescent leafy stems and woody stems following the terminology of MAHALL and PARK (1976a). Above ground primary production for the helophytes was calculated according to the Smalley method (see LINTHURST and REIMOLD, 1978) based on changes in live and dead biomass. Peak live above ground biomass was used to estimate productivity for glasswort species (*Arthrocnemum fruticosum* and *Arthrocnemum glaucum*). This method has been successfully used before in the Camargue and elsewhere (BERGER *et al.*, 1978; MAHALL and PARK, 1976 a). Turnover rates were calculated as the ratio of annual production to mean yearly live biomass. In order to have an idea of the turnover and growth of leafy stems, 5 shoots on each of 8 different plants of *Arthrocnemum fruticosum* (from Palissade Impoundment) were tagged and total length, and the number and length of green and senescent leafy stems (after MAHALL and PARK 1976a), were measured on seven occasions.

Decomposition of above and below ground biomass of *Arthrocnemum fruticosum*, *Typha angustifolia* and *Phragmites*

*australis* was determined from the disappearance of materials from litter bags (MASON and BRYANT, 1975; HACKNEY and DE LA CRUZ, 1980; BUTH and DE WOLF, 1985; HIETZ, 1992) at six sites (Digue North, Digue South, Palissade Impoundment and Tour du Valat CNRS for *Arthrocnemum fruticosum* and Palissade Exclosure and Relongues Out for the two helophytes). Litter bags were placed in the field in February 1993, using dead above ground biomass and roots collected from entire plants excavated from the primary production plots during the previous two months. Root material was washed of soil material before drying. The litter bags were 10 × 45 cm with a mesh size of 1.5 mm. For *Arthrocnemum fruticosum*, each bag had 5 compartments: one for shoots and one for woody stems (both placed on the ground surface) and three for roots, placed at three different depths (5, 15 and 25 cm). For the helophytes, each bag had 4 compartments: one for above ground biomass (placed on the ground surface) and three for roots, placed at the same depths. All the samples of each compartment contained 3 gr of dry biomass, except the shoots and woody stems of *Arthrocnemum fruticosum*, which contained 3 gr of fresh weight and 5 gr of dry weight, respectively. The *Arthrocnemum fruticosum* material used for the decomposition experiments was collected from the Palissade Impoundment site while *Typha angustifolia* and *Phragmites australis* material used was collected from the plots in which the litter bags were placed. *Typha angustifolia* and *Phragmites australis* material was placed in separate litter bags. Two replicates from each plot and each species were removed after 1, 4, 8, 16 and 43 weeks. The samples were carefully rinsed, invertebrates removed, and the remaining biomass was dried at 70 °C until constant weight.

The decomposition data were fit to an exponential function as follows:

$$y = e^{-kt}$$

where  $y$  = percent of material remaining,  $k$  = decomposition constant,  $t$  = time (weeks).

The  $k$  parameter was estimated for each replicate of species, location and depth using non-linear regression (NLIN) and the SAS statistical analysis package. A series of ANOVA's with a 2-way cross classified design were used to test the null hypothesis that the  $K$  coefficient was equal for all levels of each factor in the models. A significant result is interpreted to mean that the rate of decomposition differs among the levels of the given factor.

## RESULTS

### Above Ground Biomass Changes

There were strong seasonal patterns of live and dead above ground biomass for the three sites with helophytic species (Figure 2), with statistically significant differences among locations and sampling periods for both live and dead biomass (Table 1). In all cases, live biomass was zero from January to March, when the growing season started. Patterns were very similar and strongly seasonal, with maximum live biomass occurring between July (Relongues Out, 396 g m<sup>-2</sup>) and September (Relongues In, 861 g m<sup>-2</sup> and Palissade Exclosure,

522 g m<sup>-2</sup>), and maximum dead biomass occurring in fall and winter. Species at Relongues Out, which is dominated by *Scirpus maritimus*, had a shorter growing season and a more marked (but much lower) peak live biomass than plants at the other two sites. Relongues In (dominated by *Typha angustifolia*) and Palissade Exclosure (dominated by *Phragmites australis*) had a period of rapid increase in biomass at the beginning of the growing season (from March to May) followed by a period of slower growth (from May to August). The decrease of live biomass was also rapid in all three cases, but it occurred earlier in Relongues Out (from August to November) than in the other two sites (from November to January). Standing dead biomass was highest in the fall and winter months and decreased through the spring and reached lowest levels during the summer.

The measured seasonal patterns of biomass for the glasswort species did not show statistically significant differences either for live and dead components, but they did among locations (Table 1). The sites dominated by *Arthrocnemum fruticosum* (Palissade Impoundment and Digue South) had much higher average (2094 and 1540 g m<sup>-2</sup>) and peak biomass (2779 and 2157 g m<sup>-2</sup>) levels than those dominated by *Arthrocnemum glaucum* (Digue North and Tour du Valat CNRS) (Figure 3). Maximum live biomass was measured in June or July for all sites although high biomass occurred in late October for *Arthrocnemum glaucum* at Tour du Valat CNRS. Minimum live biomass occurred in March; in Digue North, the October value was only slightly higher than that in March. After the winter, the percentage of green leafy stems was low due to the occurrence of low temperatures, so most of the live biomass was in the form of lignified parts. Dead biomass was generally higher in the fall and winter periods.

The total number of leafy stems did not vary much over the year for the measured shoots of *Arthrocnemum fruticosum* from the Palissade Impoundment site, but the proportion of those stems which were green changed significantly over time (Figure 4). The total number of leafy stems was generally between 20–40 per shoot but sometimes with an increase in July, however the percentage which were green was close to zero in the winter and early spring and varied from 60–100% in the summer and early fall. Leafy stems were red during the winter probably due to a cessation in growth as a result of low temperatures. The increase in total leafy stems from April to July was due to ramification -the growth of new leafy stems- and the lignification of old stems (as described by CAMERON 1972).

### Above Ground Primary Production

Primary production (Table 2) was maximum (2989 g dry wt m<sup>-2</sup> yr<sup>-1</sup>) at Relongues In, the freshwater *Typha* marsh protected from cattle grazing. For Relongues Out, the site subject to grazing, production was much lower (452 g m<sup>-2</sup> yr<sup>-1</sup>). In the brackish Palissade Exclosure site which was protected from grazing, primary production of the *Phragmites-Scirpus* dominated wetland was 824 g m<sup>-2</sup> yr<sup>-1</sup>. In the adjacent grazed area at Palissade Exclosure, above ground vegetation was virtually absent. In the salt marshes dominated

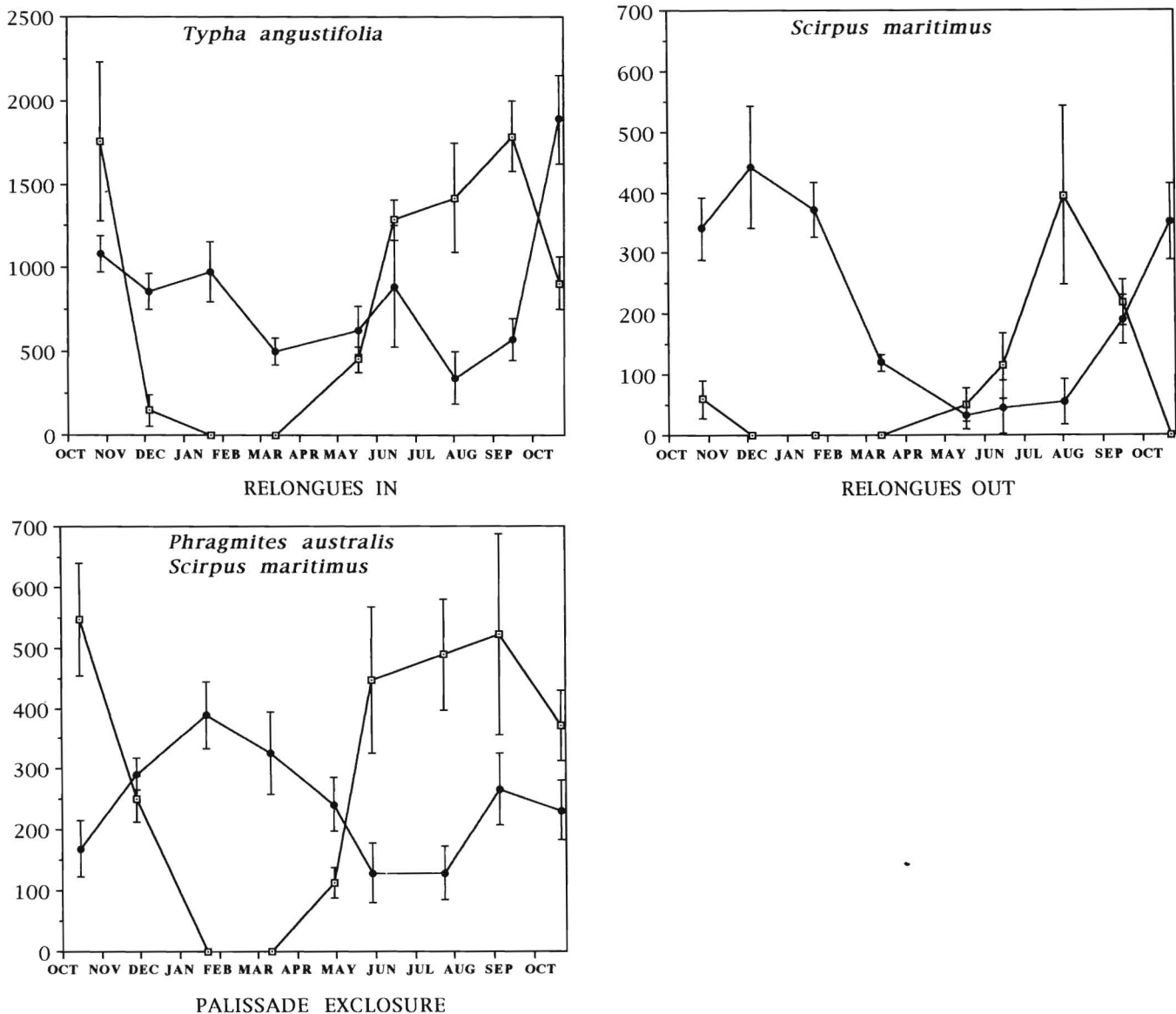


Figure 2. Seasonal changes in live (open squares) and dead (closed squares) biomass ( $\text{g m}^{-2} \text{yr}^{-1}$ ) during the study period in the helophytic sites. Vertical bars are  $\pm$  one standard error.

by *Arthrocnemum fruticosum*, productivity was considerably higher (Digue South,  $1262 \text{ g m}^{-2} \text{yr}^{-1}$ ; Palissade Exclosure,  $1123 \text{ g m}^{-2} \text{yr}^{-1}$ ) than salt marshes dominated by *Arthrocnemum glaucum* (Digue North,  $244 \text{ g m}^{-2} \text{yr}^{-1}$ ; Tour du Valat CNRS,  $294 \text{ g m}^{-2} \text{yr}^{-1}$ ).

Turnover rates (production/mean biomass) were considerably higher for the helophytic species than for the glassworts. The highest turnover occurred in Relongues Out ( $4.9 \text{ yr}^{-1}$ ), a grazed site dominated by *Scirpus maritimus*, whereas the minimum was in the Palissade Impoundment, a site located in a well developed *Arthrocnemum fruticosum* salt marsh ( $0.5 \text{ yr}^{-1}$ , Table 2).

### Conductivity, Water Levels and Temperature

There were highly significant differences among locations for mean water level and conductivity (Table 3) which showed statistical differences among locations (Kruskal-Wallis test,  $P = 0.0001$ ), but differences were not significant for temperature (Kruskal-Wallis test,  $P = 0.67$ ). The conductivity of the salt marshes with glasswort vegetation had significantly higher levels than the sites with helophytic vegetation. The highest conductivity values, with a mean of  $84.6 \text{ mS cm}^{-1}$ , occurred at Digue North, which was hypersaline all the year. By contrast, Digue South, less than 100 m away on the sea side of the dike, had a mean conductivity of  $34.6 \text{ mS cm}^{-1}$ .

Table 1. Results of the analysis of variance (2-way ANOVAs) of helophytes and glasswort species for live and dead biomass. Factors are location and sampling period. Significant for  $p < 0.05$ .

Variable	df	Sum of Squares	F	p
<b>HELOPHYTES</b>				
Live biomass				
Location	2	14195062	73.341	0.0001
Month	8	1430015	18.471	0.0001
Station $\times$ month	16	9889011	6.387	0.0001
Dead Biomass				
Location	2	11961940	86.790	0.0001
Month	8	4559839	8.271	0.0001
Station $\times$ month	16	5062158	4.591	0.0001
<b>GLASSWORTS</b>				
Live biomass				
Location	3	15760351	13.258	0.0001
Month	3	1357620	1.142	0.3417
Station $\times$ month	9	3431400	0.962	0.4824
Dead biomass				
Location	3	1065046	5.217	0.0034
Month	3	327986	1.607	0.2001
Station $\times$ month	9	746720	1.219	0.3057

Palissade Impoundment was hypersaline for much of the year but with values lower than Digue North. The mean conductivity was  $57.4 \text{ mS cm}^{-1}$  with the lowest values during the spring. The Tour du Valat CNRS site had a mean value of  $47.8 \text{ mS cm}^{-1}$ . The freshest site was Relongues, with a mean value of  $2.7 \text{ mS cm}^{-1}$ , whereas the Palissade Exclosure site was brackish (mean value of  $14.9 \text{ mS cm}^{-1}$ ) with the lowest values in the spring.

The salt marsh sites with glassworts generally had little or no surface water during the study period. The deepest ground water levels occurred at Tour du Valat CNRS because of the high elevation of this site. Digue North had shallower ground water levels than Digue South. The Palissade Impoundment site had the shallowest ground water levels and was flooded during the spring period of high river flow. The Palissade Exclosure site also often had surface water due to riverine flooding. The Relongues site was always flooded due its location in the relic river channel. There were no significant differences in mean water temperature among the different sites but there was a seasonal temperature signal with the highest values in summer and the lowest in winter. Temperature ranged from a low of  $9.5 \text{ C}$  at Palissade Exclosure in January to  $23.7$  at Digue North in June.

### Decomposition

The K values, regression coefficients and t values for significance of regression are shown in Table 4 and Figure 5. All regressions were statistically significant except two, for roots at 25 cm from Digue North and Palissade Impoundment. Table 5 shows the ANOVA's results of testing the K values for each species as a function of the plant part and the location. For *Arthrocnemum fruticosum*, decomposition rates were significantly different between leafy stems and woody stems ( $p = .0001$ ), but there were no significant differences in decomposition of either leafy stems or woody stems among sites. Root decomposition was not significantly different with

depth. Leafy stems had the highest decomposition rates with K values ranging from  $0.044$  to  $0.023 \text{ wk}^{-1}$ . K ranged from  $0.0039$  to  $0.0033 \text{ wk}^{-1}$  for woody stems and from  $0.0067$  to  $0.0015 \text{ wk}^{-1}$  for roots. Results from Relongues Out are not shown because litter bags were destroyed by cattle during the experiment.

There were significant differences in below ground decomposition between *Phragmites australis* ( $p = .0103$ ) and *Typha angustifolia* ( $p = .033$ ) but there were no differences with depth. There were no significant differences in above ground decomposition between species and sites. Above ground K values were  $0.024$  and  $0.019 \text{ wk}^{-1}$  for *Phragmites australis* and *Typha angustifolia*, respectively. K for roots ranged from  $0.025$  to  $0.019 \text{ wk}^{-1}$  for *Phragmites*, and from  $0.040$  to  $0.034 \text{ wk}^{-1}$  for *Typha*. Although the exponential fitting is satisfactory in general terms, in most of cases decomposition data can be divided in two nearly linear periods: the initial period of 10–15 weeks characterized by high decomposition rates followed by another with much slower rates (Figure 5).

### DISCUSSION

#### Comparison of Biomass Changes, Productivity and Decomposition Rates with Other Areas

Marked seasonal patterns of biomass and low or absent live above ground biomass in winter are characteristic of temperate zone coastal marshes. In the Rhône Delta, growth of *Phragmites* and *Typha* began in March, one month earlier than in Norfolk, England (MASON and BRYANT, 1975). In the Mississippi Delta, growth of *Phragmites communis* starts at the end of January when live biomass was low (HOPKINSON *et al.*, 1978). Standing biomass and primary production values obtained in this study for reed-type species are in the low range for *Phragmites* and in the high range for *Typha* (MASON and BRYANT, 1975; HOPKINSON *et al.*, 1978; BRINSON *et al.*, 1981). The Smalley method, used in this study for helophyte species, yields production estimates somewhat greater than methods based on peak live biomass, but it is inadequate for species in which growth, mortality and the disappearance of dead plant material occur at a relatively constant rates throughout the year (HOPKINSON *et al.*, 1980). However, our results show rapid and pronounced changes in live and dead biomass, and thus the underestimates of the Smalley method in this study may be small.

In the case of glasswort species, biomass changes among sampling periods were not statistically significant, so primary production estimates based on biomass changes can not be considered as statistically significant. This problem is common in studies of net primary production for perennial glasswort species because of a number of factors. These include less marked seasonal patterns and, in some cases, green leafy stems remaining during winter, as well as the large lignified standing stock, a non-homogeneous spatial distribution of vegetation, and the time-consuming processing of biomass samples. It was also difficult to accurately estimate loss rates of standing leafy stems, either when the litter method was used (due to the very fast decomposition rate) or when the tagging method was used (due to its small size and particular growth pattern). BERGER *et al.* (1978), using the

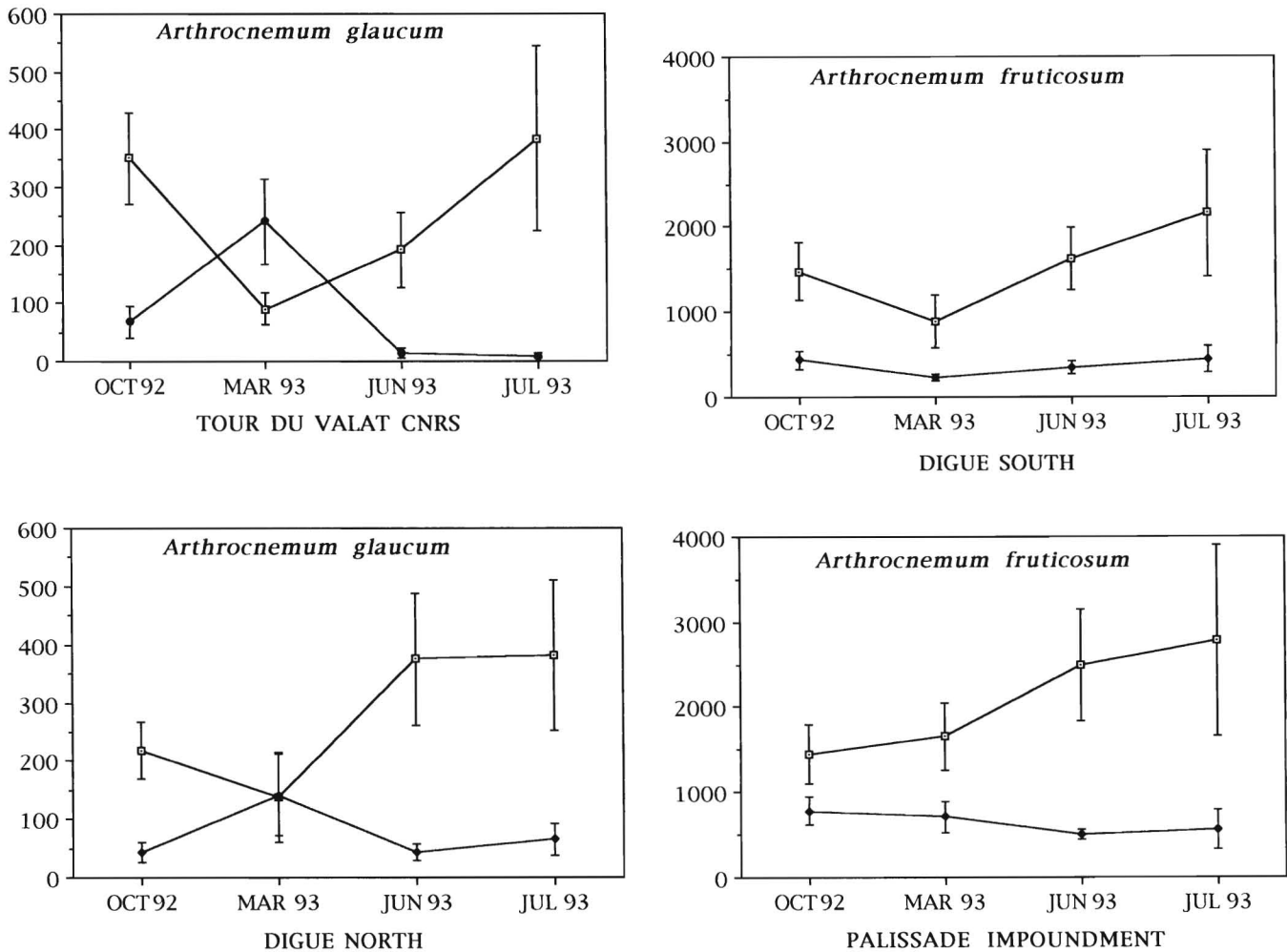


Figure 3. Live and dead biomass changes ( $\text{g m}^{-2} \text{yr}^{-1}$ ) of sites dominated by glassworts (Chenopodiaceae) during the study period. Palissade Impoundment and Digue South are dominated by *Arthrocnemum fruticosum* and Tour du Valat CNRS and Digue North are dominated by *Arthrocnemum glaucum*.

same methods, reported similar values to ours for productivity and biomass of *Arthrocnemum fruticosum* and *Arthrocnemum glaucum* at different locations in the Rhône delta. They reported biomass of 2000–3500  $\text{g m}^{-2}$  and primary production of 950–1000  $\text{m}^{-2} \text{yr}^{-1}$  for *Arthrocnemum fruticosum* and a biomass of around 400  $\text{g m}^{-2}$  for *Arthrocnemum glaucum*. In California, the above ground biomass of *Salicornia virginica* ranged from 400–2700  $\text{g m}^{-2}$ , and the primary production from 550 to 960  $\text{g m}^{-2} \text{yr}^{-1}$ , using the same method as our study (MAHALL and PARK, 1976; MALL, 1969).

The decomposition rates of *Arthrocnemum fruticosum* showed large differences between leafy stems and lignified parts (woody stems and roots). Leafy stems lost around 75% of the initial weight after 43 weeks, but it should be noted that most of the remaining material was small lignified parts that form the base of the leafy stems, and also that ash content of leafy stems is high (30% of dry weight in the study of BERGER *et al.*, 1978). This indicates that the organic matter in leafy stems decomposes almost completely during the first

year. In contrast, woody stems and roots only lost around 20% of initial weight after 43 weeks. These differences in decomposition, together with the fact that most of the leafy stems remain on the plant and become lignified, are reflected in the litter, which is composed almost entirely of lignified material. We know of no previous study of decomposition of *Arthrocnemum*-like species, but it has been reported that woody material decomposes slowly (BRINSON *et al.*, 1981).

By contrast, decomposition studies of helophytic species are quite common (see BRINSON *et al.*, 1981; HIETZ, 1992). The decomposition patterns and rates for *Typha angustifolia* and *Phragmites australis*, both for below and above ground biomass, were similar. The decomposition rate of above ground biomass was almost constant for the two species, as has been reported elsewhere for these two species (MASON and BRYANT, 1975). Approximately 50% of the material remained after 39 weeks for leaves of both species and roots of *Phragmites*, and around 25% for roots of *Typha*. The decomposition rates obtained by MASON and BRYANT (1975) for above

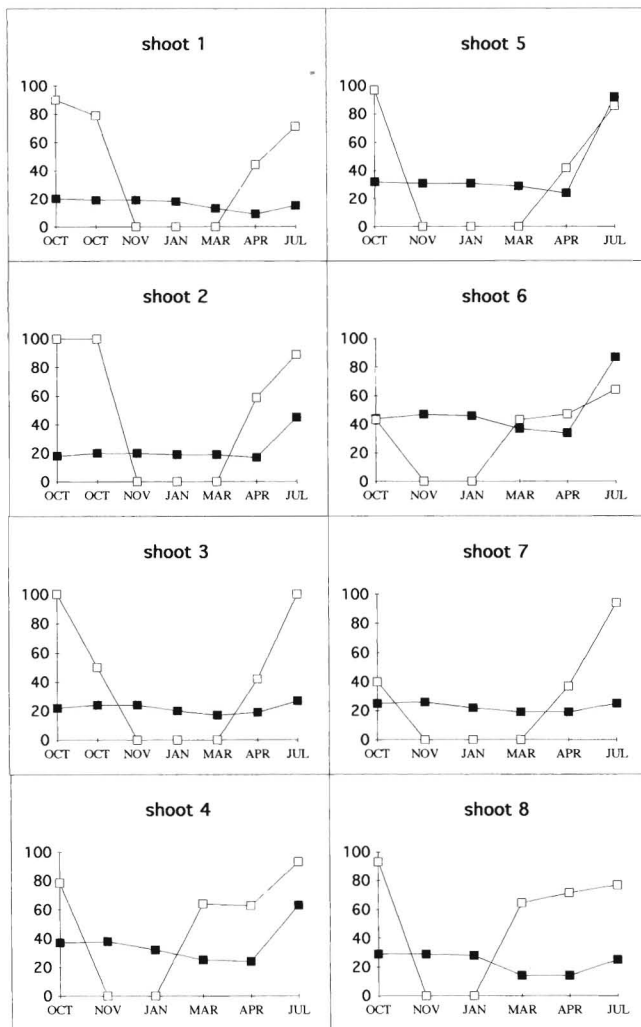


Figure 4. Changes during the study period in the total number of leafy stems (black squares) and the percentage of the total leafy stems which were green (white squares) in 8 different shoots of *Arthrocnemum fruticosum* from the Palissade Impoundment site.

Table 2. Biomass, production, and turnover values of the different study sites. Biomass parameters show the standard error.

Site	Annual Mean Biomass ( $\text{g m}^{-2}$ )		Peak Live Biomass ( $\text{g m}^{-2}$ )	Production ( $\text{g m}^{-2}$ over $\text{yr}^{-1}$ )	Turnover ( $\text{yr}^{-1}$ )
	LIVE	DEAD			
Palissade					
Exclosure	305 ± 74	242 ± 30	522 ± 165	824	2.7
Relongues In	862 ± 244	861 ± 152	1785 ± 213	2989	3.5
Relongues Out	93 ± 45	217 ± 53	396 ± 148	452	4.9
Digue North	278 ± 60	73 ± 23	382 ± 130	244	0.9
Digue South	1540 ± 260	364 ± 50	2157 ± 747	1262	0.8
Palissade					
Impoundment	2094 ± 321	635 ± 65	2779 ± 1118	1123	0.5
Tour du Valat					
CNRS	254 ± 69	84 ± 54	384 ± 160	294	1.2

Table 3. Conductivity ( $\text{mS cm}^{-1}$ ), temperature ( $^{\circ}\text{C}$ ) and water level (cm) during the study period at the different sampling sites. Blanks indicate no data.

	TV CNRS	TV REL	DIG N	DIG S	PAL IMP	PAL EXC
<b>Conductivity</b>						
22/10/92	46.7	1.6	102.7	43.2	74.7	17.2
11/11/92	57.0	2.0	95.3	38.8	74.5	16.7
30/11/92	43.0	2.8	84.4	33.1		
7/12/92			91.9	36.2	72.9	
19/1/93	40.7		84.6	28.4	72.2	10.8
10/2/93	55.7	2.2	83.2	30.6	71	
10/3/93		2.7			68.5	
27/4/93					14.3	
6/5/93		3.3			9.9	
1/6/93	43.6	4.4	49.9	31.7	58.8	
Mean	47.8	2.7	84.6	34.6	57.4	14.9
Std. error	2.8	0.3	6.4	1.9	8.7	2.0
<b>Temperature</b>						
22/10/92	14.8	17	15.1	13.6	14.1	11.8
11/11/92	14.3	11.7	13.3	13	16.5	15
30/11/92	13.3	9.6	13.4	12.3		
7/12/92			11.1	9.8	11.3	
19/1/93	11.3				10.7	9.5
10/2/93	10	14.4	11.6	10.2	10.9	
10/3/93		14.8			10.8	
27/4/93					13.7	
6/5/93		20.9			17	
1/6/93	20.1	23.1	23.7	22.3	23.1	
Mean	14.0	15.9	14.2	13.1	14.2	12.1
Std. error	1.4	1.8	1.7	1.6	1.4	1.6
<b>Water level</b>						
10/9/92	-6.3					
14/10/92						20
22/10/92	.22	1.5	0	-10	4	10
11/5/92		9				2
11/11/92	.30	6	-4	-13.5	-5.5	1
30/11/92	.39	4	-9	21.5	26	25.7
7/12/92			-6	-10	5	
19/1/93	-45	9.2	8.5	25	.9	-22
10/2/93	65	9	.8	28	-10	
3/3/93		9	2			6
10/3/93		11.7			-13	
19/3/93		6	3			
7/4/93		4			10	
27/4/93					20	
6/5/93		19.2			2	2
26/5/93	46				2	0
1/6/93	49	9.2	15	15	2	
Mean	44.9	8.1	-5.1	17.6	0.3	5.0
Std. error	5.2	1.3	2.0	2.7	3.0	4.5

ground biomass, were a little higher for *Phragmites* (50% remaining after 30 weeks) but a little lower for *Typha* (50% remaining after 1 year).

### Factors Affecting Productivity and Decomposition

A number of factors affected the patterns of production and decomposition that we observed including species, soil salinity, waterlogging, nutrients and grazing pressure. The highest productivity measured was for the Relongues In site, which is dominated by *Typha angustifolia*. This site is fresh, fed by nutrient-rich Rhône water, and is not affected by grazing. By contrast, the lowest productivity was at the Digue



Table 4. Decomposition constants (K), regression coefficients and t values (for significance of regression) obtained for different study sites, species and plant parts. \*  $p < 0.05$ . ns = not significant.

Site	Species	Plant Part	K Weeks	r <sup>2</sup>	t
Digue South	<i>Arthrocnemum fruticosum</i>	leaf stems	0.033	0.897	9.3*
		woody stems	0.0038	0.782	6.0*
		roots - 5 cm	0.0050	0.623	4.1*
		roots - 15 cm	0.0036	0.444	2.8*
		roots - 25 cm	0.0032	0.356	2.3*
Digue North	<i>Arthrocnemum fruticosum</i>	leaf stems	0.031	0.938	12.3*
		woody stems	0.0033	0.648	4.3
		roots - 5 cm	0.0039	0.601	3.9*
		roots - 15 cm	0.0036	0.551	3.5*
		roots - 25 cm	0.0026	0.250	1.8 ns
Palissade Impoundment	<i>Arthrocnemum fruticosum</i>	leaf stems	0.044	0.961	15.7*
		woody stems	0.0039	0.891	9.0*
		roots - 5 cm	0.0058	0.711	4.9*
		roots - 15 cm	0.0030	0.410	2.6*
		roots - 25 cm	0.0015	0.109	1.1 ns
Tour du Valat CNRS	<i>Arthrocnemum fruticosum</i>	leaf stems	0.023	0.886	8.8*
		woody stems	0.0036	0.872	8.3*
		roots - 5 cm	0.0055	0.656	4.4*
		roots - 15 cm	0.0067	0.750	5.5*
		roots - 25 cm	0.0058	0.672	4.5*
Palissade Exclosure	<i>Typha angustifolia</i>	shoots	0.019	0.965	18.8*
		roots - 5 cm	0.039	0.908	10.9*
		roots - 15 cm	0.040	0.903	8.6*
		roots - 25 cm	0.034	0.830	7.6*
Palissade Exclosure	<i>Phragmites australis</i>	shoots	0.024	0.942	15.1*
		roots - 5 cm	0.025	0.890	10.6*
		roots - 15 cm	0.019	0.897	11.0*
		roots - 25 cm	0.019	0.784	7.1*

North site, which has hypersaline ground water at or near the surface for much of the year, is affected by grazing and receives very little fresh water or nutrient input. High productivity has been often reported for *Typha* spp. (WESTLAKE, 1963; MASON and BRYANT, 1975) especially in nutrient rich situations (KADLEC and KNIGHT, 1996). The effect of grazing is clear at the Relongues site; the protected area had much higher productivity than the grazed site. In the Norfolk Broadlands of England, MASON and BRYANT (1975) reported values of 1081 and 551 g m<sup>-2</sup> yr<sup>-1</sup> for the same site in two successive years. The lower productivity the second year was due to grazing. Extensive stands of *Phragmites* are commonly found in the Mediterranean at river mouths and around coastal lagoons receiving freshwater inputs, where nutrients are abundant and salinity stress is low. The biomass and productivity of *Phragmites* found in our study is similar to values reported elsewhere in the Mediterranean (IBAÑEZ *et al.*, in press). In the Mississippi Delta, HOPKINSON *et al.* (1978) measured a higher above ground productivity (2318 g m<sup>-2</sup> yr<sup>-1</sup>) using the Wiegert-Evans method.

The growth rate of glasswort species seemed to be affected primarily by salinity but also by waterlogging, low nutrients, and grazing. Our values of above ground productivity are similar to those reported in other Mediterranean areas (IBAÑEZ *et al.*, in press). The highest production rates were at Palissade Impoundment and Digue South where salinities were near sea water. The soil was well drained at Digue South and neither site was strongly affected by grazing. The

Tour du Valat CNRS site had high soil salinity while the Digue North site had hypersaline ground water which was at or near the surface for much of the year. Although both sites were enclosed during the study, they had been affected by grazing prior to the study. These observations are similar to earlier reports on the factors affecting *Arthrocnemum fruticosum* and *Arthrocnemum glaucum* growth. BERGER *et al.* (1978) reported that low summer rainfall caused low growth and seed production for these two species in the Rhône delta. Long periods of waterlogging are stressful for *Arthrocnemum fruticosum*, probably due to anoxic conditions. ABDULRAHMAN and WILLIAMS (1981) reported that *Arthrocnemum fruticosum* growing on the Mediterranean coast of Libya had decreased production at high temperatures and salinities. ZEDLER *et al.* (1980) found that increased flooding can cause a decrease in productivity if soil salinities increase but can also result in higher production if salinities are lowered due to rainfall or upland runoff. FERREN (1985) reported that prolonged inundation can reduce the cover of, or totally eliminate, *Salicornia virginica*. MAHALL and PARK (1975) also reported that tidal immersion inhibits growth of *Salicornia virginica*.

Decomposition of organic matter in litter bags is not only influenced by temperature and flooding time, but also by tidal flushing which removes litter (WHITE and TRAPANI, 1982). However, lunar tides are very low in the Mediterranean (about 20 cm in the Rhône Delta), and they do not flush most of marshes. Marsh flushing is usually associated with episod-

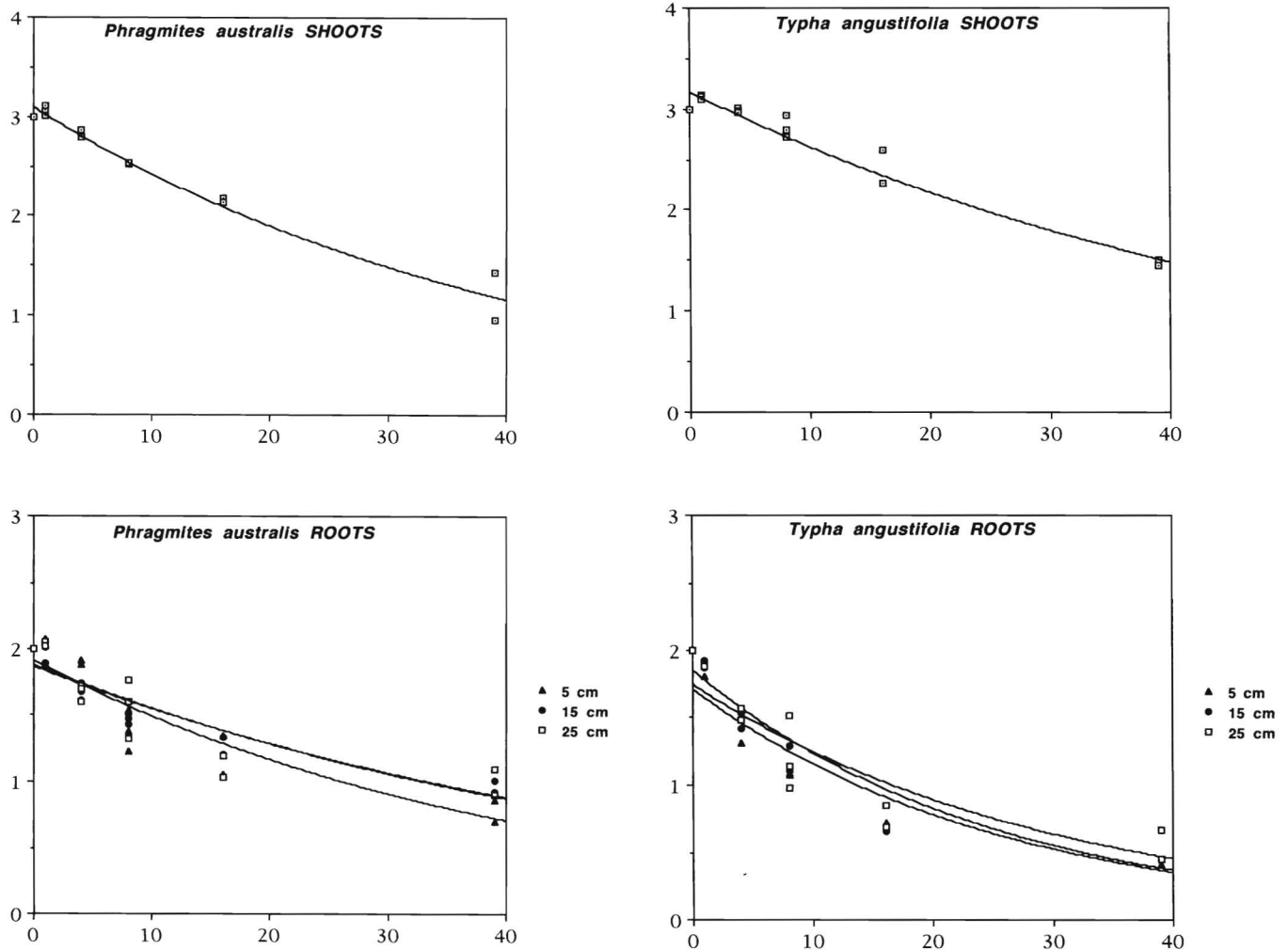


Figure 5. Decomposition curves obtained for the studied sites. The regression coefficient and the k values are shown in Table 4.  $x = \text{wk}$ ,  $y = \text{gr}$ .

ic events like storms or strong winds causing higher changes in water levels. We suspect that litter removal is more affected by these climatological forcings but that overall litter export is probably lower than in regularly flushed coastal marshes. Our study, in which decomposition experiments of *Arthrocnemum fruticosum* were carried out in four different sites, does not show significant differences among sites. This may be attributed to similar flooding conditions for all sites.

### Patterns of Productivity Related to Vegetation Succession

The data and observations presented here suggest successional patterns for both species and wetland productivity over the natural cycle of deltaic evolution, especially as affected by human activities. The factors affecting these patterns are soil salinity, soil waterlogging, grazing and nutrients. The Rhône like all other deltas has gone through a number of cycles of deltaic lobe building and abandonment (L'HOMER, 1992). There are at present two active arms of the river, but

a number of relic channels have been identified, including the Relongues channel where two of our sites are located. In freshwater areas such as these, which receive high inputs of riverine water and nutrients, very high biomass and productivity can be maintained by communities of *Scirpus* and *Typha*. Further seaward in the delta, in the vicinity of the river mouths, marshes of *Phragmites* develop in low salinity, microtidal areas, like in La Palissade. In the Rhône delta, these have a rather limited distribution because dikes limit the river's influence. However, in some deltas such as the Po and Mississippi, there are extensive *Phragmites* marshes. Productive salt marshes dominated by *Arthrocnemum fruticosum* occur in well drained areas where soil salinities are near that of sea water such as in the Digue South and Palissade Impoundment sites.

In isolated areas of the delta that do not receive direct flooding from the river or sea, hypersaline conditions can develop because of the lack of fresh water input, strong evaporation, and migration of hypersaline ground water towards

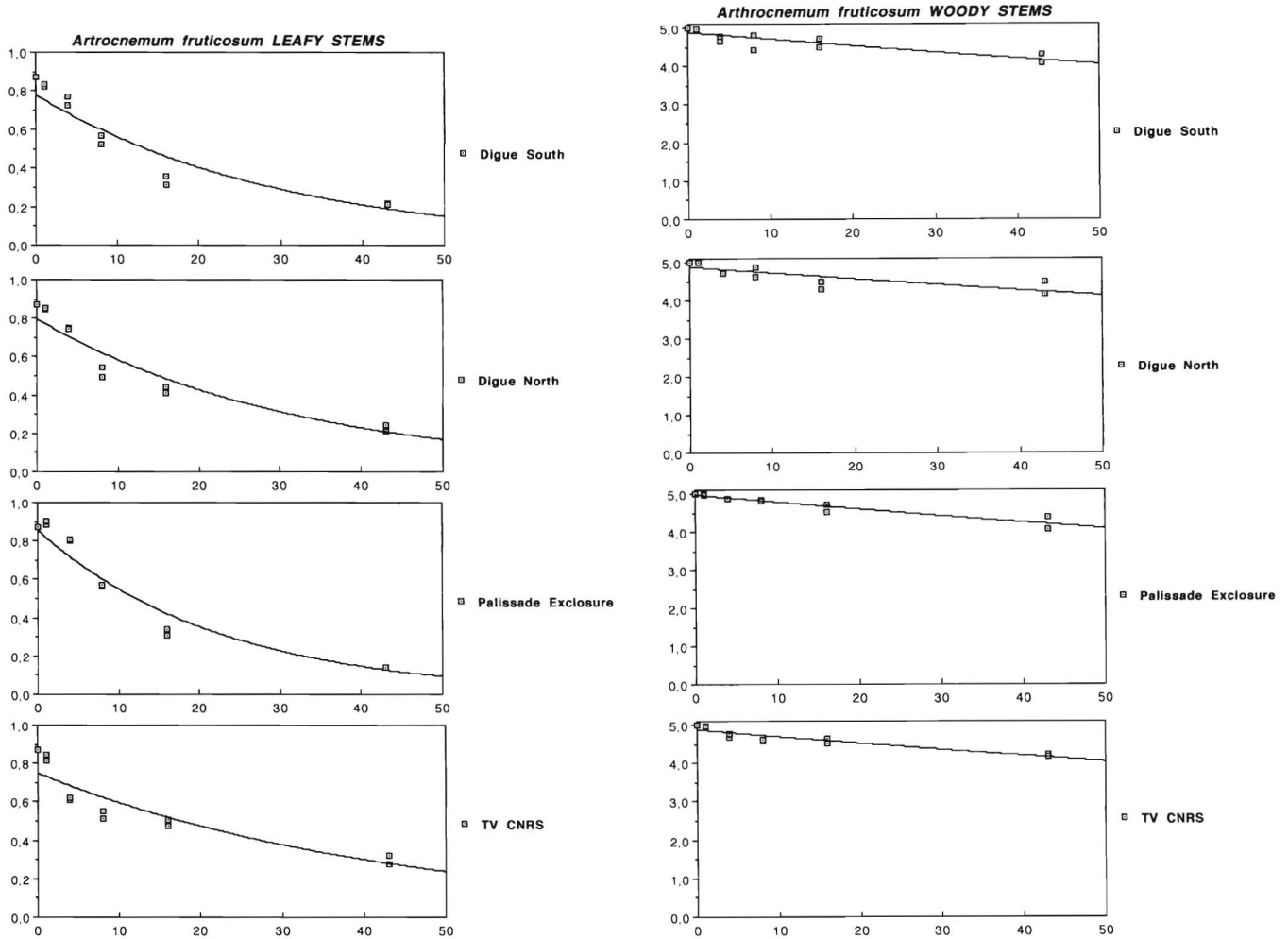


Figure 5. Continued.

the surface (HEURTEAUX, 1969). These areas also have low rates of accretion because external inputs of mineral sediments are low (HENSEL *et al.*, 1998) and *in situ* organic soil formation is also low due to low productivity exacerbated by low nutrients. Thus, these areas become progressively more flooded as accretion is unable to offset relative sea level rise (DAY *et al.*, 1995; HENSEL *et al.*, 1998). An extreme example of this situation is Digue North, which has the lowest productivity of all the sites. Here water levels are near the surface for much of the year, soil salinity is nearly twice that of sea water, and vegetation is dying over extensive areas. Coastal vegetation death due to sediment deficits, excessive waterlogging and salinity intrusion has been demonstrated for a number of coastal areas, especially the Mississippi delta (CAHOON, 1994; DELAUNE *et al.*, 1983; NYMAN *et al.*, 1990).

Grazing has a profound effect on both productivity and species composition. This was especially notable in the Relongues sites, where in addition to the decreased productivity noted above, there was a species shift from a *Typha* to a *Scirpus* community in the grazed area. Likewise, there was quite

high *Phragmites* biomass in the Palissade Exclosure site, while in the adjacent unfenced area, there was essentially no above ground vegetation. In 1994, grazing was excluded from the whole of the Palissade and there has been an invasion of helophytic genera such as *Scirpus*, *Juncus*, and *Phragmites* in areas formerly dominated by *Arthrocnemum fruticosum* and *Arthrocnemum glaucum*. We also noted invasion of grass species inside the exclosure at the Tour du Valat CNRS site which is also subjected to grazing. BASSETT (1980) also reported that in the *camargue*, *Phragmites* and *Scirpus* increased greatly when grazing was excluded and that *Arthrocnemum fruticosum* marshes remained relatively unchanged when there was grazing. Digue North is the only site where there has not been an invasion of grass species inside the exclosures, despite the fact that this area is occasionally grazed. We believe that this is due to the extremely stressful conditions of hypersalinity and continuous waterlogging in the root zone. Others have shown the effect of grazing on coastal wetlands. EVERS *et al.* (1998) reported that a combination of waterfowl and nutria grazing in the Atchafalaya

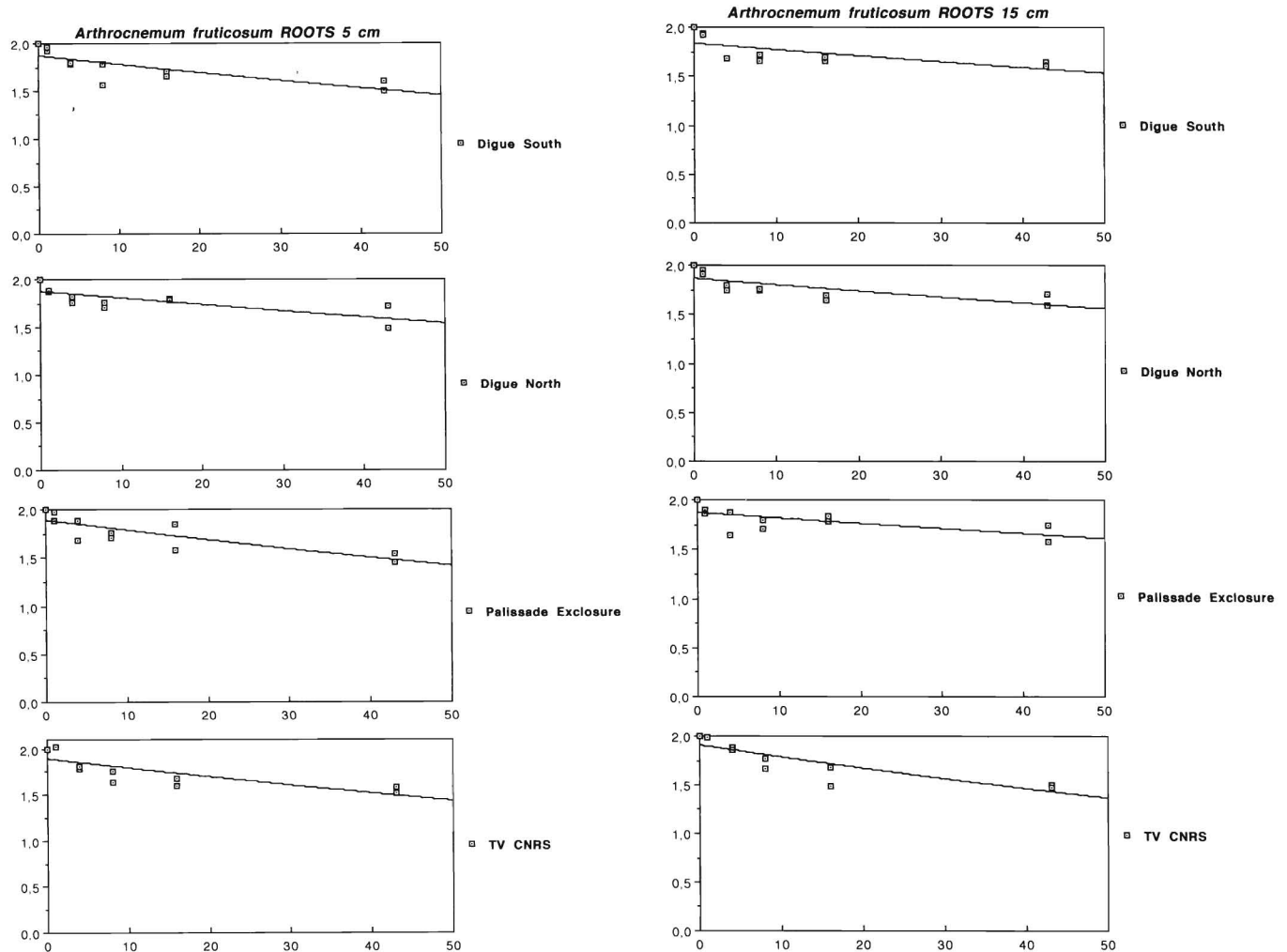


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delta, Louisiana, resulted in almost complete removal of vegetation. In the Netherlands, cattle grazing caused retrogressive succession in a salt marsh (BAKKER 1985).

In the absence of human activity, relatively high levels of productivity are maintained as species assemblages shift to those well adapted to prevailing conditions. Human activity has altered this cycle by changing the hydrology of the delta and by introducing grazing. Much of the area of the central and southern Rhône delta is similar to the conditions at Digue north, and wetlands will likely progressively disappear if management is not changed. Introduction of river water and reduction of grazing pressure would increase productivity of these areas. A similar situation exists in the Mississippi delta. Under natural conditions, when a deltaic lobe is abandoned, vegetation shifts from fresh to salt. This is compensated for by wetland formation in the area of active deltaic lobe formation (ROBERTS, 1997). However, suppression of channel switching and restricting the river to channel flow

by dikes has resulted in widespread wetland loss (DAY and TEMPLET, 1989; DAY *et al.*, 1997).

### Implications of Different Management Practices on Sustainability

The results of this study, in conjunction with findings by others, have implications for sustainable wetland management in the Rhône delta. This delta, like most deltas, has a relatively high rate of relative sea level rise (RSLR) due both to eustatic sea level rise and regional subsidence (L'HOMER, 1992; DAY *et al.*, 1995). In order to survive in the long term, deltaic wetlands must be able to grow vertically at a rate equal to RSLR (DAY and TEMPLET, 1989). The high productivity sites dominated by *Phragmites* and *Typha* are in areas of relatively high accretion. In the Palissade area, high accretion is due to riverine flooding. Accretion at the *Typha* site protected from grazing is mainly due to organic soil formation. This suggests that input of river water with suspended

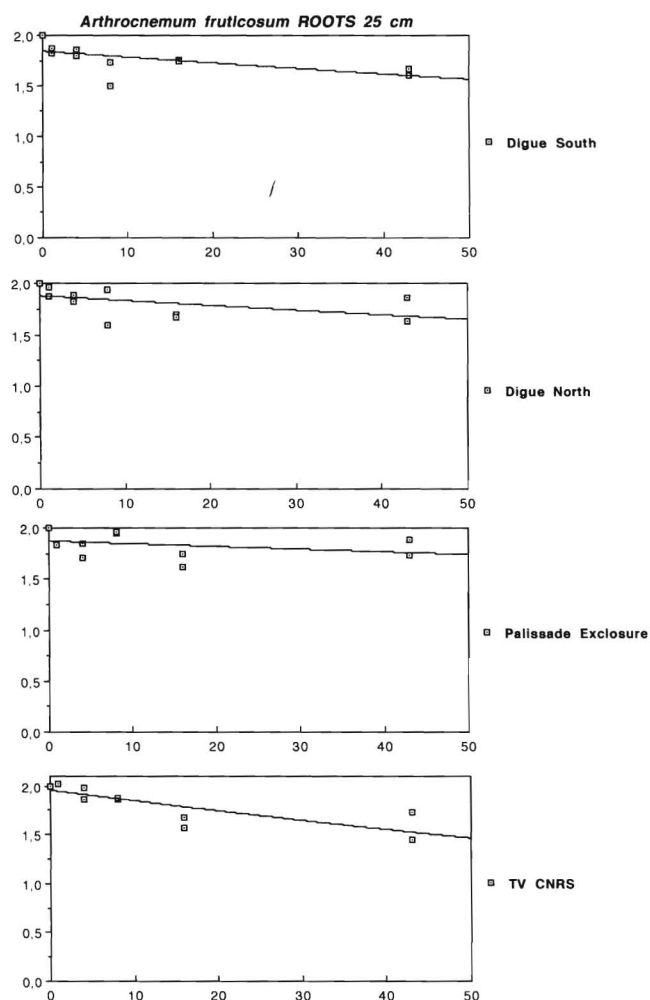


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mineral sediments and nutrients can contribute to sustainability of wetlands in the Rhône delta. Without sufficient input of river water, problems of hypersalinity and waterlogging are increased. Impounded sites, such as Digue North and Tour du Valat CNRS, have low production and low rates of vertical accretion (DAY *et al.*, 1995; HENSEL *et al.*, 1998). These sites, like the Relongues Out site, are also grazed. These results suggest that exclusion of riverine input combined with grazing is leading to non-sustainable conditions for Rhône delta wetlands. We believe that controlled inputs of river water can offset lack of accretion, waterlogging and high salinity. In a general sense, this is an example of using the natural energy pulses of the system to maintain ecosystem integrity and sustainability (DAY *et al.*, 1995). Future studies are needed to define how various grazing levels will affect diversity and productivity in a restored deltaic system.

#### ACKNOWLEDGMENTS

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Table 5. Results of the analysis of variance (2-way ANOVAs) of the  $k$  parameter for each species and plant part. Significant for  $p < 0.05$ .

Variable	df	Sum of Squares	F	p
<b>ABOVE-GROUND</b>				
<i>Arthrocnemum fruticosum</i>				
Location	3	0.24209	0.955	0.4591
Plant part	1	4.07590	48.24	0.0001
Location $\times$ plant part	3	0.24253	0.957	0.4584
<i>Typha</i> and <i>Phragmites</i>				
Location	1	0.00010	3.110	0.1760
Species	1	0.00024	7.155	0.0754
Location $\times$ species	1	0.00001	0.170	0.7081
<b>BELOW-GROUND</b>				
<i>Arthrocnemum fruticosum</i>				
Location	3	0.000083	1.961	0.1738
Depth	2	0.000077	2.724	0.1058
Location $\times$ depth	6	0.000042	0.494	0.8014
<i>Phragmites australis</i>				
Location	1	0.00815	13.566	0.0103
Depth	2	0.00004	0.030	0.9703
Location $\times$ Depth	2	0.00027	0.225	0.8051
<i>Typha angustifolia</i>				
Location	1	0.00830	14.114	0.0330
Depth	2	0.00010	0.850	0.5099
Location $\times$ depth	2	0.00013	0.113	0.8972

talunya" and, in part, by the EC Environment Research Programme "Climatology and Natural Hazards": MEDDELTE. Impact of Climate Change on Northwestern Mediterranean Deltas (contract EV5V-CT94-0465). Support was also supplied by the Franco-American Commission through a Fulbright Fellowship to J.W. Day. We thank Philippe Hensel, Jason Day and Hero Prins for their help in field surveys and sample processing. We also thank Frank Torre and Glenn Garson for their help in statistical analyses. We acknowledge the Station Biologique du Tour du Valat, Reserve National de Camargue and Reserve de La Palissade for permitting us to carry out the study in these protected areas and for providing logistical support and valuable advice.

#### LITERATURE CITED

- ABDULRAHMAN, F.S. and WILLIAMS, G., 1981. Temperature and salinity regulation of growth and gas exchange of *Salicornia frutescens* (L.) L. *Oecologia* 48, 346-352.
- BAKKER, J.P., 1985. The impact of grazing on plant communities, plant populations and soil conditions on salt marshes. *Vegetatio*, 62, 391-398.
- BASSETT, P.A., 1980. Some effects of grazing on vegetation dynamics in the Camargue, France. *Vegetatio*, 43, 173-184.
- BERGER, A.; CORRE, J.J., and HEIM, G., 1978. Structure, productivité et régime hydrique de phytocénoses halophiles sous climat méditerranéen. *La Terre et la Vie*, 32, 241-78.
- BRINSON, M.M.; LUGO, A.E., and BROWN, S., 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. *Annual Review of Ecology and Systematics*, 12, 123-161.
- BUTH, G.J.C. and DE WOLF, L., 1985. Decomposition of *Spartina anglica*, *Elytrigia pungens* and *Halimione portulacoides* in a Dutch salt marsh in association with faunal and habitat influences. *Vegetatio*, 62, 337-355.
- CAHOON, D., 1994. Recent accretion in two managed marsh impoundments in coastal Louisiana. *Ecological Applications*, 4, 166-176.

- CALLAWAY, R.M.; JONES, S.; FERREN, W.R., and PARIKH A., 1990. Ecology of a mediterranean-climate estuarine wetland at Carpinteria, California: plant distributions and soil salinity in the upper marsh. *Canadian Journal of Botany*, 69, 1139–1146.
- CAMERON, G.N., 1972. Analysis of insect trophic diversity in two salt marsh communities. *Ecology*, 53, 58–73.
- CLARK, J.S., 1986. Coastal forest tree populations in a changing environment, southeastern Long Island, New York. *Ecological Monographs*, 56, 259–277.
- CONNER, W.H. and DAY, J.W., 1989. Response of coastal wetland forests to human and natural changes in the environment with emphasis on hydrology. pp. 34–43. In: HOOK, D.D. and LEA, R. (eds.) *Proceedings of the symposium: The forested wetlands of the Southern United States*; Orlando, Florida General Technology Report SE-50. Asheville, NC: U.S. Depart. of Agriculture, Forest Service, Southeastern Forest Experiment Station. 168 pp.
- COOPER, A., 1982. The effects of salinity and waterlogging on the growth and cation uptake of salt marsh plants. *New Phytologist*, 90, 263–275.
- DAY, J.W., JR. and TEMPLET, P.H., 1989. Consequences of sea level rise: Implications from the Mississippi Delta. *Coastal Management*, 17, 241–257.
- DAY, J.W., JR.; HALL, C.; KEMP, W., and YAÑEZ-ARENCEBIA, A., 1989. *Esuarine Ecology*, New York: Wiley-Interscience, 558 p.
- DAY, J.W., JR.; PONT, D.; HENSEL, P.H., and IBAÑEZ, C., 1995. Impacts of sea level rise on deltas in the Gulf of Mexico and the Mediterranean: the importance of pulsing events to sustainability. *Estuaries*, 18(4), 636–647.
- DAY, J.; MARTIN, J.; CARDOCH, L., and TEMPLET, P., 1997. System functioning as a basis for sustainable management of deltaic ecosystems. *Coastal Management*, 25, 115–153.
- DELAUNE, R.; BAUMANN, R., and GOSSELINK, J., 1983. Relationship Among vertical accretion, coastal submergence, and erosion in a Louisiana Gulf Coast marsh. *Journal of Sedimentary Petrology*, 53(1), 147–157.
- EVERS, E.; SASSER, C.; GOSSELINK, J.; FULLER, D., and VISSER, J., 1998. The impact of vertebrate herbivores on wetland vegetation in Atchafalaya Bay, Louisiana. *Estuaries*, 21, 1–13.
- FERREN, W.R., 1985. Carpinteria salt marsh: environment, history and botanical resources of a southern California estuary. *The Herbarium* (University of California, Santa Barbara), 4, 108–120.
- GORNITZ, V.; LEBEDEFF, S., and HANSEN J.E., 1982. Global sea level trends in the past century. *Science*, 215, 1611–1614.
- GROENENDIJK, A.M. and VINK-LIEVAART, M.A., 1987. Primary production and biomass on a Dutch salt marsh: emphasis on the below-ground component. *Vegetatio*, 70, 21–27.
- HACKNEY, C.T. and DE LA CRUZ, A.A., 1980. In situ decomposition of roots and rhizomes of two tidal marsh plants. *Ecology*, 61, 226–231.
- HACKNEY, C.T. and CLEARY, W.J., 1987. Saltmarsh loss in southeastern North Carolina lagoons: importance of sea level rise and inlet dredging. *Journal of Coastal Research*, 3, 93–97.
- HENSEL, P.F.; DAY, J.W., JR.; PONT, D., and DAY, J.N., 1998. Short-term sedimentation dynamics in the Rhône River delta, France: the importance of riverine pulsing. *Estuaries*, 21, 52–65.
- HEURTEAUX, P. 1969. Rapports des eaux souterraines avec les sols halomorphes et la végétation en Camargue. *Actes de la Reserve de Camargue*, 37, 467–510.
- HIEZ, P., 1992. Decomposition and nutrient dynamics of reed (*Phragmites australis* (Cav.) Trin. ex Steud) litter in Lake Neusiedl, Austria. *Aquatic Botany*, 43, 211–30.
- HOPKINSON, C.S.; GOSSELINK, J.G., and PARRONDO, R.T., 1978. Aboveground production of seven marsh plant species in coastal Louisiana. *Ecology*, 59(4), 760–769.
- HOPKINSON, C.S.; GOSSELINK, J.G., and PARRONDO, R.T., 1980. Production of coastal Louisiana marsh plants calculated from phenometric techniques. *Ecology*, 61(5), 1091–1098.
- IBAÑEZ, C.; CURCO, A.; DAY, J.W., JR., and PRAT, N., In press. Productivity of Mediterranean coastal marshes and estuaries: differences with macrotidal systems. In: WEINSTEIN, M.P. and KREGER, D.A. (eds.), *Concepts and Controversies in Tidal Marsh Ecology*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- IPCC (INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE), 1996. *Climate Change: Adaptation and Mitigation of Climate Change: Scientific-Technical Analysis. Contribution of Working Group II to the IPCC In: WATSON, R.T.; ZINVOWERA, M.C., and MOSS, R.H. (eds.). Cambridge Univ. Press, New York. 880p*
- KADLEC, R. and KNIGHT, R., 1996. *Treatment Wetlands*. Boca Raton, Florida, Lewis Publishers, 893p.
- KANA, T.W.; BACA, B.J., and WILLIAMS, M.L., 1986. *Potential impacts of sea level rise on wetlands around Charleston, South Carolina*. U.S. Environmental Protection Agency, EPA 230-10-85-014. 65p.
- L'HOMER, A., 1992. Sea-level changes and impacts on the Rhône coastal lowlands. pp 136–152 In: TOOLEY, A. and JELGERSMA, M. and S. (eds.) *Impacts of Sea-level Rise on European Coastal Lowlands*. Oxford, UK: Blackwell Publishers.
- LINTHURST, R.A. and REIMOLD, R.J., 1978. An evaluation of methods for estimating the net aerial primary productivity of estuarine angiosperms. *Journal of Applied Ecology*, 15, 919–931.
- MAHALL, B.E. and PARK, R.B., 1976a. The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay. I. Biomass and production. *Journal of Ecology*, 64, 421–433.
- MAHALL, B.E. and PARK, R.B., 1976b. The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay. II. Soil water and salinity. *Journal of Ecology*, 64, 793–809.
- MAHALL, B.E. and PARK, R.B., 1976c. The ecotone between *Spartina foliosa* Trin. and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay. III. Soil aeration and tidal immersion. *Journal of Ecology*, 64, 811–819.
- MALL, R.E., 1969. *Soil-water-salt relationships of waterfowl food plants in the Suisun Marsh of California*. California Department Fish and Game, Wildlife Bulletin N° 1.
- MASON, C.F. and BRYANT, R.J., 1975. Production, nutrient content and decomposition of *Phragmites communis* and *Typha angustifolia*. *Journal of Ecology*, 63, 71–95.
- MITTSCH, W.J. and GOSSELINK, J.G., 1986. *Wetlands*. New York: Van Nostrand Reinhold.
- NYMAN, J.; CHABRECK, R., and LINScombe, R., 1990. Effects of Weir Management on Marsh Loss, Marsh Island, Louisiana, USA. *Environmental Management*, 14(6), 809–814.
- PENNINGS, S.C. and CALLAWAY, R.M., 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. *Ecology*, 73(2), 681–690.
- REY, J.R.; SHAFFER, J.; CROSSMAN, R., and TREMAIN, D., 1990. Above-ground primary production in impounded, ditched, and natural batis-salicornia marshes along the indian river lagoon, Florida, U.S.A. *Wetlands*, 2(10), 151–171.
- ROBERTS, H.H., 1997. Dynamic changes of the Holocene Mississippi River Delta Plain: The delta cycle. *Journal of Coastal Research*, 13(3), 605–627.
- SCHUBAUER, J.P. and HOPKINSON, C.S., 1984. Above and below-ground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. *Limnology and Oceanography*, 29(5), 1052–1065.
- SESTINI, G., 1992a. Implications of climatic changes for the Po delta and Venice lagoon. pp 428–494. In: L. JEFTIC, J. MILLIMAN and G. SESTINI (eds.), *Climatic Change and the Mediterranean*. London: Edward Arnold.
- SESTINI, G., 1992b. Implications of climatic changes for the Nile delta. pp 535–561. In: L. JEFTIC, J. MILLIMAN and G. SESTINI (eds.), *Climatic Change and the Mediterranean*. London: Edward Arnold.
- SOKAL, R.R. and ROHLF, F.J. 1995. *Biometry* (third edition). W.H. New York: Freeman and Company.
- STANLEY, D., 1988. Subsidence in the northeastern Nile delta: rapid rates, possible causes, and consequences. *Science*, 240, 497–500.
- STANLEY, D., 1990. Recent subsidence and northeast tilting of the Nile delta: Egypt. *Marine Geology*, 94, 147–154.
- TAMISIER, A., 1990. *Camargue: Milieux et Paysages, Evolution de 1942 à 1984*. Association Pour les Recherches en Camargue Sur la Nature et l'Environnement, Montpellier, France, 33p.

- TAMISIER, A. and GRILLAS, P., 1994. A review of habitat changes in the Camargue: An assessment of the effects of the loss of biological diversity on the wintering waterfowl community. *Biological Conservation*, 70, 39–47.
- WEBSTER, J.R. and BENFIELD, E.F., 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics*, 17: 567–594.
- WESTLAKE, D.F., 1963. Comparisons of plant productivity. *Biological Review*, 38, 385–429.
- WHITE, D.A. and TRAPANI, J.M., 1982. Factors influencing the disappearance of *Spartina alterniflora* from litter bags. *Ecology*, 63, 242–245.
- WHITE, D.A.; WEISS, T.E.; TRAPANI, J.M., and THIEN, L.B., 1978. Productivity and decomposition of the dominant saltmarsh plants in Louisiana. *Ecology*, 59, 751–759.
- ZEDLER, J.B.; WINFIELD T.P., and WILLIAMS, P., 1980. Salt marsh productivity with natural and altered tidal circulation. *Oecologia*, 44, 236–240.