Tidal regime, salinity and salt marsh plant zonation

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Received 24 October 2003; accepted 12 August 2004

Abstract

Salt marsh morphology is known to be strongly correlated to vegetation patterns through a complex interplay of biological and physical processes. This paper presents the results of field surveys at several study salt marshes within the Venice Lagoon (Italy), which indicate that salt-marsh macrophyte species may indeed be associated with narrow ranges of soil topographic elevation. Statistical analyses show that several properties of the frequency distributions of halophytes presence are sensitive not only to variations in soil elevation, but also to the specific marsh considered. Through direct in situ sampling and by use of a finite-element hydrodynamic model the role of plant submersion duration and frequency in determining the observed variability of vegetation species is then studied. Measurements of soil salinity have also been performed at selected salt marshes to address its influence on vegetation occurrence. With implications for tidal marshes in general, the distribution of halophytes in the salt marshes considered is found not to be responding to simple rules dictated by the tidal cycle or to salinity, and that such factors, when singularly considered, cannot explain the observed spatial distribution of halophytes. On the basis of observations and modelling results it is thus concluded that a combination of multiple factors, likely dominated by saturated/unsaturated flow in the soil, may be responsible for the observed macrophyte distribution.

1. Introduction

Tidal marshes are colonized by halophytic vegetation species, i.e. macrophytes adapted to complete their life-cycle in salty environments. The spatial distribution of halophytic vegetation over salt marshes is not random nor spatially uncorrelated but is, on the contrary, organized in characteristic patches whose observation (Chapman, 1976; Pignatti, 1966; Silvestri et al., 2000; Marani et al., 2003) has stimulated an increasing interest in the phenomenon (*zonation*). A number of authors (e.g. Waisel, 1972; Chapman, 1976; Beeftink, 1977; van Wijnen et al., 1997; Rogel et al., 2001; Bockelmann

et al., 2002; Costa et al., 2003) have described plant zonation in salt-marsh environments and have evaluated the environmental factors affecting the distribution of halophytes. Some of the first hypotheses (Chapman, 1976; Pignatti, 1966) linked zonation to the concept of "succession" (Clements, 1916; Odum, 1969; Glenn-Lewin et al., 1992), i.e. the replacement of plant species in an orderly sequence of colonization and development. This hypothesis is based on the assumption that, on emerging salt marshes, after an initial colonization phase, the substrate would be more stable and sediments would be trapped by the vegetation. This would allow other species to invade the marsh, producing changes directed towards a mature and stable *climax* ecosystem (Odum, 1971). Results of long-term monitoring, however, reveal that the dynamics of salt-marsh vegetation

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does not always proceed according to succession schemes (De Leeuw et al., 1993). Furthermore, paleo-ecological analyses suggest that, at some sites, the present species existed for several thousands of years with relatively stable plant communities boundaries and that, if a change occurs, it usually does not follow specific succession schemes (Redfield, 1972; Beeftink, 1977; Adam, 1990). Salt-marsh vegetation dynamics is thus seen to be quite complex and a deeper understanding of halophyte spatial and temporal patterns (with relevant consequences for ecogeomorphic issues) requires accurate studies of the physical, chemical and biotic factors affecting plant physiology.

The reproduction, germination and development of halophytes depend on a number of physiological needs, broadly related either to a sufficient input of energy and vital substances (e.g. water, oxygen, light, salt ions, macro-nutrients and micro-nutrients, etc.) or to the limitation of stressing factors (e.g. soil waterlogging, toxic substances in soils, sudden thermal changes, inter- and intra-specific competition). Numerous edaphic and biotic factors have been found to be related to salt-marsh plant distribution, for example, nutrient availability (see Gallagher, 1975; Jefferies, 1977; Buresh et al., 1980; Mitsch and Gosselink, 1993; van Wijnen and Bakker, 1999; Rogel et al., 2001), inter- and intra-specific competition (see Snow and Vince, 1984; Ellison, 1987; Bertness, 1991; Bertness et al., 1992; Pennings and Callaway, 1992; Grosshans and Kenkel, 1997; Levine et al., 1998; Costa et al., 2003; Lenssen et al., 2004), grazing and human management (see Adam, 1990; Laffaille et al., 2000; Tessier et al., 2003; Lenssen et al., 2004). The present work addresses the influence of two basic factors: soil water salinity and oxygen availability.

Experimental evidence indicates that soil salinity gradually increases with soil elevation, reaching a maximum just above mean high sea level (MHSL) to again decrease beyond it (Mahal and Park, 1976; Adam, 1990). These observations, which provide a link between the presence of halophytes and topographic elevation, may be explained by noting that evaporation periods (occurring when the marsh is not flooded) are longer at higher elevations and thus salts in surface soils may become very concentrated (e.g. Adam, 1990). At very high soil elevations, above MHSL, soil water salinity tends to decrease due to progressively less frequent flooding of the marsh and the associated reduced salt input. The dependence of soil salinity on elevation may thus partly explain zonation, since physiological responses of plants to salinity are heavily species-dependent.

Oxygen availability crucially affects plant growth, and is determined, for a given soil type and given topographic characteristics, by the frequency and the duration of salt-marsh flooding, which affect root respiration, germination and early seedling growth

(Chapman, 1976; Ungar, 1991; Mitsch and Gosselink, 1993), and change soil chemistry, possibly leading to toxic conditions for the plants (Pezeshki, 2001). Salt-marsh plants have adopted different strategies in order to survive periodic soil saturation (e.g. aerenchyma, to allow transport of oxygen from above-water tissues to the roots [e.g. Visser et al., 2000; Ungar, 1991], and increased above-ground tissue pore volumes to store oxygen for respiration [Armstrong, 1982]), which are quite species-dependent, thus providing a mechanism through which vegetation zonation may take place. The dependence of halophytes on morphology through soil aeration is more complex than in the case of salinity, since aeration does not simply depend on flooding frequency and duration, but also on soil conductivity, surrounding topography, position of the channels from which flooding occurs, etc. (Ursino, 2004).

Even though the physiology of halophytes in the laboratory has been the subject of numerous studies for at least the past four decades, there is still a need for work on the interactions of halophytes with multiple biotic and abiotic factors in their own environment. While it is quite difficult to simultaneously monitor a large number of parameters through field surveys, this type of approach could be implemented through the use of mathematical models describing the main physical components affecting salt-marsh macrophytes. This study presents an example of this approach and investigates the distribution of halophytic species with respect to flooding period duration and frequency and soil salinity within the Venice lagoon (northeastern Italy) using field data and by applying a two-dimensional numerical model to describe tide propagation within the lagoon.

2. Materials and methods

2.1. Study area

The salt marshes studied are located in the northern part of the Venice lagoon (Fig. 1), NE Italy, which has an area of about 550 km^2, with a mean water depth of approximately 1.5 m. The tidal regime is semi-diurnal and the maximum excursion (at the inlets) is about ± 70 cm around mean sea level. The mean water volume of the lagoon is about 700×10^6 m^3, the semi-diurnal volume exchange with the sea is about 350×10^6 m^3 during spring tides and 175×10^6 m^3 during neap tides (Silvestri et al., 2000). The total freshwater input into the lagoon is 900×10^6 m^3 per year, discharged by 27 channels, while the rainfall volume directly falling on the lagoon (i.e. not through its watershed) is 440×10^6 m^3 per year (Silvestri et al., 2000). Freshwater inputs from rivers are rich in nutrients and high in pesticides but very low in transported sediments so that there is no
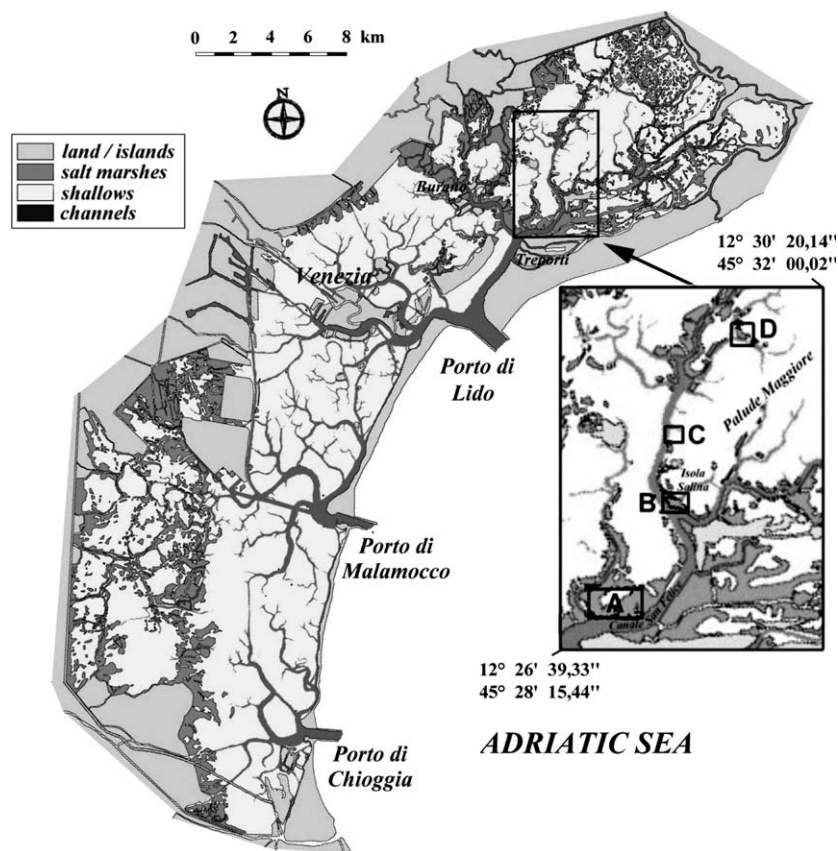
Fig. 1. The Venice lagoon and the four salt marshes studied: (A) San Lorenzo, (B) Salina, (C) Salina Nord, (D) Palude Maggiore.

appreciable variability of sediment load during ebb or flood periods. With an input of 7000 tons per year of nitrogen and of 1500 tons per year of phosphorous, the lagoon can be considered as an eutrophic environment.

Human activities have historically had a strong impact on the lagoon morphology: the three main rivers that used to run into the lagoon were diverted directly to the sea during the 15th and 16th centuries. Deep channels have been dredged and long jetties have been built at the three inlets. Very few areas unaffected by human intervention may currently be found within the lagoon, and, in particular, the southern and central parts of the lagoon are undergoing strong erosional trends. Hence, the field campaigns described in the present study focused on the northern part of the lagoon, which is still characterized by (modest) sediment inputs from two small rivers and from the sea. In particular, the study sites are located on the sides of the San Felice channel that, from the inlet *Porto di Lido*, runs north-east, ending in the large shallow water area called Palude Maggiore (Fig. 1). Proceeding along this channel (starting from the inlet) four salt marshes were selected, indicated by A, B, C, and D in Fig. 1, which are characterized by networks of small creeks and are covered by dense populations of halophytes. Soil elevation ranges

in the four study sites exhibit appreciable differences: soil elevation of salt marsh A lies between 10 and 50 cm above mean sea level (a.m.s.l.), between 0 and 25 cm a.m.s.l. in salt marsh B, between 5 and 30 cm a.m.s.l. in salt marsh C, and between 10 and 40 cm a.m.s.l. in marsh D.

The number of halophytic species present in these marshes is limited. They are: *Salicornia veneta* (Sal), *Spartina maritima* (Sp), *Limonium narbonense* (Li), *Sarcocornia fruticosa* (Sa), *Juncus maritimus* (Ju), *Puccinellia palustris* (Pu), *Inula crithmoides* (In), *Halimione portulacoides* (Ha), *Suaeda maritima* (Su), *Arthrocnemum macrostachyum* (Ar), and *Aster tripolium* (As) (nomenclature follows Caniglia et al., 1997).

2.2. Sampling

A typical soil transect from salt marsh A is shown in Fig. 2, where soil elevation and the presence of different species have been sampled every 10 m. It can be noticed that the inner areas of the marsh are lower than the edges, in accordance with previous observations (Pignatti, 1966; Caniglia et al., 1997). *Spartina maritima* usually occupies the inner and lower areas, while *Sarcocornia fruticosa*, *Puccinellia palustris* and *Inula crithmoides* usually grow only on higher soils, along the
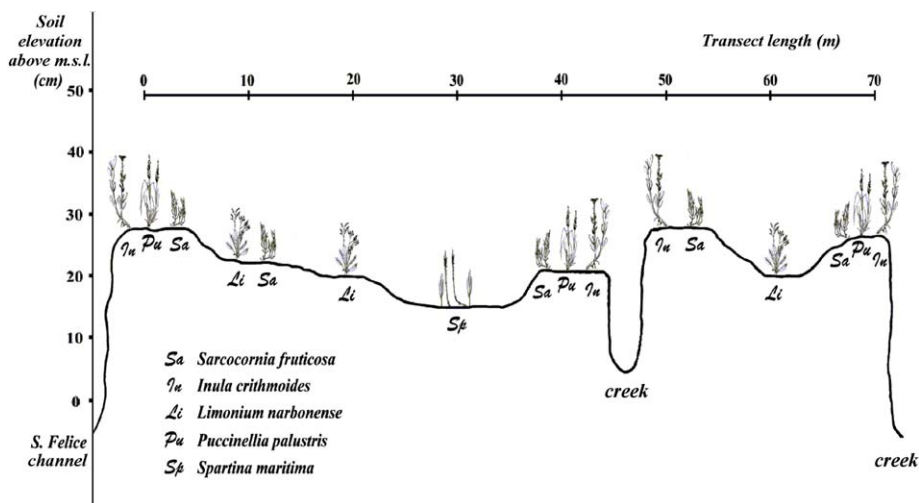
Fig. 2. Soil profile along a transect in salt marsh A.

edges of creeks and channels. In the intermediate areas a wide presence of *Limonium narbonense* is observed.

Accurate topographic surveys were performed by randomly sampling the selected salt-marsh areas. Geographic position and elevation were measured at each sampling site using a laser theodolite (precision of ± 2 mm in elevation with respect to the local geoid) and an area of $1m^2$ was surveyed by estimating the relative abundance of vegetation species by the Braun–Blanquet method (Pignatti, 1953a,b,c; Mueller-Dombois and Ellenberg, 1974) using six classes ($<1\%$, 1–20%, 21–40%, 41–60%, 61–80%, 81–100%). During the summer of 2000 more than 240 measurements were performed at salt marsh A, 35 at B, 27 at C and 53 at D. The number of observations was varied as a function of the size of the salt marshes and, even though observations at sites B, C and D have been less extensive, samples are large enough to provide reasonably converging estimates of population statistics.

In the case of salt marsh A, the distance d of each sampling site from the nearest channel or creek was computed using a rectified and georeferenced aerial photo acquired in August 1998. Soil salinity measurements were carried out on soil samples acquired within two transects on salt marshes B (25 soil samples) and D (20 soil samples). Marshes B and D were selected because they are representative of the two types of halophytes distributions with elevation observed in the following. Because of the low rainfall of that period (summer 2000) these measurements provide a reasonable description of the variability of soil salinity due to flooding, infiltration and evaporation processes. Cores were taken with a circular sampler with an inner diameter of 5 cm, for a depth of 20 cm, and were then stored in plastic boxes for subsequent laboratory analyses. Soil elevation and position of each sampling site were determined with a laser theodolite. The inner part of each core was sampled for the actual salinity measurements, to avoid possible contaminations, and samples were dried at 70 °C for 36 h, pressed and homogenized. Twenty grams from each sample was then mixed with 100 g of distilled water and the solution was allowed to reach an equilibrium salt concentration for 12 h. Given the extremely high salt concentration of the solution, titration could not be used, and salinity was evaluated by measuring conductivity (WTW MultiLine P4 conductivity meter, http://www.wtw-inc.com).

2.3. The hydrodynamic model

The four salt marshes considered lie along the S. Felice channel and are sequentially reached by the entering tidal wave with a delay which depends on the distance from the inlet and a tidal attenuation due to frictional effects. For a fixed soil elevation in the four marshes considered, the tidal attenuation along the channel determines differences in the frequency and the duration of floods, the evaluation of whose magnitude is of great ecogeomorphologic importance. To this end, a two-dimensional finite element model (D'Alpaos and Defina, 1993, 1995; Defina and Zovatto, 1995; D'Alpaos et al., 1995) was used to accurately describe tidal propagation within the Venice lagoon and to study the time evolution of water levels at the four marshes considered. The mathematical model uses a particular formulation of the shallow water equations (Defina, 2000), which allows the detailed simulation of wetting and drying fronts which considerably affect tidal propagation within a tidal embayment. The model is based on a discretized 2D description of shallow water hydrodynamics (for tidal flats and salt marshes), coupled to 1D elements describing the flow in the

numerous smaller channels, which decisively impact tidal propagation. Both the two-dimensional and the one-dimensional sets of equations are solved by a finite element scheme, which uses 2280 triangular elements and 985 linear elements to discretize the Venice lagoon. The model was calibrated on an extended set of water level observations performed within the Venice lagoon and on the values of the discharges exchanged between the lagoon and the sea through the three inlets. The validation of the model shows that the maximum difference between observed and computed water levels is 2 cm in the areas where the analyses on vegetation presence described below were performed.

In the simulations used to determine duration and frequency of salt marsh flooding, sea levels measured at the Porto di Lido inlet were assigned as boundary conditions, using hourly measurements performed in 1995, 1997 and 1998, which constituted the most complete recent dataset available. Within the selected periods analyses of model results were separately performed for a spring period (March–May) and a summer period (June–September).

3. Results

3.1. Field data

The topographic observations, together with the estimates of vegetation cover, allowed the study of the frequency distribution of each species with respect to distance (d) from the nearest creek and to soil elevation. The experimental frequency distributions for marsh A were computed by specifying intervals of equal length for d and by computing how many times a given species occurred within each of the intervals. The results are in good agreement with observations shown in Fig. 2. Some species, in fact (e.g. *Puccinellia palustris, Inula crithmoides* and *Spartina maritima*), almost exclusively grow along the edges of creeks and channels, while *S. maritima, Limonium narbonense* and *Juncus maritimus* do not seem to have a preferential distance from the tidal network.

The analysis of vegetation species and the associated elevation values as expected shows a strong dependence of vegetation presence on soil elevation. Fig. 3 shows, for salt marsh A, the frequency distribution of soil elevation z conditioned to the presence of each species, computed by specifying intervals of elevation values and by computing how many times a given species occurred within each of the intervals. Fig. 3 shows that *Spartina, Limonium* and *Sarcocornia* are characterized by a nearly symmetric distribution, in which the mean and the mode coincide, suggesting an approximately normal distribution (within the elevation range of observation). *Juncus*
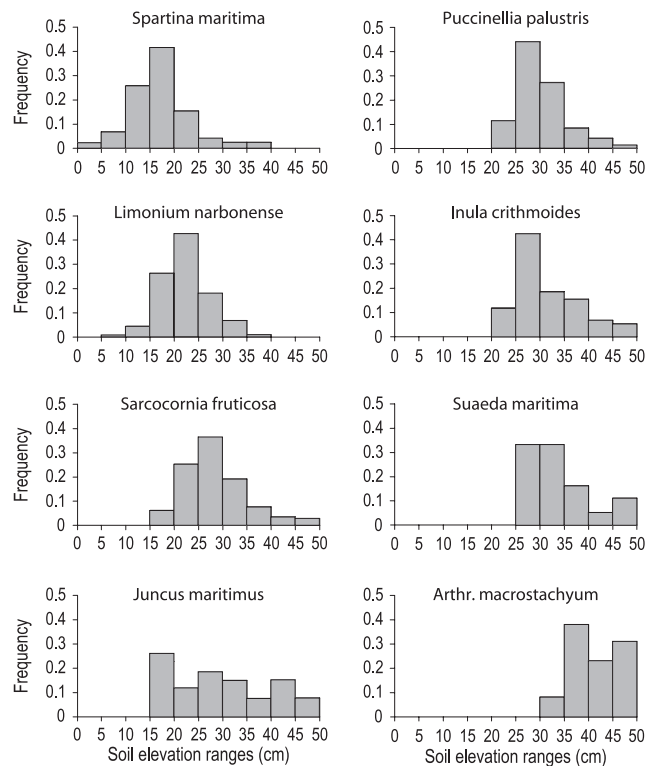

Fig. 3. Frequency distribution of halophytes with respect to the soil elevation for salt marsh A.

maritimus is the only species exhibiting a flat distribution, indicating a relative indifference to soil elevation.

Differences and overlaps between elevation ranges typical to each halophyte are summarized in Fig. 4 for marshes A, B, C and D. An identical vegetation sequence of species with increasing soil elevation can be observed at the four marshes: i.e. *Spartina maritima* grows on the lowest soils, *Limonium narbonense* over slightly higher areas, *Sarcocornia fruticosa* on even higher soils, etc.. However, our results show that a given species is found at preferential elevations which are different in the four marshes: the identical plant sequence is shifted vertically at different sites. Fig. 5 shows how *Spartina, Salicornia, Limonium, Sarcocornia* and *Inula* develop at different soil elevations within each salt marsh and live over relatively high soils in marshes A and D, and at minimum elevations in marsh B.

Species richness and density are often used as indicators of stress levels (e.g. Tilman, 2000), and are usually significantly higher near channel banks than in the inner areas of marshes (e.g. Pignatti, 1966; Sanderson et al., 2000, 2001). To describe how diversity, and thus stress level, varies with elevation not only the number of species, but also the shape (evenness) of the probability of occurrence of each species is here considered. Shannon's entropy (e.g. Odum, 1983; Chapin et al., 2000) is a measure of diversity which combines these two factors, providing a single index of
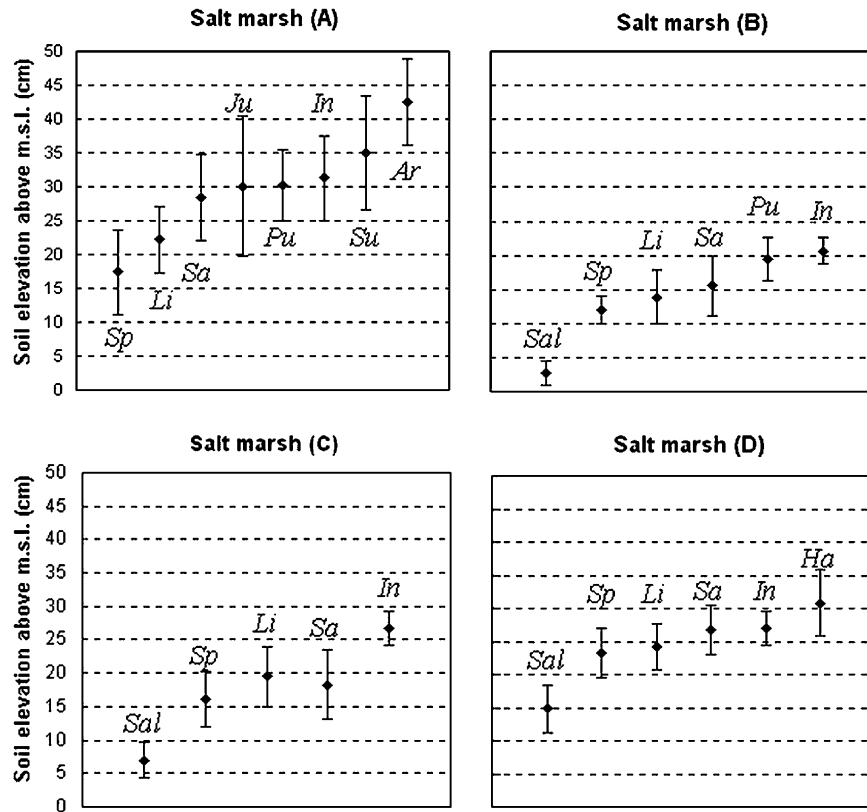
Fig. 4. Mean elevation for each vegetation species and their standard deviations for the four considered salt marshes.

environmental stress level. An elevation-dependent Shannon's entropy, $S(z)$, was determined by dividing the total elevation range of each marsh in elevation intervals of size Δz, and by computing for each of them:

$$S(z) = - \sum_{i=1}^{N} P_i(z) \ln P_i(z) \qquad (1)$$

where $P_i(z)$ is the probability that the ith species be present in the elevation range within z and $z + \Delta z$, and N is the total number of species in the marsh. Fig. 6 shows the function $S(z)$ computed for marshes A, B, C and D. It may be observed that entropy increases with soil elevation and that, at two of the sites considered, it exhibits a maximum for intermediate elevation values. Since entropy may be considered to be a measure of environmental pressure, the highest values of $S(z)$ may be associated with environmental conditions which are most favourable to vegetation development. In lower salt-marsh areas, frequently flooded for longer periods of time, only the most resistant species can survive to prolonged anaerobiosis conditions, and usually mono-specific populations are observed. Less frequently flooded soils are characterized by larger oxygen avail-ability and hence host a wider variety of species occurring with similar likelihood. The behaviour

of $S(z)$ is also consistent with the observation that increased diversity is, on average, associated to increased biomass (Tilman, 2000): vegetation density is, in fact, particularly large along elevated creek edges in Venetian salt marshes (Marani et al., in press).

Soil salinity was measured with the purpose of determining its link to soil elevation and to the distance from the channel network and to characterize its variability from one marsh to another. For these purposes salt marsh B (the lowest) and D (high and far from the inlet) were selected. The average salinity values (throughout the paper in Practical Salinity Units) of all samples from the two salt marshes are very similar: 93.0 (± 51.7) for site B and 103.9 (± 26.3) for site D. Considering only samples taken in the low marsh areas, from 0 to 35 cm a.m.s.l., the average salinity is almost identical for both marshes: 103.8 ± 45.0 for site B and 103.9 ± 26.3 for site D. Soil total salinity seems to be poorly correlated to soil elevation: no definite trend is observed (Fig. 7) except for very high soil elevation values (never reached by the tide), which exhibit very low salinity concentrations. In salt marsh B, 20 of the 25 measurements were performed along a transect, from the edge of the S. Felice channel to the inner area, ending on a small artificial hill, with a spacing of 5 m. Observations performed along this transect are shown in Fig. 8, where
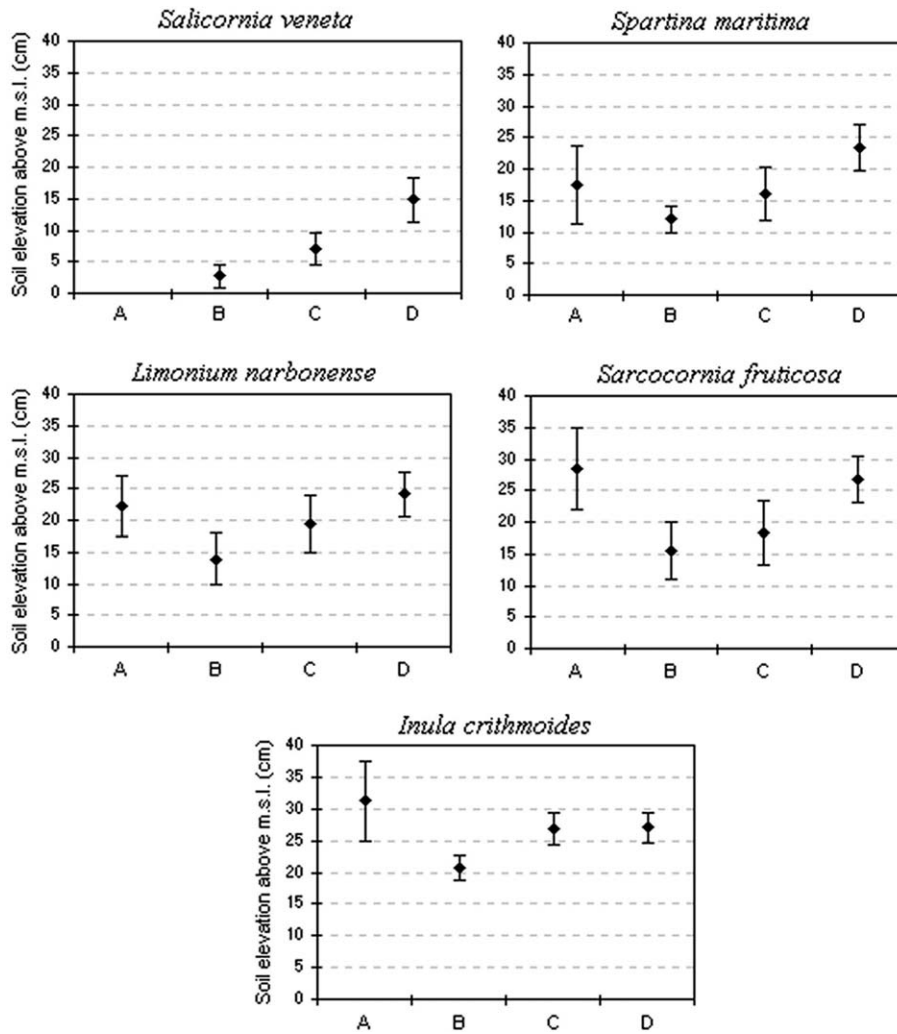
Fig. 5. Comparison among soil elevations characteristic of each halophytic species at the four study salt marshes. Bars indicate standard deviations around the means.

it may be seen that total salinity does not appear to be correlated to the distance from the channel.

3.2. Hydrodynamic model results

The finite-element hydrodynamic model described earlier was used to compute tidal levels at the study sites A, B, C and D within the S. Felice channel, located 7.7, 12.1, 13.1 and 15.1 km away from the Porto di Lido inlet, respectively. Fig. 9 shows sample results of the computations for the first two days of June 1997, which shows the phase delay between peaks and troughs of the level oscillations at different sites and the attenuation of the tidal wave in its propagation from the inlet. It may be noticed that differences in tidal oscillations at different sites do not show a trivial behaviour and hence a detailed finite element model is needed to correctly describe salt-marsh flooding.

Model-computed tidal levels data have been used to compute the following parameters:

(1) Mean duration of flooding periods τ, computed for different periods of the year (spring and summer):

$$\tau = \sum_{i=1}^{n} d_i / n \tag{2}$$

where d_i = duration of a single flood, n = number of floods; τ may be connected to the *hydroperiod* (e.g. Kadlec and Knight, 1996), which may be defined as the percentage of time during which the marsh is flooded (computed by dividing total flood duration, $n\tau$, by the reference time, T_r).

(2) Flood frequency, f, defined as the mean number of floods occurred during a reference period (Mitsch and Gosselink, 1993):
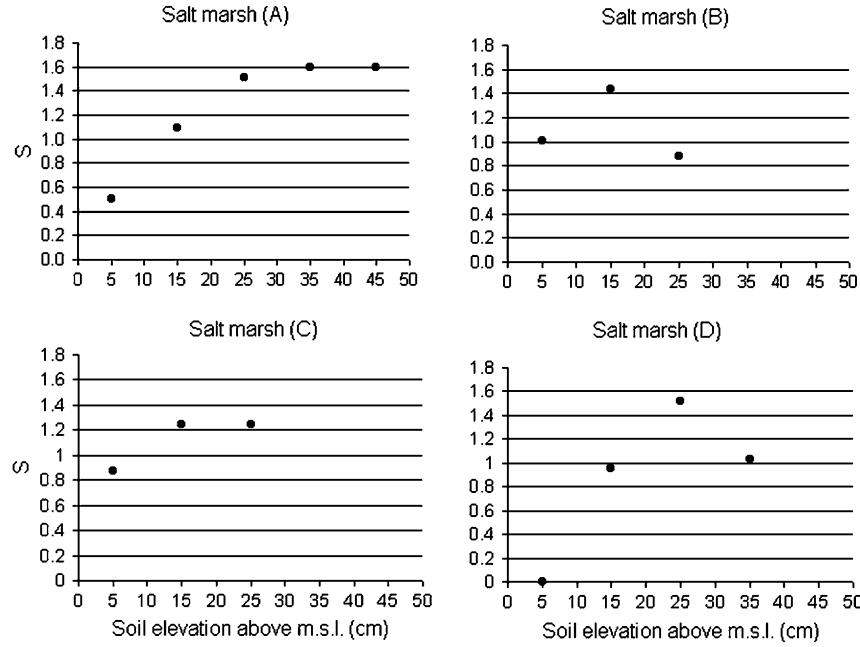
$$f = n / T_r \tag{3}$$

Fig. 6. Dependence of entropy, $S(z)$, on soil elevation, z, at the four study salt marshes.

where n = number of floods, T_r = reference time.

(3) Average water height above mean sea level, $\hbar$:

$$\hbar = \frac{\int_0^{T_r} h(t)u(h)\,\mathrm{d}t}{\int_0^{T_r} u(h)\,\mathrm{d}t} \qquad (4)$$

where $h(t)$ = water height at time, and $u(h) = 1$ if $h(t) \geq 0$, while $u(h) = 0$ if $h(t) < 0$.

The mean water height above mean sea level, $\hbar$, is shown in Table 1, where it may be noticed that very little variability among different sites is observed.

Fig. 10 plots the mean flood duration, τ, against soil elevation during the three summer periods considered (spring plots yield very similar results), while Fig. 11
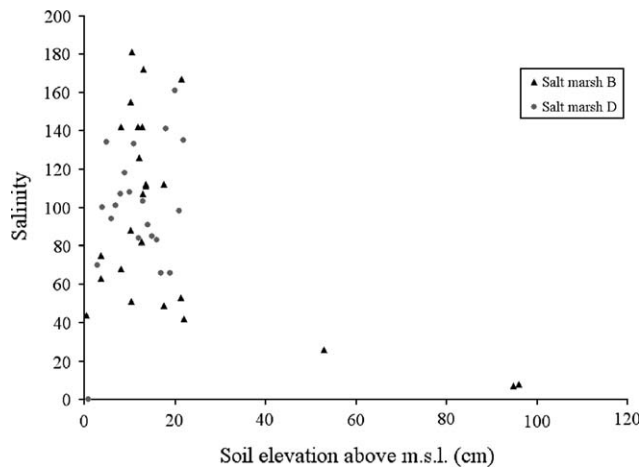
shows the mean duration of flooding periods experienced by some halophytes in the four salt marshes. Fig. 12 shows the frequency of floods computed for fixed soil elevation values, characteristic of some halophytes at the four sites.

4. Discussion

The topographic surveys discussed in the previous section yield distributions of the distance to the nearest creek for each vegetation type which are quite uniform and no preferential location with respect to the channel network thus seems to emerge. This may be explained with the observation of Ursino (2004) that only a narrow area near the network is influenced, in terms of soil aeration, by channel drainage. The remaining part of the marsh is characterized by quasi-vertical, one-dimensional,

Fig. 7. Soil total salinity vs. soil elevation from observations in marshes B and D.
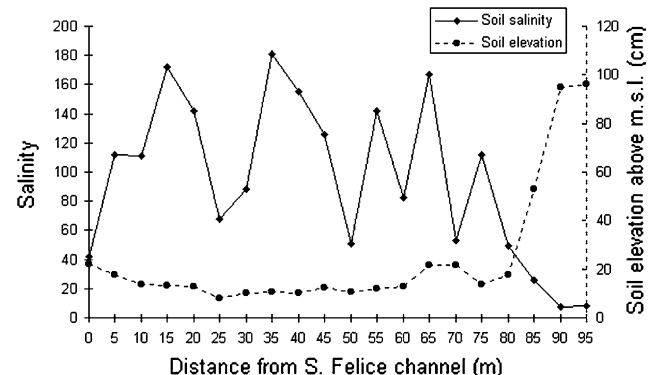

Fig. 8. Soil total salinity and soil elevation along a transect in marsh B.
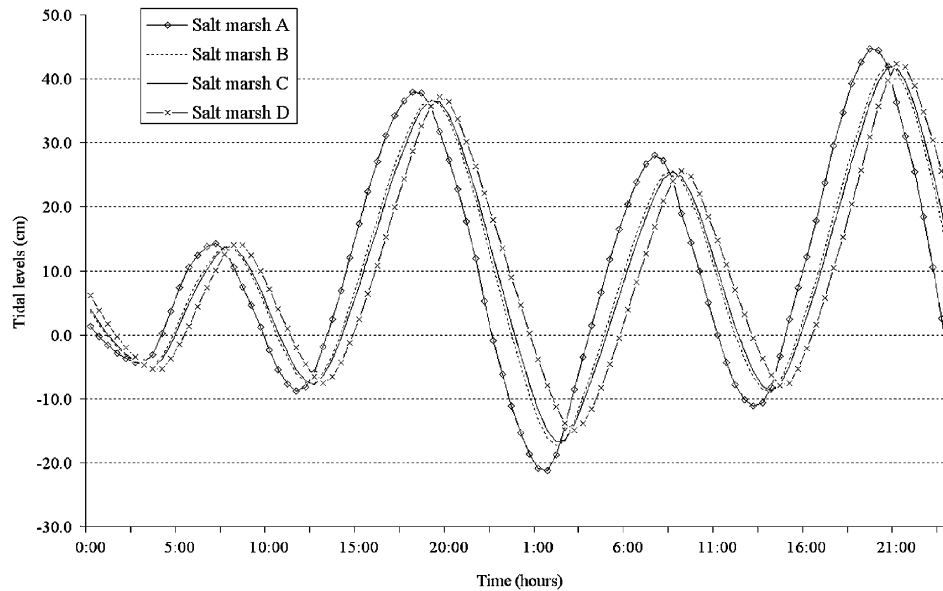
Fig. 9. Typical tidal fluctuations at the four study sites.

moisture dynamics which is quite insensitive to the presence and location of the channel network. The evident zonation of *Spartina*, *Limonium* and *Juncus* must therefore be explained in terms of factors related to the vertical movement of water above the soil and in the soil and, likely, to soil properties. Soil elevation is certainly a major factor as evidenced by previous literature (e.g. Bockelmann et al., 2002) and confirmed by the results presented for the Venice lagoon in terms of preferential soil elevations for a given halophytic species (Fig. 3) and of biodiversity, as represented by Shannon's entropy (Fig. 6). As shown in Figs. 4 and 5, the same halophyte grows at different characteristic soil elevations in different salt marshes: the explanation of this difference may provide a decisive clue as to the identification of zonation controlling factors. It is interesting to note that entropy as a function of elevation seems to correctly capture environmental pressure. In fact, a given value of entropy, and thus of stress level, corresponds at sites A and D (Fig. 1) to higher soil elevation values than at sites B and C, consistently with the observation (Fig. 5) that a given species typically lives at higher elevations on A and D than on B and C. It is clear from these results that the role of soil elevation must be related to local marsh properties, whose variability may explain the observed differences across the study sites.

A first, perhaps obvious, candidate is the local water fluctuation, as determined by the tidal forcing at sea and tidal wave dissipation and deformation in the course of its propagation. The hydrodynamic model used accounted for all these effects and determined whether the different soil elevations characterizing the same species on different salt marshes corresponded to similar edaphic conditions, such as flooding durations and frequencies. The analyses could not establish correlations between the characteristics of marsh flooding and the spatial distribution of vegetation. Flooding duration, τ, for a fixed value of elevation above mean sea level slightly decreased when moving from marsh A to marsh D, but differences were quite small and did not seem to justify the difference in the observed typical vegetation soil elevations. As it may be seen in Fig. 10, mean flooding periods present large variations for soils below mean sea level. On the contrary, soils above mean sea level experience almost identical flooding durations, even when different years are compared (Fig. 10). Furthermore, Fig. 11 shows that, for example, *Spartina maritima*, growing at site A at a mean soil elevation of 17.5 cm a.m.s.l., is flooded on average for 5.5 h every tide. At site B it grows at a mean soil elevation of 12 cm a.m.s.l., which is flooded on average for 6.8 h every tide. The difference in flooding durations experienced by *S. maritima* is therefore almost 20% and suggests that other physical factors must play a role in determining similar habitats at the two sites despite the different flooding durations.

Similar considerations are valid for the computed frequency of floods, *f*. Flooding frequency of soils above

Table 1
Mean water height $\hbar$ above mean sea level (in cm) calculated for spring and summer 1998 at the four salt-marsh sites studied

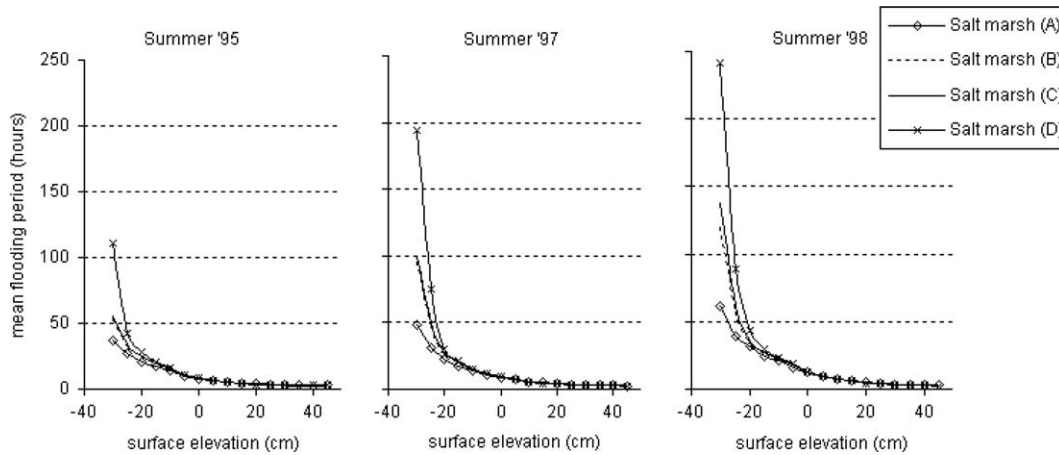| Mean water height $\hbar$ (cm above m.s.l)	Period	Salt marsh (A)	Salt marsh (B)	Salt marsh (C)	Salt marsh (D)
	Spring 1998	22.1	20.4	20.3	20.3
	Summer 1998	28.6	27.5	27.6	27.8

Fig. 10. Mean flood duration vs. soil elevation during three summer periods in 1995, 1997 and 1998.

mean sea level (Fig. 12) tend to decrease with the distance from the Porto di Lido inlet, but it is interesting to note that the observed values are very similar for the four sites and that differences in flood frequency values do not seem to justify the differences in vegetation zonation at the study sites. Attempts to correlate halophytic species to the product of frequency and flooding period similarly produced negative result.

5. Conclusions

Field campaigns on salt marshes within the Venice lagoon have indicated that the distribution of halophytes was strongly correlated to marsh topography and morphology. This circumstance had been observed previously (Mahal and Park, 1976; Snow and Vince, 1984; Vince and Snow, 1984; Olff et al., 1988; Adam, 1990; Sánchez et al., 1996; Grosshans and Kenkel, 1997; Sanderson et al., 2000, 2001; Bockelmann et al., 2002), but the analyses presented show that simple correlations of plant zonation to soil elevation or distance from the

nearest creek did not have a general validity and could not be extended to different marshes, even within the same tidal environment. This is consistent with results obtained in different tidal environments (e.g. Adam, 1990; Bockelmann et al., 2002).

Analogies and differences in the distribution of plants were seen in the present study. At all marshes observed species diversity, as epitomized by an entropy measure, increased with ground elevation through most of the range explored. In particular, more elevated soils along creek edges were observed to host a wider variety of halophytes than inner marsh zones and entropy was shown to provide a concise description of environmental stress. All marshes considered were populated by the same species: *S. maritima*, for example, grows on the most depressed soils, *L. narbonense* over slightly higher areas, *S. fruticosa*, *I. chritmoides* and *P. palustris* on the most elevated soils. Apart from these analogies, species-characteristic soil elevation or distance from the channels of a general validity could not be defined. On the contrary, each species was found to grow at different
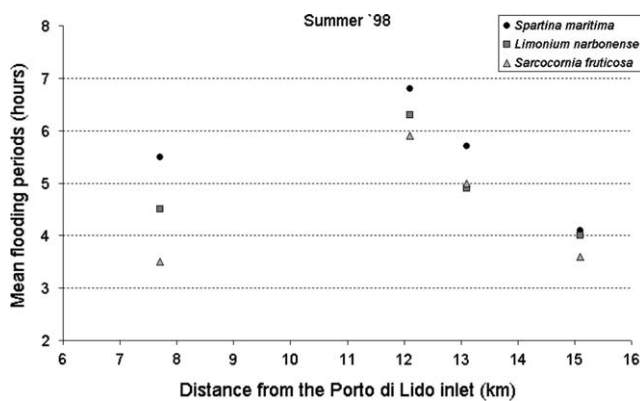

Fig. 11. Mean duration of flooding periods experienced by some halophytes at the four study sites labelled according to the distance from the nearest lagoon inlet.
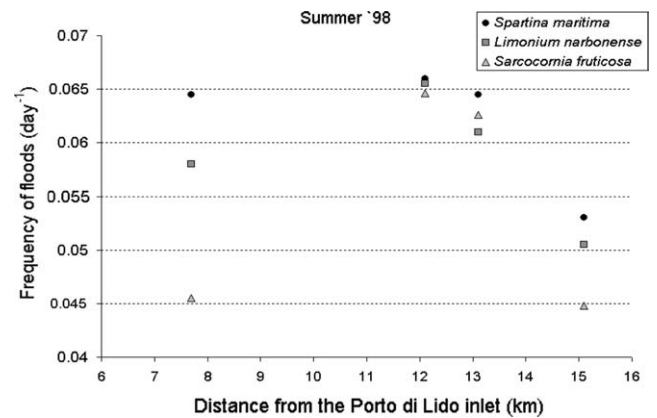

Fig. 12. Mean flooding frequency experienced by some halophytes at the four study sites labelled according to the distance from the nearest lagoon inlet.

ranges of soil elevations over the marshes studied: even when marshes are very close to one another, site-dependent physical characteristics crucially influence vegetation distribution. These results suggest that the distribution of halophytic plants should be related to the space-time variability of the relevant processes, rather than by trying to define empirical correlations between vegetation occurrence and single edaphic factors.

The use of mathematical models is thus required to describe the environmental variables controlling plant growth. In this view, lower salt marshes, flooded for longer periods of times, were initially hypothesized to host a smaller variety of species, adapted to prolonged anaerobiosis conditions, than higher, less frequently flooded marshes with greater oxygen availability. To test this hypothesis, a hydrodynamic finite element model was used to determine if frequency and duration of tidal flooding were correlated with observed plant patterns. However, no correlation could be established between species and submersion period/frequency: a given species was found to experience different submersion periods and frequencies in different salt marshes.

No correlation between soil salinity and soil topography was observed, and the values found in a very low salt marsh were very similar to those found in a much higher one. No characteristic soil salinity values have been found for different species and no correlation between plant distribution and distance from channels could be established. It should nevertheless be noted that, given its high variability, a larger number of measurements of soil salinity, sampling different salt marshes, will need to be performed to conclusively determine the role of this factor with higher statistical significance.

On the basis of previous literature and the observations and modelling results presented, soil salinity and tidal regime, albeit important factors, are concluded to be unable to explain the observed distribution of halophytic species over salt marshes. Since the influence of above-ground submergence of plants is unable to account for vegetation zonation, its explanation is likely to be found in the dynamics determining root oxygen availability. Water dynamics in the salt-marsh sub-surface must exert a fundamental control on vegetation patterns, since oxygen is necessary for aerobic respiration in roots, and could provide the source of heterogeneity accounting for the different halophytes patterns observed in different marshes. Subsurface saturated/unsaturated dynamics forced by tidal level fluctuations and surface evapotranspiration (Ursino, 2003W) could yield an interpretation for the evidences presented in this study. Subsurface flow, in fact, mediates the influences of soil properties (e.g. conductivity), which crucially affect soil aeration times, and of marsh non-local topography. Finally, subsurface unsaturated flow may provide a physical mechanism through which the plants themselves may deeply modify, through evapotranspiration fluxes, the aeration regime of the soil, thereby introducing an ecogeomorphological feedback. Therefore, the different zonation patterns observed in the present study (but with possible implications of somewhat general nature) may not be explained solely in terms of local elevation, flooding periods or induced soil salinity, but should be related to spatial heterogeneities of soil properties and to the interplay between evapotranspiration patterns and sub-surface water flow.

Acknowledgments

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