Primary colonisation of mudflat estuaries by *Spartina maritima* (Curtis) Fernald in Northwest Spain: vegetation structure and sediment accretion

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Abstract

Spartina maritima in Northwest Spain follows a colonisation pattern similar to that described from other latitudes and other *Spartina* coloniser species. After the establishment of vegetative fragments on the mudflat, rhizomes grow centrifugally forming rounded patches that act like sediment traps, becoming dome-shaped due to the accumulation of sediment towards the centre of the patch. Patch size has been marked as one of the main determinants of the accretion due to the presence of *Spartina*. We propose a model to relate patch size and sediment accretion at the first stages of colonisation, which seems to be logarithmic rather than linear as had been previously suggested. Other factors such as distance to water exchange source and elevation prior to *Spartina* colonisation have proved to be important accretion determinants. Shoot size within patches increased from the edge towards the centre, while shoot density showed a complex distribution characterised by a series of concentric belts of different densities, with the lowest density at the centre of the patch. Despite, the higher elevation and the lower *Spartina* density at the centre of the patches, no other species have been found colonising those spots. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Sediment accretion in coastal salt marshes is enhanced by marsh vegetation (e.g. Ranwell, 1963; Cahoon et al., 1996), and species of the genus *Spartina* are among the most efficient trappers of sediment (Bird and Ranwell, 1964; Van Eerdt, 1985; Hutchinson et al., 1995; Daehler and Strong, 1996). The rigid and densely packed stems and leaves decrease the

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speed of tidal flow, causing the precipitation of suspended sediments, while dense root mats trap the sediment so precipitated (Daehler and Strong, 1996). Sediment entrapment by *Spartina* results in an elevation of the marsh surface, which induces a number of changes in the soil characteristics, and the subsequent replacement of *Spartina* by other species (Lewis and Dunstand, 1975; Bertness and Callaway, 1994; Bertness and Yeh, 1994; Castellanos et al., 1994; Hacker and Bertness, 1995).

Colonisation of mudflats by *Spartina* sp. occurs mainly by vegetative reproduction from rhizome fragments transported by tidal currents. Once rooted, these plants grow in discrete circular domed patches separated by open mud, which may eventually coalesce into continuous swards. These patches have been identified as genetic clones in previous studies (Castellanos et al., 1994; Daehler and Strong, 1994).

Sediment deposition dynamics follows a complex multifactorial model, which makes the evaluation of the relationship between sediment accretion and vegetation difficult (Warren and Niering, 1993). In addition, Hutchinson et al. (1995) have found that sediment deposition in salt marshes may not follow a clear pattern, but is often 'catastrophic', since isolated and unpredictable episodes like severe storms may account for most of the accretion. However, the discrete circular patches of *Spartina*, isolated on the mudflat, offer a good opportunity to evaluate some of the plant characteristics and their relationships with accretion. For example, Castellanos et al. (1994) found a linear relationship between patch size and accretion in two *S. maritima* (Curtis) Fernald marshes situated in a wide estuary in Southwest Spain.

In this study, we test the model of Castellanos et al. (1994) in a long and narrow estuary of Northwest Spain. We also characterise the plant distribution patterns within patches, which are compared with the patterns described in the literature on this topic.

Although it is still abundant on the Atlantic Iberian coasts, *S. maritima* is considered to be at risk on the European coast, since it is being displaced by the more aggressive hybrids *S. anglica* C.E. Hubbard and *S. townsendii* H. & J. Graves at its northern limit of distribution (Géhu, 1991), and by the American neophyte *S. densiflora* Brong. at its southern limit (Figueroa and Castellanos, 1988).

2. Methods

2.1. Study area

The study was carried out in the salt marshes of the Ría de Betanzos (Northwest Spain) which is a long and narrow estuary at the mouth of the rivers Mendo and Mandeo (Fig. 1). This area has been declared as protected by the local government, which has also proposed that it will be included in the European network of protected natural areas *Natura 2000*. The salt marsh is relatively undisturbed, being affected only by the non-aggressive activities of shellfish gathering and rush (*Juncus maritimus* L.) mowing.

Tidal range between mean springs is about 3.27 m, and tidal periodicity is semi-diurnal. Following Thornwaite's classification, climate in this area is humid, mesothermic and oceanic (Carballeira et al., 1983), with monthly temperatures fluctuating only slightly from the annual mean of 12.3°C (January and August means were 8.2 and 16.7°C,
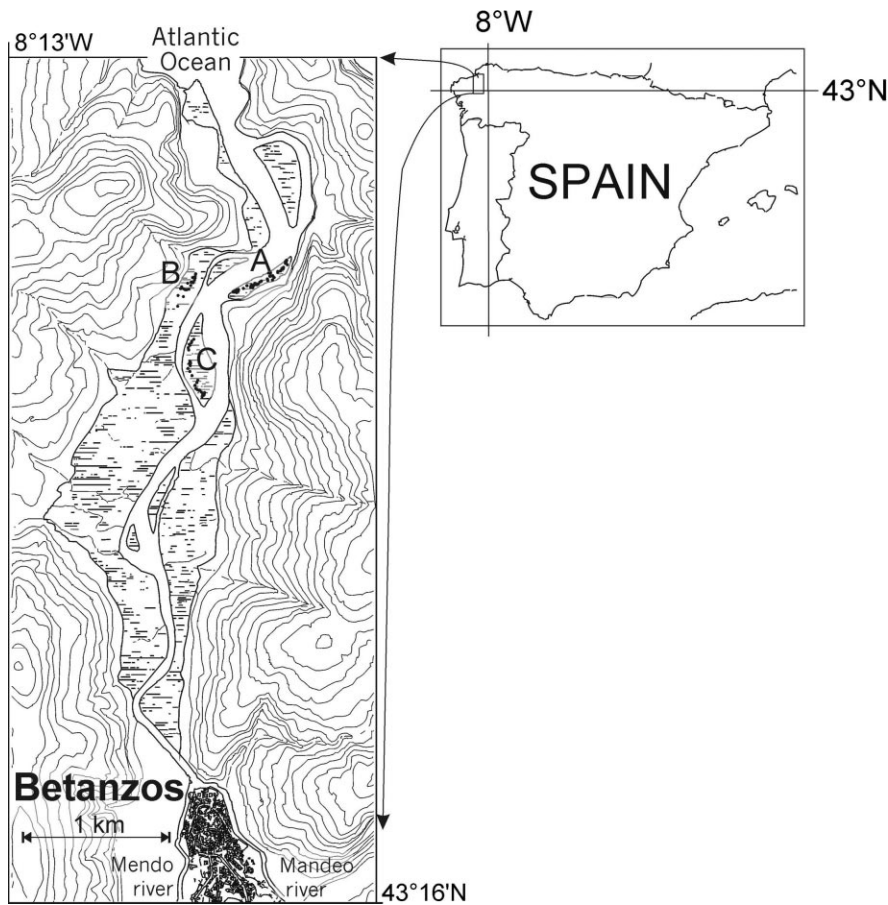
Fig. 1. Location map of the study site and distribution of the studied patches in the estuary (contour lines are separated by 10 m).

respectively). Mean annual precipitation is about 900 mm, and summer is the driest period, although drought conditions rarely occur. Underlying bedrock is mostly gneiss and slate, which give rise to a fine sediment when weathered.

The salt marsh vegetation of the area has been previously described in detail (Sánchez, 1991) and is clearly zoned, with *S. maritima* at the lower and outermost places. *Spartina* forms monospecific continuous stands at the upper end of its distribution, as well as a lot of rounded patches at the lower end, where it is colonising the open mud of the tidal flat. It is assumed that the individual genetic clones constitute each one of the patches ("clones", henceforth) which expand by vegetative reproduction, since a similar growing pattern has been reported previously from other latitudes (Castellanos et al., 1994), and for other *Spartina* species (Callaway and Josselyn, 1992; Daehler and Strong, 1994).

2.2. Relationship between patch characteristics and topography

In order to evaluate the relationship between clone size and topography, a survey was conducted on 102 *Spartina* clones growing on the tidal flat. Three different situations were considered (Fig. 1), corresponding to three different places along the estuary ("populations", henceforth, although they are not real genetically isolated populations).

Between September and October of 1996 the following variables were measured in each clone: maximal diameter; distance to open sea (i.e. distance from external sediment source, either the sea at one end of the estuary, or inversely the rivers at the other end, see Fig. 1); maximal elevation (i.e. elevation at clone centre); and external elevation (i.e. elevation at clone perimeter). For each clone, accretion due to the action of *Spartina* was considered as the difference between minimal and maximal clone elevation.

All topographical data were determined with an engineer's total station (SOKISA 3/B), and referred to the lowermost point of this study, i.e. the elevation at the perimeter of the outermost clone of population A. Distance to open sea was also considered as the distance from each clone centre to the centre of the outermost clone of population A.

2.3. Spartina patterns within patches

In order to assess the distribution patterns of plant characteristics within clones, we performed 24 belt transects, in 8 randomly selected clones of population A, and 16 of population C. The following variables were measured in contiguous 15×15 cm quadrats: vegetative shoot density, flowering shoot density and quadrat elevation at sediment level. All transects were radially laid from the lowest point on the perimeter to the highest (centre) of each clone. Quadrat elevation was measured with an automatic level (Fuji-Koh FL25M) and a calibrated rod.

2.4. Data analysis

The main clone variables were compared between populations with the Kruskall–Wallis single-factor analysis of variance by ranks.

Maximal clone elevation was compared between populations with ANCOVA, considering "minimal clone elevation" (elevation outside the clone), "clone diameter" (log transformed), and "distance to sea" as concomitant variables, in order to know whether there is any difference in plant ability to enhance accretion between populations (concomitant variable "distance to sea" was excluded because it failed to fit the ANCOVA requirement of slope homogeneity between groups).

The relationships between maximal clone elevation and clone characteristics were evaluated with multiple regression analysis. Regression analysis was also used to evaluate the relationship between shoot characteristics and topographical descriptors within clones.

Correlation analysis were calculated as the Spearman rank correlation coefficient (r_s), unless otherwise stated.

Normality was confirmed with the Korlmogorof–Smirnof test, and data were transformed when their distribution was not normal. All analyses were performed with the SPSS software package (Anon., 1999).

3. Results

3.1. Relationship between patch characteristics and topography

Average elevation at the edge of the clone and clone size increase from the outermost population A to the innermost C, although the differences for the second variable were not significant (Table 1). When compared within groups, only population A showed any correlation between elevation at clone edge and clone size ($r_s = 0.43$, $p < 0.01$, $n = 47$), while no correlation was found in the other populations ($r_s = 0.19$, $p < 0.40$, $n = 22$; $r_s = 0.01$, $p < 0.95$, $n = 32$ for populations B and C, respectively).

ANCOVA results show that "minimal clone elevation" and "clone diameter" are rather important factors determining the maximal elevation that a clone will reach, while the effect of the factor "population" is only marginally significant ($p = 0.041$) (Table 2).

The best-fit model (i.e. the model that minimises the determination coefficient) relating maximal elevation and clone characteristics for every population is shown in Table 3. The influence of "minimal clone elevation" on the model is significant in two of the populations, and its correlation with accretion (difference between maximal and minimal clone elevation) is negative ($r_s = -0.30$, $p < 0.01$ for sum of the populations; $n = 102$); the lower the altitude outside a clone, the higher is its ability to capture sediments. The influence of the "distance to sea" was only important in the outermost population A.

Clone diameter is the only factor shared by the models from all populations and thus can be considered as the main determinant of accretion. There is a positive logarithmic relationship

Table 1

Main descriptors of the studied patches (clones) at the three populations considered (between population Kruskall–Wallis test)

Population	n	Variable	Minimum	Maximum	Average ± S.E.
A	47	Diameter (cm)	128.0	1107.0	475.3±30.5
		Elevation at edge (cm)	0.0	61.2	47.1±2.0
		Distance from sea (m)	0.00	508.12	260.71±23.63
		Accretion (cm)	4.8	40.4	16.9±1.3
B	22	Diameter (cm)	136.0	2412.0	600.8±96.4
		Elevation at edge (cm)	32.2	64.0	49.9±1.7
		Distance from sea (m)	628.31	975.44	754.59±18.77
		Accretion (cm)	2.7	35.5	13.4±1.9
C	32	Diameter (cm)	131.00	2643.00	793.3±134.9
		Elevation at edge (cm)	43.4	69.0	59.4±1.4
		Distance from sea (m)	1078.23	1571.22	1365.86±30.03
		Accretion (cm)	2.7	37.8	15.8±1.4
Total	101	Diameter (cm)*	128.00	2643.00	584.2±422.6
		Elevation at edge (cm)**	0.0	69.0	51.6±1.2
		Distance from sea (m)**	0.00	1571.22	713.95±50.06
		Accretion (cm)[a]	2.7	40.4	15.8±0.9

* $p < 0.05$.
** $p < 0.01$.
[a] Not significant.

Table 2
Results of ANCOVA to evaluate the effect of factor "population" and the concomitant variables "clone diameter" (log transformed) and "minimal elevation" on the maximal elevation reached by each clone

Variable	d.f.	M.S.	F	P
Population	2	1.403E−2	3.304	0.041
Concomitant variables				
ln(diameter)	1	0.283	66.719	<0.001
Minimal elevation	1	0.471	110.877	<0.001
Error	96	4.246E−3		

between both variables; accretion increases with clone size until it reaches a limit where it stabilises independently of clone size (Fig. 2). On the other hand, untransformed clone diameter was not significant, and so excluded from every model, making it clear that the relationship between clone diameter and maximal elevation is non-linear.

Other plant characteristics such as mean shoot size or mean shoot density of the clone were not correlated with accretion ($r_s = -0.10$, $p = 0.63$; $r_s = -0.16$, $p = 0.45$, respectively, for all clones from belt transect survey [$n = 24$]).

There is no relationship between the topographical elevation where a clone is located (elevation at the edge) and mean shoot size ($r_s = 0.05$, $p = 0.81$; $n = 24$) or mean shoot density ($r_s = -0.10$, $p = 0.65$; $n = 24$). On the other hand, there is a positive correlation between clone distance to the sea and mean shoot density ($r_s = 0.51$, $p = 0.01$; $n = 24$), but there is no correlation with mean shoot size of the clone ($r_s = -0.05$, $p = 0.82$; $n = 24$).

3.2. Spartina patterns within patches

Mean shoot size increased from the edge towards the centre of the clone (Fig. 3A), up to a maximum located at about 190 cm from the edge. Shoot density showed a more complex

Table 3
Results of the stepwise regression analysis on "maximal clone height"

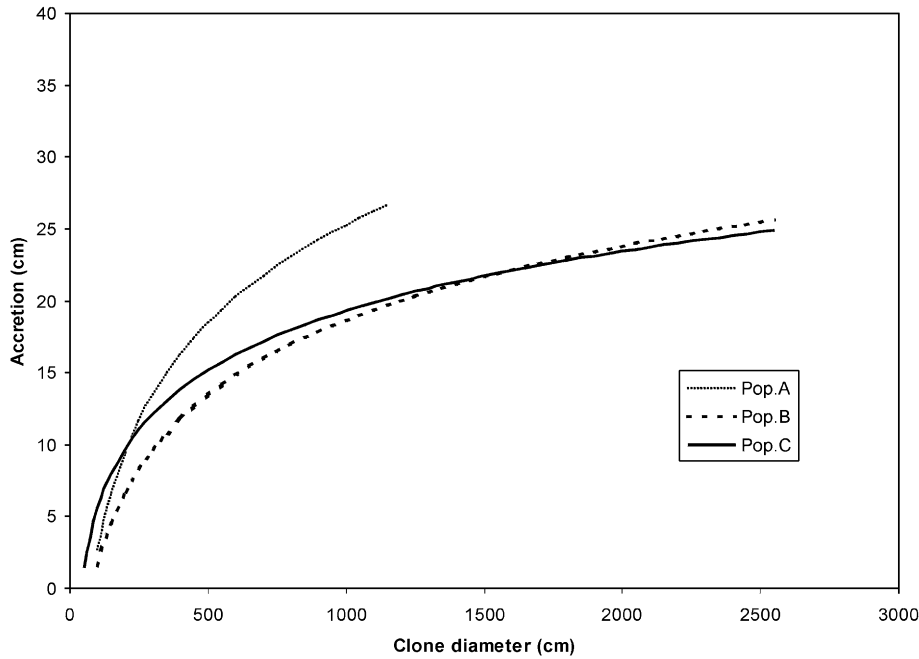| Population	Independent variable	R^2	B	β
A	Constant		−1.88**	
	Minimal elevation	0.84	0.50**	0.49
	ln(diameter)		0.11**	0.38
	Distance to sea		2.99E−4**	0.35
B	Constant	0.68	−3.1**	
	ln(diameter)		0.11**	0.82
C	Constant		−1.29**	
	Minimal elevation	0.65	0.57**	0.49
	ln(diameter)		6.48E−2**	0.58
A + B + C	Constant		−1.193**	
	Minimal elevation	0.73	0.67**	0.64
	ln(diameter)		8.40E−2**	0.43

** $p < 0.01$.

Fig. 2. Best-fit curves relating clone diameter and accretion calculated from the three studied populations (note that population A contains no clone with a diameter exceeding 11 m).

distribution, with a succession of belts with different densities (Fig. 3B). The pattern of flowering shoot density was similar to that of the vegetative shoots, and some belts with different densities could be detected too, but its maximum is slightly moved inwards (around 120 cm from clone edge; mean density about 156 flowering shoots/m^2). Flowering shoot density decreased from that point, but it did not seem to follow a clear pattern (Fig. 3C).

The relationship between shoot size and the distance to the clone edge is positive and logarithmic (standardised coefficient = 0.39), while its relationship with topographical height is linear and also positive (standardised coefficient = 0.22) (Table 4).

Table 4
Regression models for the relationship between shoot size with distance to clone edge (log and square-transformed, respectively), and quadrat elevation (considering elevation at clone edge as zero for each clone)

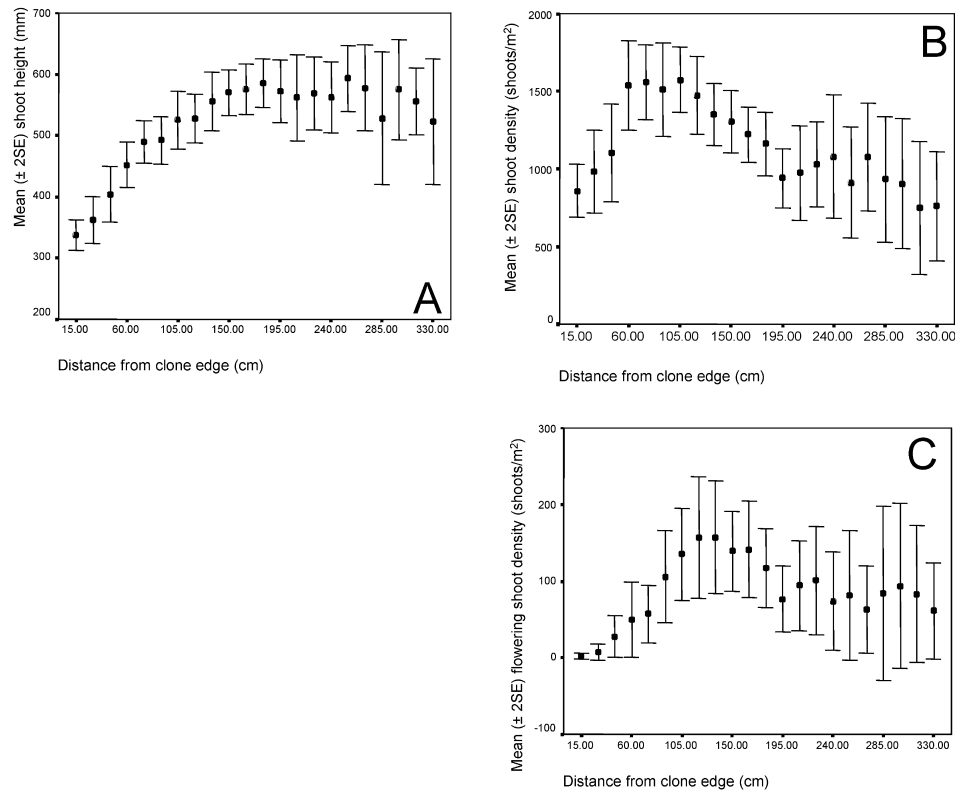| Dependent variable	R^2	Independent variable	B	β
Shoot size	0.33	Constant	354.38**	
		ln(distance to edge)	60.31**	0.39
		Quadrat elevation	0.48**	0.22
Shoot density	0.13	Constant	26.64**	
		(Distance to edge)^2	−0.05**	−0.49
		Quadrat elevation	0.09**	0.36

** $p < 0.01$.

Fig. 3. Mean vegetative shoot size (A), vegetative shoot density (B), and flowering shoot density (C), from the edge to the centre of the clones. Bars stand for ± 2 standard errors of the mean.

The relationship between shoot density and the factors considered is weak, and the regression model cannot explain most of the variance ($R^2 = 0.13$). Moreover, there seems to be no correlation with topographical elevation or distance to clone edge ($r_s = 0.06$, $p = 0.23$; $r_s = -0.14$, $p < 0.01$, respectively, $n = 413$).

4. Discussion

4.1. Relationship between Spartina patches and accretion

Clone size is considered as one of the most important factor conditioning accretion (Castellanos et al., 1994), and our results agree with this view, although it has been previously stated, the accretion process follows a rather complex multifactorial model (e.g. Hutchinson et al., 1995; Moy and Levin, 1991). Other factors, some as evident as time (Bird and Ranwell, 1964), basal elevation (Hutchinson et al., 1995, present results) or distance to the water exchange source (Cahoon, 1994, present results) can also modulate the sediment

deposition. On a larger spatial scale, tidal variables (e.g. tidal range) are also conditioning the distribution (and therefore the accretional action) of *Spartina* in the altitudinal gradient (see McKee and Patrick, 1988; Daehler and Strong, 1996). It has been stated that the larger the tidal amplitude, the larger the *S. alterniflora* altitudinal range (McKee and Patrick, 1988), and this seems to be the case for *S. maritima* also; its altitudinal range in Southwest Spain is about 58 cm, for a tidal amplitude of 2.97 m (Castellanos et al., 1994), while in Northwest Spain those values are 66 cm for 3.27 m, respectively (present results).

Regardless of the multifactorial determination of accretion, some clear patterns have been found associating accretion and *Spartina* patch size. Castellanos et al. (1994) have found a linear relationship between clone size and elevation at clone centre (maximal elevation), so accretion increases with clone size. In this study, we have found a logarithmic relationship: while clone size is small, the relationship between clone diameter and accretion is almost linear, as the model of Castellanos et al. (1994) predicted; in larger sized clones, accretion stabilises around a maximum, and no sediment deposition seems to take place despite the increase in clone size (Fig. 2). Accretion models in populations B and C are almost identical, probably because both populations are composed of clones of all sizes, while population A has no clone with a diameter exceeding 11 m; the model from population A is less reliable in predicting the accretion of the clones with a larger diameter.

According to our data, basal (mudflat) elevation is also a rather important determinant of accretion (Table 3), since it is directly correlated with the duration of inundation (and therefore with exposition to tidal currents carrying sediments). Our regression model predicts that sediment accretion diminishes with increasing marsh surface elevation, as previous studies have shown for other *Spartina* species (Hutchinson et al., 1995 and references therein). Variable "distance to sea" is an important factor only in population A, which is closer to open sea than the others.

This study also supports the hypothesis of Castellanos et al. (1994), who suggested that larger clone size corresponds to older clones. In this case, as the *Spartina* colonisation progresses outwards on the open mudflats, clone size becomes smaller. This is specially clear in population A, as its situation at the lowermost part of the elevation gradient made this tendency more evident.

4.2. Shoot size and density within patches

Spartina patches are characterised by several concentric rings with different shoot density, although maximal density is regularly close to the patch edge (Castellanos et al., 1994). According to our data, maximal shoot density occurs at about 90 cm from the clone edge. Density at the centre of the patches is significantly lower than that near the edge, as has been previously stated in other latitudes (Castellanos et al., 1994) and for other *Spartina* coloniser species (e.g. Caldwell, 1957; Callaway and Josselyn, 1992). The higher elevation and the lower shoot density at the centre of the clones ameliorate the environmental conditions, making it possible for other species to colonise ('nucleation' sensu Yarranton and Morrison, 1974), as has been described by Castellanos et al. (1994): an elevation at the centre of one *S. maritima* clone of only 15 cm above the perimeter is enough to facilitate the installation of *Sarcocornia perennis* (Miller) A.J. Scott in some populations of Southwest Spain. Nonetheless, this is not the case in our latitude, despite the fact that the mean

accretion for two populations was higher than 15 cm (Table 1), and that *Sarcocornia* is a very common plant in this salt marsh (Sánchez, 1991).

Our data support previous studies which have documented that *Spartina* flowering is related to shoot density (Thompson et al., 1990; Castellanos et al., 1998). It has been proved that shoot mortality increases after flowering (Castellanos et al., 1998), and this loss may contribute to the observed decrease of vegetative shoot density inside the clones. Other works have proved that flowering is not a direct effect of vegetative shoot density; Mullins and Marks (1987) have found that the density of flowering shoots of *S. anglica* is significantly lower in mature zones of the salt marsh, independent of vegetative shoot density.

In conclusion, we propose a model that relates clone size and accretion, which is a modification of that proposed earlier for this species for other latitudes (Castellanos et al., 1994), and that takes into account a larger number of clone sizes. When this variation is considered, the relationship seems to be logarithmic rather than linear. Other factors like distance to water exchange source and height prior to *Spartina* colonisation have proved to be important to condition accretion. Once established, *S. maritima* patches in Northwest Spain follow a colonisation pattern similar to that described from other latitudes and other *Spartina* coloniser species.

Acknowledgements

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