

Primary succession in an Atlantic saltmarsh: from intertidal flats to mid-marsh platform in 35 years

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Abstract

1. Although saltmarsh is a classic example of primary succession, the underlying mechanisms and their timescales are poorly understood. As saltmarsh succession depends on sediment accretion, the amelioration of abiotic conditions associated with increasing elevation suggests potential explanatory roles for facilitation, competition and the stress-gradient hypothesis.
2. We present a 35-year longitudinal study of saltmarsh development from intertidal flat to a mid-marsh platform at Odiel Marshes in southwestern Iberia. Using permanent plots, this work chronicles changes in elevation and marsh morphology, their evolving effects on sediment redox potential and salinity, and the colonisation and changing patterns of dominance of halophytic species.
3. Sporadically colonizing clumps of the low-marsh species *Spartina maritima* trapped sediment to form raised tussocks, which increased in elevation and area. Reduced tidal inundation and locally improved drainage promoted higher redox potentials and allowed colonization by a sequence of species less tolerant of reducing conditions: *Sarcocornia perennis*, its hybrid with high-marsh *S. fruticosa*, and *Atriplex portulacoides*. Unlike its centrifugally colonising predecessors, *A. portulacoides* invaded from the tussock edges. Transplant experiments designed to investigate its late establishment on tussocks showed that seedling survival depended on elevational differences as small as 4 cm.
4. After increasing in elevation by c. 1 m (c. 29 mm/year), coalescence of the tussocks formed a marsh platform at a level corresponding with mean high tides. This supports a theoretical punctuated transition from ‘submergence marsh’ to ‘emergence marsh’, previously postulated for this tidal elevation.
5. *Synthesis*. The unexpected rapidity of this primary succession highlights the central role of facilitation. Vertical sediment accretion, locally engineered by colonizing species, progressively alleviates abiotic stress and allows colonisation by species that are less tolerant of chemically reducing conditions but are ultimately better competitors.

KEYWORDS

Atriplex portulacoides, elevation, emergence marsh, facilitation, invasion, redox potential, sediment accretion, stress-gradient hypothesis

1 INTRODUCTION

Succession has been of enduring interest since the inception of ecological theory and remains central to contemporary ecological questions (Meiners et al., 2015; Chang & Turner, 2019). Primary succession involves changes in the abiotic environment that modulate the outcome of biotic interactions but the mechanisms, notably facilitation, inhibition and tolerance, have been contentious (Connell & Slatyer, 1977; Pickett, Collins, & Armesto, 1987; Farrell, 1991; Pulsford, Lindenmayer, & Driscoll, 2016). Nevertheless, the fundamental role of facilitation in the structure and ontogeny of natural ecosystems is now recognised (Brooker et al., 2008); for primary succession it is widely accepted that tolerance of abiotic stress and facilitation dominate in the early stages, whereas interspecific competition becomes more important as abiotic conditions ameliorate, consistent with the stress gradient hypothesis (He & Bertness, 2014). Because of the timescales involved, much of the evidence has come from chronosequence studies and thus from space-for-time substitutions. Although valuable, they have limitations and inappropriate inferences have been drawn from them (Walker et al., 2010). Longitudinal studies, coupled with experimentation, are likely to provide more reliable insights into mechanisms. In particular, they may clarify the extent to which successional trajectories are gradual or are determined by thresholds (e.g. Corenblit, Steiger, & Tabacchi, 2010); non-linear dynamics have previously been associated mainly with the disturbances initiating secondary successions (e.g. Jager et al., 2018).

Coastal saltmarshes represent the earliest recorded examples of successional development (Davy, 2000) and succession is integral to our understanding of saltmarsh geomorphology (Allen, 2000). However, space-for-time substitutions have not satisfactorily distinguished it from static vegetational zonation associated with the elevational gradient from sea to land, particularly in the light of changing relative sea levels, and associated sediment dynamics. Because the relationship between tidal submergence and elevation is not linear, a distinction has often been made between lower marshes (dominated by factors associated with submergence) and upper marshes (dominated by those associated with emergence); the threshold between submergence and emergence marsh is widely accepted as around Mean High Water (MHW) tidal level (Chapman, 1960; Ranwell, 1972; Long & Mason, 1983). Succession implies a transition between these zones but such punctuated changes and their dynamics have not been observed in longitudinal studies. Long-term studies based on permanent quadrats (Leendertse, Roozen, & Rozema, 1997; Roozen & Westhoff, 1985; Bos, Bakker, de Vries, & van Lieshout, 2002) or historical maps and aerial photographs (Gray, 1972; Willis, 2000) have focused on the changing extent and composition of plant communities, offering circumstantial insight into succession.

Primary saltmarsh succession was initiated at Odiel Marshes (southwestern Iberian Peninsula) in 1977, when the construction of a dyke to protect an estuarine shipping channel allowed sedimentation on sand flats in intertidal lagoons (Castellanos, Figueroa, & Davy, 1994). In a well-drained lagoon the primary colonist, *Spartina maritima* (Curtis) Fernald, trapped sediment to form raised tussocks that increased in diameter and elevation; this allowed invasion of the centres of the tussocks by *Sarcocornia perennis* (Mill.) A.J. Scott, which spread centrifugally, displacing *Spartina* to the periphery of the expanding tussocks (Castellanos, Figueroa, & Davy, 1994). Continued vertical accretion facilitated similar establishment and centrifugal spread of a hybrid *Sarcocornia* resulting from *in situ*

hybridisation of *S. perennis* with the high-marsh species *S. fruticosa* (L.) A.J. Scott, whose pollen had been dispersed from nearby (Figueroa et al., 2003). Subsequently this marsh and others in similar lagoons at Odiel Marshes have continued to develop, providing a model system for investigating primary succession in mineralogenic saltmarshes over a period of 35 years.

The purpose of this paper is to present the changes that have occurred in the 18 years since we reported on the establishment of the submergence marsh, to set these in the context of the overall succession, as currently understood, and to explain the processes driving change. We have investigated temporal and spatial patterns of saltmarsh structure, manifested as changing species abundance, sediment accretion and the resulting physico-chemical environment. We augment longitudinal observation with transplant experiments using *Atriplex portulacoides* L., as the emerging dominant, in examining the importance of changing position in the tidal frame, and the extent to which this influences abiotic and biotic constraints on the colonisation of plant species. We hypothesised that continued accretion would lead to: (1) a general increase in elevation in the tidal frame; (2) further amelioration of the physiochemical environment (evident as increasing sediment redox potential); (2) colonisation and subsequent domination by potentially more competitive species that are less tolerant of the consequences of submergence; (3) evolution from tussock structure to a marsh platform with dissecting creeks; and (4) a transition from submergence to emergence marsh at an elevation level similar to tidal Mean High Water.

2 MATERIALS AND METHODS

2.1 Field sites

The study was carried out at Odiel Marshes (Figure S1), in the joint Estuary of the Odiel and Tinto rivers on the Atlantic Coast of the southwestern Iberian Peninsula (37°08′ - 37°20′ N, 6°45′ - 7°02′ W). Odiel Marshes have been protected as a ‘Natural Reserve of the Biosphere’ and represent one of the largest salt marsh complexes in the Iberian Peninsula. The tidal regime is semidiurnal, with a mean range of 2.10 m and a mean spring tidal range of 2.97 m. Mean tidal levels relative to Spanish Hydrographic Zero (SHZ) are: mean high water neap (MHWN), +2.44 m; mean high water (MHW), +2.91 m; mean high water spring (MHWS), +3.37 m; and highest astronomical tides (HAT), +3.71 m. Work was located in three accreting intertidal lagoons, two with free tidal drainage (Laguna de Don Claudio and Laguna de El Manto) and another with impeded drainage (Laguna de Ludovico) – henceforth Don Claudio, El Manto and Ludovico, respectively. More details of the physiography, climate and vegetation of the sites are provided by Castellanos, Figueroa, and Davy (1994) and Figueroa et al. (2003).

2.2 Analysis of vegetation

The composition and structure of the vegetation in Don Claudio were investigated over a period of 35 years. Changing conditions necessitated certain modifications to the methodology over this period. Initially eight raised tussocks formed by colonizing clones of *Spartina maritima* were identified as permanent plots and the areas occupied by all species present on them were recorded in October-November 1984, 1990, 1997 and 2001. Subsequently, an additional eight tussocks were included as permanent plots in the sampling

programme in October–November 2004, 2007, March 2011 and November 2013, 2015 and 2018 (giving a total of 16 tussocks). From 1984 to 2007, the area of each tussock and that of its colonising species was recorded by measuring the minimum and maximum diameter at the base of the canopy and applying the formula of an ellipse. In 2007, as the vegetation became more complex in structure, the area occupied by each species was also recorded continuously along four radial, linear transects up to 5 m long; these originated at the centre of each tussock and were at 90° to one another. Estimates by the two methods corresponded closely: *A. portulacoides* ($52.0 \pm 6.2\%$ v. $67.9 \pm 5.8\%$), *Sarcocornia* hybrid (18.7 ± 5.1 v. $19.9 \pm 5.6\%$), *S. perennis* ($26.3 \pm 5.6\%$ v. $25.0 \pm 5.9\%$) and *S. maritima* ($3.8 \pm 3.4\%$ v. $2.8 \pm 1.2\%$). Thereafter, only the latter method was used, as it allowed us to measure the increasing superimposition of species' canopies and was more appropriate as tussocks became more irregular and started to coalesce. For every year the cover of each species was calculated as a percentage of the total area of the raised tussock.

Previously, above-ground plant biomass (AGB) had been harvested from transects across representative permanently marked colonizing tussocks (Castellanos, Figueroa, & Davy, 1994; Figueroa et al., 2003). In January 2005, we resampled one of these tussocks to display the radial distribution of newly invading *Atriplex portulacoides*. Each transect was a belt of contiguous quadrats (15 cm radially \times 25 cm wide) across the radius of the tussock. Dry mass was determined after drying at 80 °C for 48 h.

Similarly, measurements of the vertical distribution of below-ground biomass (BGB) made up to 2001 were augmented by new samples in 2005. Sediment cores (10.5 cm diameter \times 50 cm deep) were extracted from under the largest *A. portulacoides* patch in five replicate tussocks in April 2005. Cores were divided into 5-cm layers, and roots and rhizomes of all species present were washed from them, before being dried and weighed. Roots of *A. portulacoides* and *Sarcocornia perennis* were distinguished by their colour, size and shape. *Spartina maritima* roots were distinguished by their white colour and the presence of well-developed aerenchyma. Care was taken to maintain the attachment of small roots to the more recognisable larger ones.

To examine larger-scale plant distribution patterns in relation to the developing creeks, the continuous presence of each species, bare sediment and tidal creeks was recorded along two linear transects (298.5 m and 292.5 m long) following the main axis of the lagoon in November 2001, and along a further five transects (2 \times 30 m and 3 \times 100 m) in June–August 2005.

2.3 Sedimentary environment

Elevations relative to SHZ were surveyed to a resolution of 2 cm using a Leica NA 820 theodolite at the centre and the edge of the 16 permanent tussocks and under the canopy of each plant species ($n = 10$ –20) each time that plant cover was recorded. Elevations of extreme tidal levels were also determined as reference points. Sediment redox potential (Eh), pH and electrical conductivity (EC) were recorded in parallel with elevation under the canopy area of each plant species ($n = 5$). Eh was measured in the field using a Crison pH/mV meter and redox electrode system at two sediment depths in the rooting zone (0–10 and 11–20 cm). pH and EC (as a measure of salinity) for sediment samples collected in the field between 0–10 and 11–20 cm deep were recorded in the laboratory using a pH-meter (Crison GLP21,

Barcelona; in 1:1 mix of sediment and distilled water) and a conductivity meter (Crison-522; in 1:2 mix of sediment and distilled water), respectively, and their electrode systems.

2.4 Transplant experiments with *Atriplex portulacoides*

As the most recent coloniser to attain dominance, *Atriplex portulacoides* was transplanted into three intertidal lagoons to investigate its survival in different successional settings.

Transplants were seedlings chosen for similar size (3-5 branches, c. 15 cm height). No attempt was made to remove sediment adhering to the roots of transplants. Survival was determined at 2-monthly intervals for 6 months and a transplant was considered dead when no green leaves or shoots remained. Sediment Eh and conductivity were measured, as described previously, at five locations from each transplant/replant site; as EC measurements at the two depths were not significantly different, data were combined for analysis ($n = 10$).

2.4.1 Transplants to poorly and well drained lagoons

This experiment examined whether *Atriplex portulacoides* was able to survive on *Spartina maritima* tussocks recently colonised by *Sarcocornia perennis* at their centres, in well and poorly drained settings. Seedlings were obtained from a natural population at the periphery of Ludovico (elevation +2.9 m SHZ), where seven seedlings were also replanted as a control treatment. Seedlings were transplanted to the central areas of tussocks, colonised by *S. perennis* (patches smaller than 30 cm diameter), in the previous two years at Ludovico (poorly drained) and El Manto (well drained) lagoons. Single seedlings were planted at the centre of each of seven replicate tussocks at each lagoon in April 2005.

2.4.2 Transplants to different tussock zones

The second transplant experiment investigated the survival of *A. portulacoides* in three different radial zones of tussocks that had been colonised centrifugally by *S. perennis* and which had begun to develop raised levees at their edges, as they met, or formed creek banks. *Atriplex portulacoides* seedlings were sourced from material previously collected from Odiel Marshes and cultivated for five months in a glasshouse in commercial potting compost, to obtain a total of 60 of consistent size. Then seedlings were transplanted to Don Claudio at the edge of tussocks (levee or creek-bank), their inner areas colonised by *Sarcocornia perennis* and inner areas still occupied only by *Spartina maritima*. Five seedlings were planted in each of the three zones of four different tussocks in May 2007. Surface elevation and sediment water content were determined, as described previously, at five locations for each transplant site.

2.5 Statistical analysis

Analyses were carried out using SPSS v.15.0 (SPSS, Inc.). Data were tested for normality using the Kolmogorov-Smirnov test, and for homogeneity of variance using the Levene test. Sediment variables for the transplant experiment to poorly and well drained lagoons were compared between lagoons using t-tests for independent samples. Sediment variables for the transplant experiment to different tussock zones were compared among zones using one-way analysis of variance (ANOVA) and Tukey's Honestly Significant Difference Test post hoc test. Where normality or homogeneity of variance was not achieved by transformation, means

were compared using non-parametric Kruskal-Wallis ANOVA with a post hoc Mann-Whitney U-test. Sigmoidal and linear regressions were fitted using Sigma Plot v11.0 (Systat Software, Inc.) to examine the relationships of Eh and EC, respectively, with surface elevation of the tussocks. Differences in marsh elevation among taxa, years and their interaction were analyzed using the Gamma Generalized Linear Model (GLZ) with Chi-square (χ^2) of Wald, and Bonferroni *post hoc* test, since transformations of the data did not achieve homogeneity of variance (Ng & Cribbie, 2017).

Plant cover data for large-scale spatial distribution analysis obtained from linear transects following the main axis of Don Claudio were grouped into contiguous 50-cm sections. Data were checked for conformation to a Poisson distribution and dispersion coefficients were calculated as the ratio of variance and arithmetic mean (σ^2 / x); random distribution: $\sigma^2 / x = 1$, regular: $\sigma^2 / x < 1$; contagious: $\sigma^2 / x > 1$. Where contagion was detected, the size of clumps was estimated by the method of block variance (Greig-Smith, 1964). Association between species and tidal channels was tested by a χ^2 test for observed and expected frequencies of association, with a null hypothesis that plant species and channels were distributed randomly.

3 RESULTS

3.1 Changes in intertidal environment

Sedimentation in Don Claudio resulted in generally increasing elevation of its surface over the whole 35-year period of the study. Sporadic initial colonization by clones of *Spartina maritima* (see 3.2), when the elevation was little above the mean tidal water level (MW), was associated with increased sedimentation and the formation of raised tussocks. These tussocks increased in area and elevation with time (Figures 1, S2). Their area increased 118 m² from 1984 to 2007. The centres of the tussocks were consistently higher than their peripheries, increasing by c. 3 cm yr⁻¹ from 1984 until 2004, amounting to a total accumulation of 72 cm in 20 years. They surpassed the level of mean high water neap tides (MHWN; +2.44 m SHZ) in 1991 and approached the mean high water tidal level (MHW; +2.91 m SHZ) in 2004. After this, elevation change was slower and more erratic, with 16 cm of sedimentation from 2004 to 2018. Elevation of the tussock peripheries reached MHWN much later and oscillated around it from 2000 to 2011, before continuing to increase until 2018, at which time it was still below MHW. Elevation of the tussock peripheries decreased 27 ±7 cm from 2000 to 2011, while they were moving rapidly in a centrifugal manner to expand tussock area. After 2011, with coalescence of the tussocks, the now stationary edges resumed their increase in elevation (Figure 1a,b). The area of tussocks grew as they increased in mean diameter until 2007, eventually driving the coalescence of neighbouring tussocks. By this time, incipient drainage channels between the tussocks had either been filled with sediment or consolidated into the new marsh drainage system (Figure 1b).

Increasing elevation was associated with higher sediment Eh, changing in a sigmoid manner from values c. -300 mV to c. +200 mV, both near the surface (0-10 cm) and in deeper (10-20 cm) sediments (Figure 2). Eh values above zero were almost entirely restricted to elevations above MHWN in the superficial sediments, although the deeper ones were generally rather more reducing. Higher Eh (> +200 mV) also tended to be associated with the later stages of the succession, irrespective of elevation. The EC of sediment extracts was

significantly, if rather weakly, dependent on elevation as the marsh developed from 2001 to 2018 (Figure 3). Thus, EC from 2001 to 2013 varied between $6.0 \pm 0.0 \text{ mS cm}^{-1}$ and $17.8 \pm 0.7 \text{ mS cm}^{-1}$, increasing to values c. 30 mS cm^{-1} under the canopy of the hybrid of *Sarcocornia* and *A. portulacoides* in 2015. Sediment pH showed no discernible trend over the same period, with little deviation from neutrality, varying between 6.7 and 7.6.

3.2 Vegetation change

The initial colonisation of the Don Claudio was by *Spartina maritima*; clonal clumps of tillers formed isolated, expanding tussocks. Changes in plant species cover recorded between 1984 and 2018 showed a clear sequence of species invasion and dominance (Figures 4, 5). By 1984, although the vegetation cover was still dominated by *S. maritima* (with a mean cover of $88 \pm 6\%$), the centres of the tussocks had been invaded by *Sarcocornia perennis* (with a mean cover of $12 \pm 4\%$). Subsequently, the cover of *S. perennis* increased, at the expense of that of *S. maritima* until *S. perennis* was clearly dominant by 2001, when it achieved its maximum mean cover of $82 \pm 4\%$. However, by 1997 other species had begun to invade the tussocks, albeit with low cover. The hybrid *Sarcocornia perennis* x *fruticosa* replaced *S. perennis* at the centres of many of the tussocks through *in situ* hybridisation and expanded its cover, again centrifugally, steadily to reach mean cover of $66 \pm 5\%$ by 2018 (Figure 4). Also in 1997, the first individuals of the shrub *Atriplex portulacoides* were recorded, initially representing a mean cover of only $2 \pm 0\%$. In contrast to other species, *A. portulacoides* colonised the peripheries of the tussocks and then invaded them centripetally. This process was slow at first, with cover only $4 \pm 1\%$ in 2002, but it then rapidly achieved dominance of the tussocks by 2004 and has maintained the highest cover of c. $80 \pm 5\%$ from 2011-2018. Most of the expansion of *A. portulacoides* since 2001 has been at the expense of *S. perennis*. A very low cover of the annual *Suaeda albescens* Lázaro Ibiza was able to persist throughout the sequence but it did not show any successional change (Figure 4).

The elevational ranges of the four perennial species increased over the last 28 years (Figure 6). Although *Spartina maritima* colonized at elevations little above mean sea level (MW) its upper limit was nearer to mean high water (MHW) level, as the marsh accreted. *Sarcocornia perennis* consistently occupied a zone between MHWN and MHW level. Hybrid *Sarcocornia* and *Atriplex portulacoides* both appeared above MHWN level but were predominantly distributed around or above MHW. GLZ showed that elevation was significantly different among taxa ($\chi^2 = 135.216$, $df = 3$, $P < 0.0001$), among years ($\chi^2 = 337.732$, $df = 8$, $P < 0.0001$) and their interaction ($\chi^2 = 169.169$, $df = 20$, $P < 0.0001$). This confirms that *Spartina maritima* and *Sarcocornia perennis* colonized lower elevations ($+2.66 \pm 0.02 \text{ m SHZ}$ and $2.69 \pm 0.01 \text{ m SHZ}$, respectively) than the *Sarcocornia* hybrid and *A. portulacoides* ($+2.88 \pm 0.02 \text{ m SHZ}$ and $2.84 \pm 0.01 \text{ m SHZ}$, respectively), and all taxa except *S. perennis* increased their colonized marsh elevations over time (Figure 6).

Changes in radial distribution of above-ground biomass on a representative tussock are shown in Figure 7. Four years after its first appearance, *A. portulacoides* was distributed contagiously ($\sigma^2 / x = 1.39$) forming patches c. 2 m in diameter that were positively associated with developing tidal channels ($\chi^2 = 24.56$, $P < 0.0001$). By 2005, it was regular or random in distribution ($\sigma^2 / x = 0.89-0.98$), although still associated with tidal channels ($\chi^2 = 6.10$, $P <$

0.01), if less strongly. This trend was also reflected in the fraction of *A. portulacoides* plants appearing near the edge of developing tidal channels, which fell from $49 \pm 18\%$ in 2001 to only $20 \pm 7\%$ in 2005. The dominance of *A. portulacoides* in the canopy at this stage was reflected in its below-ground biomass (Figure 8), where it monopolised the upper 25 cm of the sediment profile, consigning the residual biomasses of earlier colonizers to greater depths.

3.3 Transplant experiments with *Atriplex portulacoides*

No seedling of *A. portulacoides* that had been transplanted to the centre of tussocks recently colonised by *S. perennis* in either poorly drained (Ludovico; Figure 9b) or well drained (El Manto; Figure 9c) lagoons survived for as long as 6 months. In contrast, survival of the replanted controls at the source locality was 100% (Figure 9a). Sediment Eh at the transplant sites in both Ludovico and El Manto was strongly reducing in comparison with Don Claudio, although even more so in the poorly drained lagoon. EC values were 30% higher at El Manto than at Ludovico (Table 1).

Survival was no better in seedlings transplanted to the inner areas of tussocks colonised by *S. perennis* at Don Claudio, whether into inner areas already occupied by *Sarcocornia perennis* (Figure 9e) or *Spartina maritima* (Figure 9f). In contrast, no seedlings died after transplantation to levees at the edge of the tussocks within the 6 months (Figure 9d). Environmental characteristics at these locations are also shown in Table 1. The favourable locations at the edges of the tussocks were on average only 4 cm higher than the unsurvivable locations but, nevertheless, had significantly lower water contents, higher superficial Eh and lower EC values.

4 DISCUSSION

Atlantic saltmarshes were mostly initiated when coastlines stabilized in their current positions some 6000-7000 years ago, after the rapid sea-level rise associated with the end of the last glaciation; subsequently, vertical sediment accretion has been accommodated by generally rising relative sea levels and auto-compaction of the sediments (Allen, 2000). This long history has obscured our view of the timescale required for successional development, especially as so much of the evidence is based on space-for-time substitutions (Walker et al., 2010). Our investigation in real time over the last 35 years revealed that after marsh formation on low-lying intertidal flats is triggered by a major physiographic change (Castellanos, Figueroa, & Davy, 1994), accretion and vegetational development can be remarkably rapid. Spontaneous development of saltmarsh plant communities (seaward of an artificial marsh) in the Wadden sea was similarly rapid between 1988 and 2016 (Hartmann & Stock, 2019). At Odiel Marshes, surface elevation increased by about 1 m in 35 years, from near mean sea level to above mean high water tidal level. In comparison, Leendertse, Roozen, and Rozema (1997) reported a rise of only 18 cm over 32 years in a marsh on the island of Terschelling (the Netherlands) that started to develop on sand flats in response to the construction of a dam. Recorded accretion rates in marshes at equilibrium with sea level rarely exceed 1 cm/year (French, 2006). Vertical elevation inevitably results in reduced frequency and duration of tidal inundation. This and the improved drainage associated with locally raised elevations, relative to the tidal platform, both led to the enhanced sediment oxygenation that we measured as higher Eh (Mossman, Grant, & Davy, 2020); furthermore, oxygenation may

have been amplified by episodic effects of tidal pumping action on the raised areas (Fivnash et al., 2019).

Vertical accretion was intimately associated with a sequence of species invasions and dominance that reveals the spatial dynamics of primary succession on an intertidal flat with little gradient from sea to land. Initial sporadic colonization was by *Spartina maritima*: clumps of its tillers trapped sediment to give rise to raised tussocks that were subsequently invaded by *Sarcocornia perennis* (Castellanos, Figueroa, & Davy, 1994) and this highlights the role of *Spartina maritima* as an ecosystem engineer. The spatial pattern of habitat heterogeneity created by *Spartina alterniflora* also influences recruitment and growth of other plant species (Proffitt et al., 2005). Continued accretion at Odiel saw colonization of many of the tussocks by a hybrid, *Sarcocornia perennis* × *fruticosa*, when pollen from stands of the latter at the upper margin of the lagoon fertilised flowers of the former *in situ* on the rising tussocks (Figueroa et al., 2003). This was not a precursor to dominance by the hybrid, however, since *Sarcocornia* hybrids have similar realized niches to their parental species and can coexist with other plant species elsewhere at Odiel (Gallego et al., 2018). Although the hybrid has indeed largely replaced its maternal parent over the subsequent 18 years, it is *Atriplex portulacoides* that has become dominant. *Atriplex portulacoides* had first appeared at a similar time to the hybrid but was less prominent in their early stages. It also had a different invasion strategy from its predecessors, colonizing the edges of the tussocks rather than the centres. As a low-growing, sprawling shrub, *A. portulacoides* is the physiognomic dominant of mid to high marshes and their creek banks around much of the European coast (Chapman, 1945; Mohamed, 1998).

The pattern of invasion with increasing elevation in the tidal frame can be explained fundamentally by the species' tolerances of the concomitantly changing environmental conditions, rather than by dispersal limitation. It is widely acknowledged that the hypoxia and toxic concentrations of reduced ions associated with low redox potentials (Pezeshki & DeLaune, 2012) are a major determinant of plant performance in wetlands. In saltmarshes, low sediment Eh is the inevitable result of the waterlogging associated with low elevation and impeded drainage (Armstrong et al., 1985; Crooks et al., 2000; Davy et al., 2011; Mossman et al., 2020). This is manifest in our results as the relationship between Eh and elevation over 28 years of the successional sequence. *Spartina maritima*, the primary colonist, is notably tolerant of low Eh, with its survival and photosynthetic performance unaffected by transplantation to low marsh settings (Castillo et al., 2000). Like its close relatives (Maricle & Lee, 2002), it has well developed aerenchyma that oxygenates its rhizomes and roots. In comparison, *Sarcocornia perennis* is intolerant of such highly reducing sites (Davy et al., 2006). The distribution, abundance and performance of *A. portulacoides* have all been shown to be limited by waterlogging or anoxia (Beefink et al., 1978; Armstrong et al., 1985; Mohamed, 1998; Crooks et al., 2002; Cot et al., 2013). Its roots show secondary thickening and do not develop the aerenchyma typical of more tolerant species (Mohamed, 1998). The relative superficiality of the root system seen in our study is another likely strategy for the avoidance of hypoxia. Its intolerance was confirmed by its inability to survive after transplantation to sites on tussocks that had marginally lower Eh than its natural distribution nearby. There is little evidence that the modest increase in mean salinity seen with elevation so far has contributed to changes in species replacement, as all of them are hydrohalophytes

characteristic of environments with near-seawater concentrations (Jensen, 1985; Nieva et al., 1999; Redondo et al., 2004; Redondo- Gómez et al., 2007).

The different tolerances of these key species to abiotic factors will also have modulated competitive interactions between them (Pennings & Callaway, 1992). Our results support the idea that early colonists in the succession require higher tolerance to abiotic constraints (low Eh), but are poorer competitors as conditions ameliorate. This is consistent also with a trade-off between abiotic tolerance and competitive ability in defining elevational limits in saltmarsh zonation, irrespective of succession (Pielou & Routledge, 1976). It was evident previously that *Sarcocornia*, with its dense sprawling canopy was a superior competitor to *Spartina* (Castellanos, Figueroa, & Davy, 1994). The fact that residual *Spartina* can occupy elevations so much higher than those of its initial colonization bears this out. Similarly, the hybrid *Sarcocornia* has a taller canopy and denser belowground biomass and thus outcompetes its parent (Figueroa et al., 2003). However, it is now *A. portulacoides* that is proving to be the competitive dominant. In northern Europe, competition from *A. portulacoides* can prevent the high-marsh species *Elymus athericus* from extending its range lower (Bockelmann & Neuhaus, 1999). Our transplant experiments showed unequivocally that *A. portulacoides* was not able to colonise the centres of tussocks already partially occupied by *Sarcocornia perennis* and it was only able to colonise at the edges, on slightly elevated levees, after tussocks had been mostly colonised by the *Sarcocornia*. Although the establishment of *A. portulacoides* at tussock edges was little later than that of the hybrid *Sarcocornia* at their centres and it was slower to get established, *Atriplex* then spread centripetally into the tussocks, where it was able to displace the *Sarcocornia* hybrid at similar elevations. At the edges its dominance was associated with incipient creek banks, as tussocks coalesced. Raised creek banks are among the best-drained and most oxidised environments on saltmarshes (Armstrong et al. 1985) and the dominance of *A. portulacoides* on them is similar to its behaviour on many European marshes. Rapid colonization and domination by *A. portulacoides* of small plots that had been artificially raised by 15 cm from the surrounding area on restored saltmarshes in the UK was also associated with locally raised Eh (Mossman, Grant & Davy, 2020).

The dominance of *A. portulacoides* coincided with a topographic transition from a patchwork of independently evolving islands into a marsh platform dissected by sinuous creeks. Such platforms are typical of mid and high marshes but their origins have rarely, if ever, been analysed. The elevation in the tidal frame at which coalescence occurred also lends support to the distinction between submergence and emergence marshes postulated by Chapman (1960), Ranwell (1972) and Long and Mason (1982). After some 23 years of sediment accumulation, accretion slowed and the elevation at the centres of tussocks stabilised at around mean high water level. This same level also represents an apparent upper limit for *Spartina maritima* and *Sarcocornia perennis*, whereas it is around the median for the elevational distribution of the hybrid *Sarcocornia* and *A. portulacoides*. The apparently sigmoidal relationship between Eh and elevation suggests a punctuation rather lower, as the surface approaches MWWN level, ahead of vegetational change. Thus, there is both topographic and floristic evidence for a transition from low (or submergence) marsh to mid (or emergence) marsh. A theoretical basis for this may lie in the essentially sigmoidal nature of tidal inundation curves, with the number of inundations per year changing fastest at mid

elevations (Mossman, Davy, & Grant, 2012).

Although the appearance of the *Sarcocornia* hybrid may be idiosyncratic to this Mediterranean system, the other species are widely distributed in European saltmarshes. Consequently our findings are likely to be widely applicable and have predictive power for saltmarsh restoration. After 35 years, we have seen a transition to a typical mid-marsh platform, dominated by *A. portulacoides*, with a well-developed creek system. However, there is vertical space in the tidal frame to accommodate further accretion. As surface elevation approaches the level of mean high water spring tides, salinity could become a more important factor in this Mediterranean climate, especially under future climate change scenarios. Then, we predict that high marsh species tolerant of hypersalinity, such as *Sarcocornia fruticosa* (L.) A.J. Scott (Redondo-Gómez et al., 2006) and *Arthrocnemum macrostachyum* (Moric.) C. Koch (Redondo-Gómez et al., 2010) might be able to invade.

Many non-exclusive mechanisms have been debated for ecological succession, including facilitation and inhibition (Slatyer & Connell, 1977; Pulsford, Lindenmayer, & Driscoll, 2016). However, when this study was initiated the ecological and evolutionary role of facilitation was far from accepted as a general rule (Brooker et al., 2008). Neither was the stress-gradient hypothesis - the idea that there would be a shift in species interactions from competition to facilitation with stress (He & Bertness, 2014). This long-term investigation has established the fundamental importance of facilitation in primary saltmarsh succession and the increasing significance of competition in the later successional stages with reduced abiotic stress.

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AUTHOR CONTRIBUTIONS

JMC, EMC, MEF and AJD conceived the ideas and designed methodology; JMC, BGT and EMC collected the data; JMC and AJD analyzed the data; JMC and AJD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data used in this study are available at Castillo et al Journal of Ecology Data Set. Figshare. Dataset. <https://doi.org/10.6084/m9.figshare.14442761>

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TABLE 1 Environmental characteristics of transplant sites for seedlings of *Atriplex portulacoides* on raised tussocks initiated by *Spartina maritima* and colonised centrifugally by *Sarcocornia perennis* in two well drained (Don Claudio and El Manto) and one poorly drained lagoon (Ludovico) at Odiel Marshes: surface elevation relative to Spanish Hydrographic Zero (SHZ), sediment water content, sediment electrical conductivity (EC) and sediment redox potential (Eh) in surface (0-10 cm) and deeper (11-20 cm) layers. Values are means \pm SE ($n = 5$; 10 for EC).

(a) Central areas of tussocks dominated by *Sarcocornia perennis* at Ludovico and El Manto. Significant differences between lagoons are indicated by different letters (t-test for independent samples, $P < 0.05$).

(b) Three zones of tussocks at Don Claudio (*Spartina*-dominated inner areas, *Sarcocornia*-dominated inner areas and *Sarcocornia*-dominated edges; Significant differences between transplant areas in Don Claudio are indicated by different letters (ANOVA or Kruskal-Wallis (EC), $P < 0.05$)

Transplant site	Elevation (m SHZ)	Water content (%)	EC (mS cm ⁻¹)	Eh (0-10 cm) (mV)	Eh (11-20 cm) (mV)
(a) Poorly and well drained lagoons:					
Ludovico (poorly drained)	-	-	12.7 \pm 0.5 ^a	-160 \pm 16 ^b	-283 \pm 24 ^b
El Manto (well drained)	-	-	17.9 \pm 0.6 ^b	-88 \pm 21 ^a	-133 \pm 10 ^a
(b) Different tussock zones (Don Claudio):					
<i>Spartina maritima</i> inner areas	+2.30 \pm 0.00 ^a	72.5 \pm 0.6 ^c	16.5 \pm 0.0 ^b	+74 \pm 28 ^a	-53 \pm 46 ^a
<i>Sarcocornia perennis</i> inner areas	+2.30 \pm 0.01 ^a	67.5 \pm 1.1 ^b	16.9 \pm 0.2 ^c	+173 \pm 5 ^b	+172 \pm 21 ^b
Edge with <i>Sarcocornia perennis</i>	+2.34 \pm 0.01 ^b	57.1 \pm 0.7 ^a	14.8 \pm 0.2 ^a	+192 \pm 9 ^b	+192 \pm 314 ^b

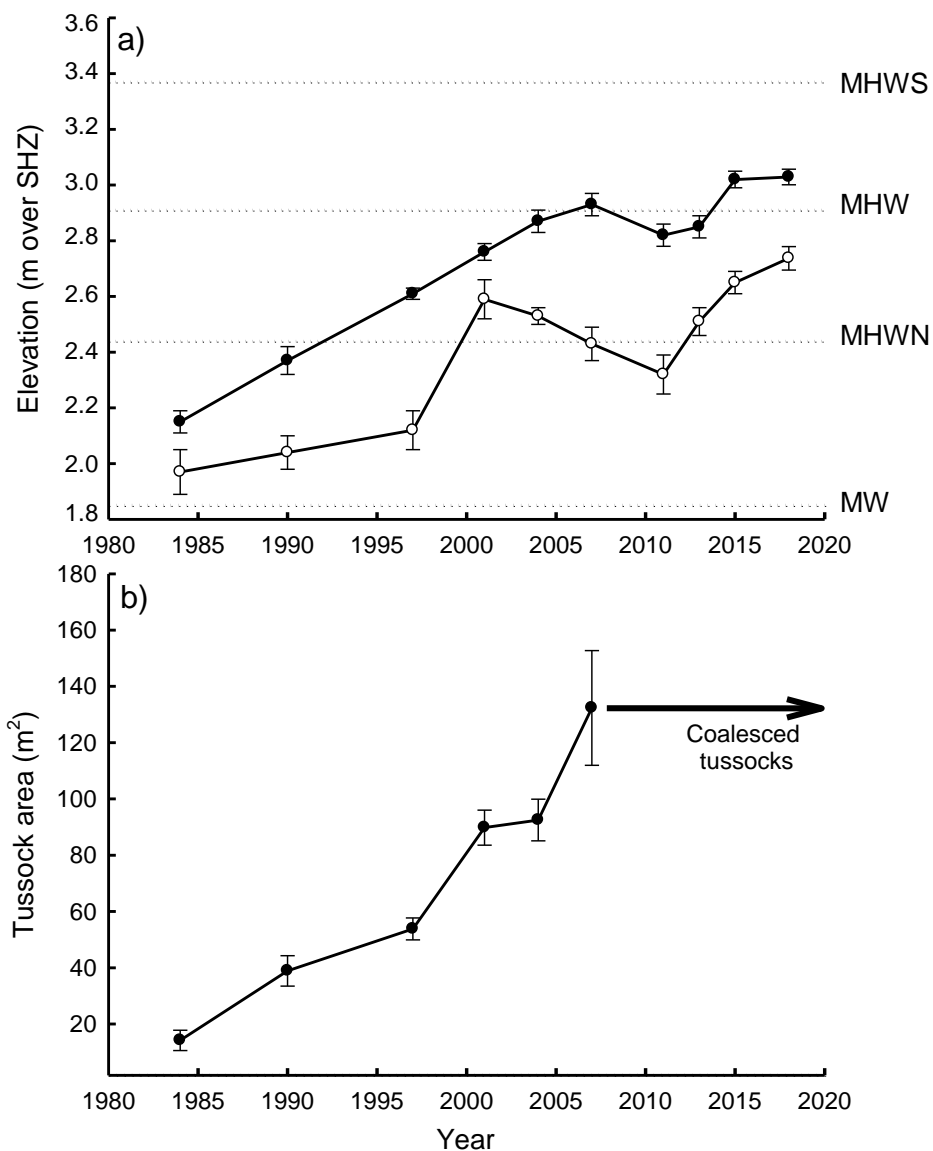


FIGURE 1 Changes in (a) surface elevation at the centre (●) and the periphery (○) and (b) corresponding tussock area of tussocks in a well-drained intertidal lagoon (Don Claudio) at Odiel Marshes (southwestern Iberian Peninsula) between 1984 and 2018. Values are means \pm SE ($n = 8-16$). Tidal levels: MW, Mean Water; MHW, Mean High Water; MHW, Mean High Water; MHWS, Mean High Water Spring; HAT, Highest Astronomical Tide.

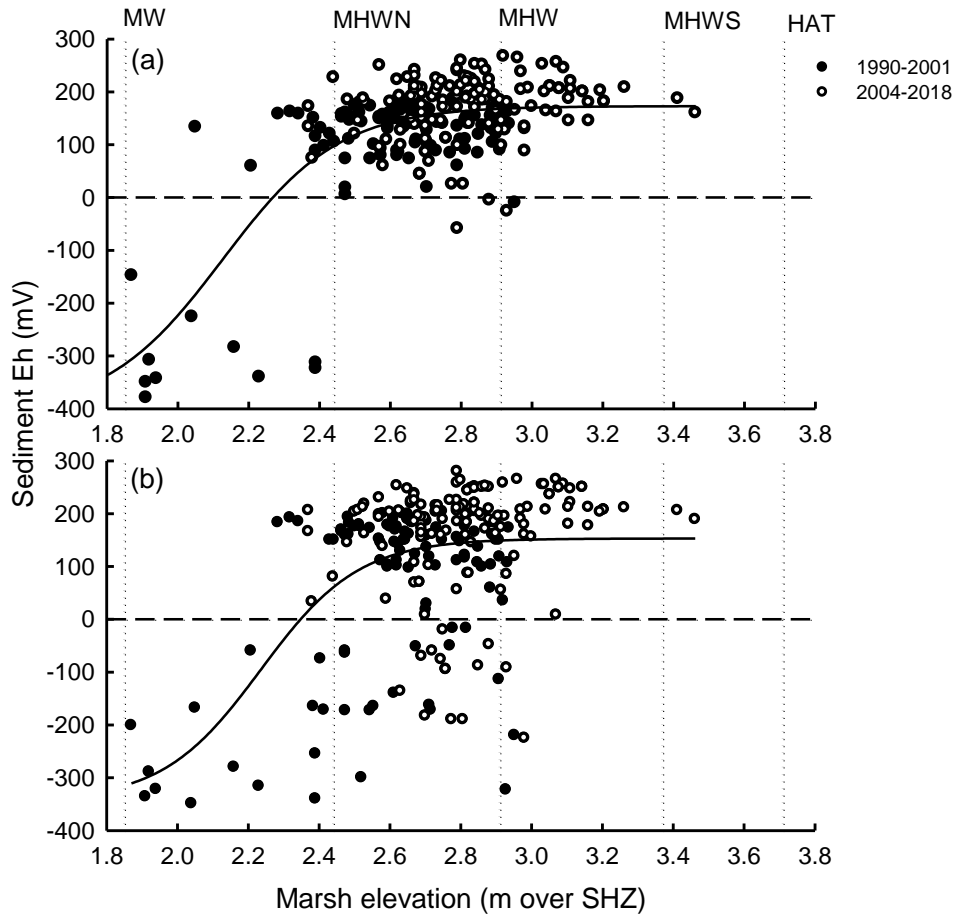


FIGURE 2 Relationship between sediment redox potential (Eh) and surface elevation relative to Spanish Hydrographic Zero (SHZ) on tussocks in a well-drained intertidal lagoon (Don Claudio) at Odiel Marshes (southwestern Iberian Peninsula) between 1990 and 2018 at two depths: (a) 0-10 cm; (b) 11-20 cm. 1990-2001 (●), 2004-2018 (○). Tidal levels: MW, Mean Water; MHWN, Mean High Water Neap; MHW, Mean High Water; MHWS, Mean High Water Spring; HAT, Highest Astronomical Tide. Regression equations: (a) $y = -407.106 + 580.128 / (\exp(-(x - 2.127) / 0.165))$ ($R = 0.738$, $P < 0.0001$); (b) $y = -343.924 + 496.906 / (\exp(-(x - 2.235) / 0.139))$ ($R = 0.526$, $P < 0.0001$).

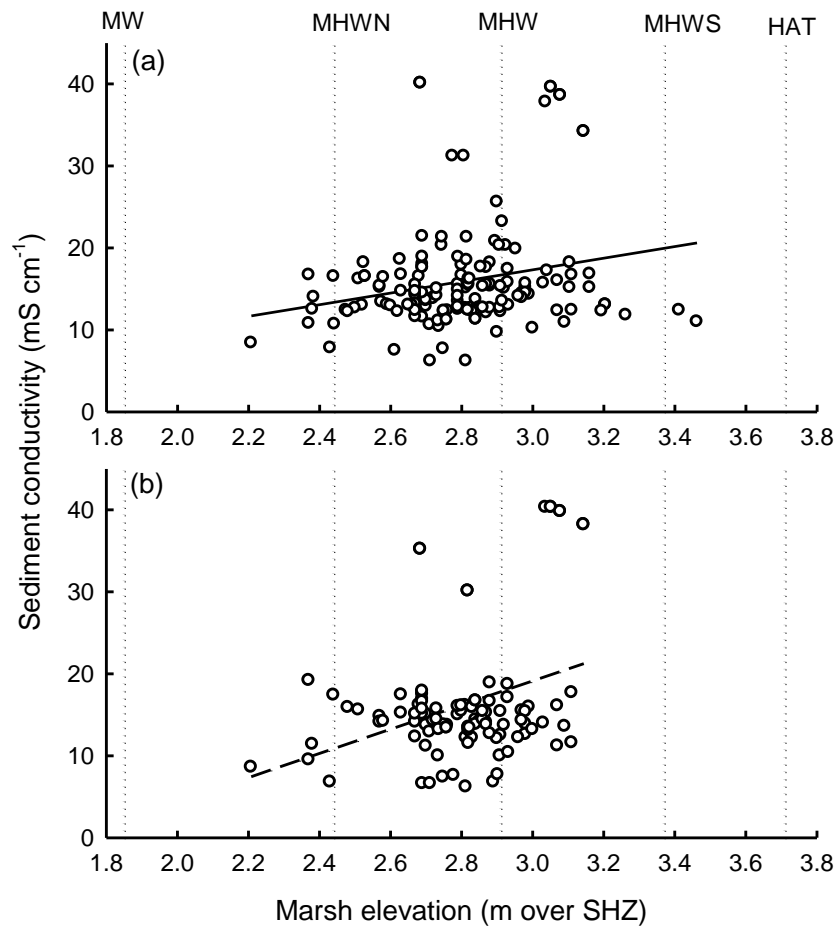


FIGURE 3 Relationship between electrical conductivity (EC) of sediment extracts and surface elevation relative to Spanish Hydrographic Zero (SHZ), on tussocks in a well-drained intertidal lagoon (Don Claudio) at Odiel Marshes (southwestern Iberian Peninsula), between 1990 and 2018 at two depths: (a) 0-10 cm, $y = -3.947 + 7.093x$, $r = 0.222$, $P < 0.01$, $n = 155$; (b) 11-20 cm, $y = -25.068 + 14.729x$, $r = 0.339$, $P < 0.0001$, $n = 104$. Tidal levels: MW, Mean Water; MHWN, Mean High Water Neap; MHW, Mean High Water; MHWS, Mean High Water Spring; HAT, Highest Astronomical Tide.

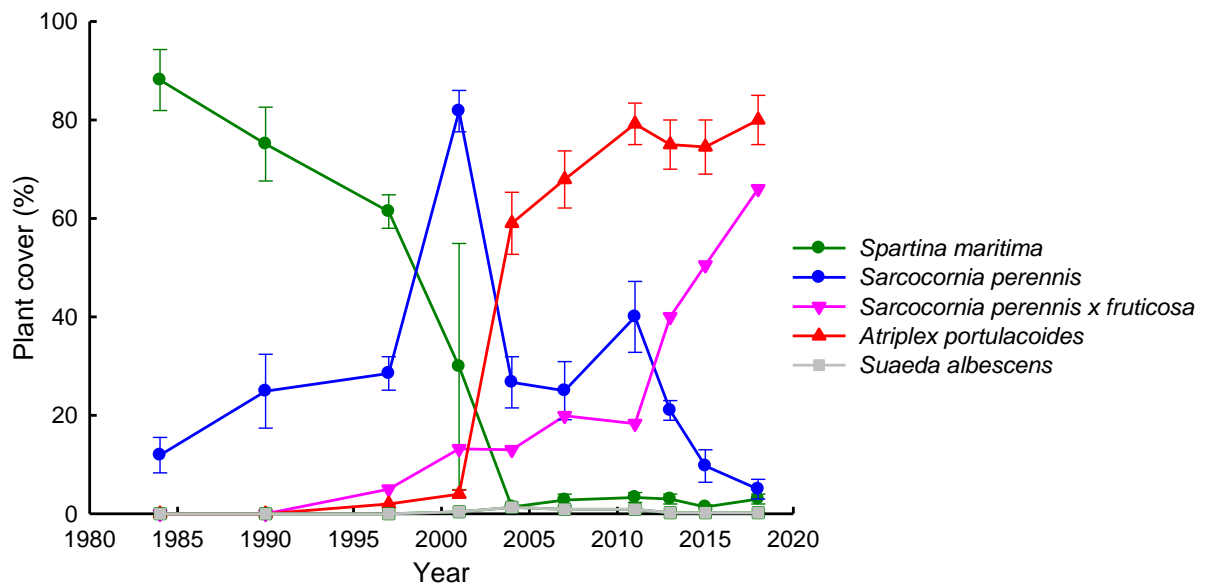


FIGURE 4 The sequence of change in the fractions of the tussock area occupied by five plant taxa colonising a well-drained intertidal lagoon (Don Claudio) at Odiel Marshes (southwestern Iberian Peninsula) between 1984 and 2018. Values are means \pm SE ($n = 8-16$).

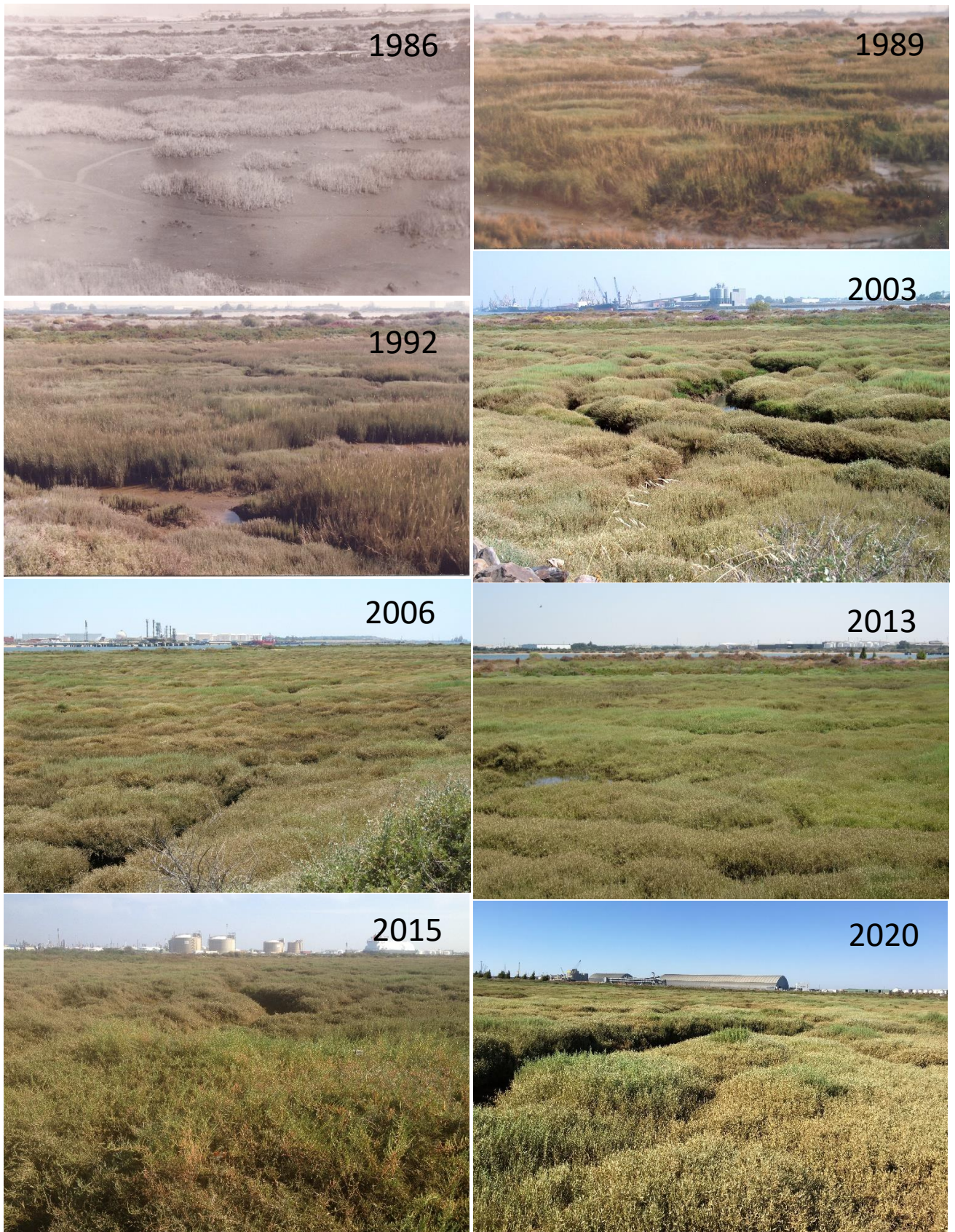


FIGURE 5 Photographs illustrating the development of the saltmarsh at Laguna de Don Claudio, Odiel Marshes, taken from various aspects between 1986 and 2020.

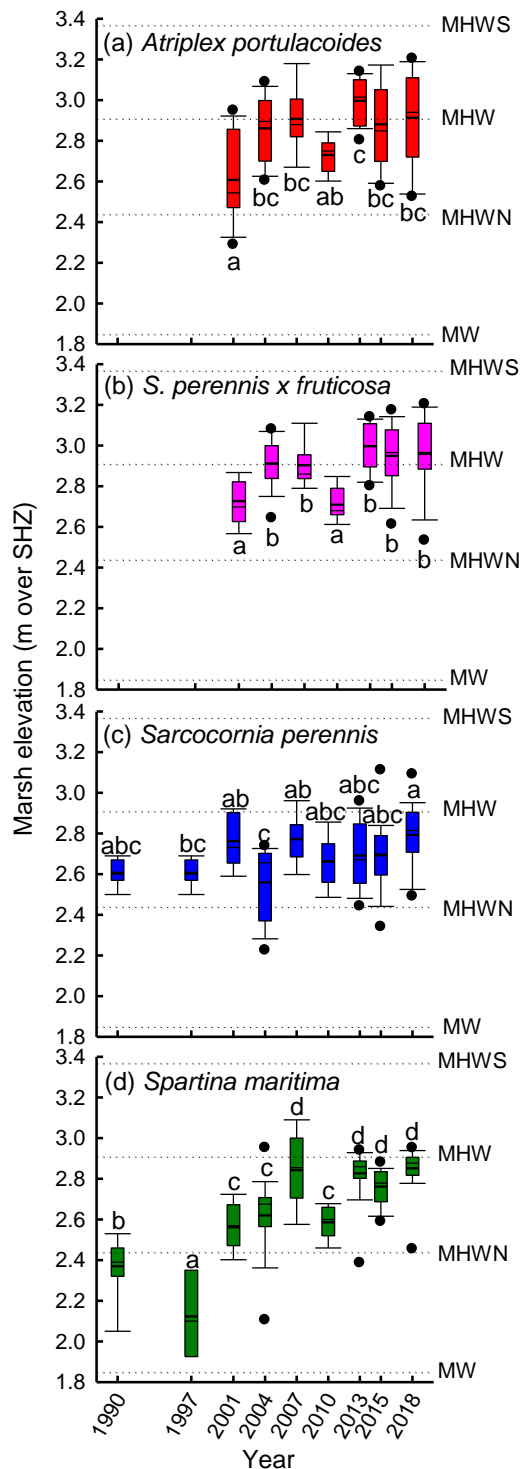


FIGURE 6 Box plots of changes in elevational range (relative to Spanish Hydrographic Zero, SHZ) of four perennial plant taxa on tussocks in a well-drained intertidal lagoon (Don Claudio) at Odiel Marshes (southwestern Iberian Peninsula), between 1990 and 2018. $n = 10-20$. Tidal levels: MW, Mean Water; MHWN, Mean High Water Neap; MHW, Mean High Water; MHWS, Mean High Water Spring; HAT, Highest Astronomical Tide. Different letters indicate significant differences between elevations for the same taxa (Bonferroni test, $P < 0.05$).

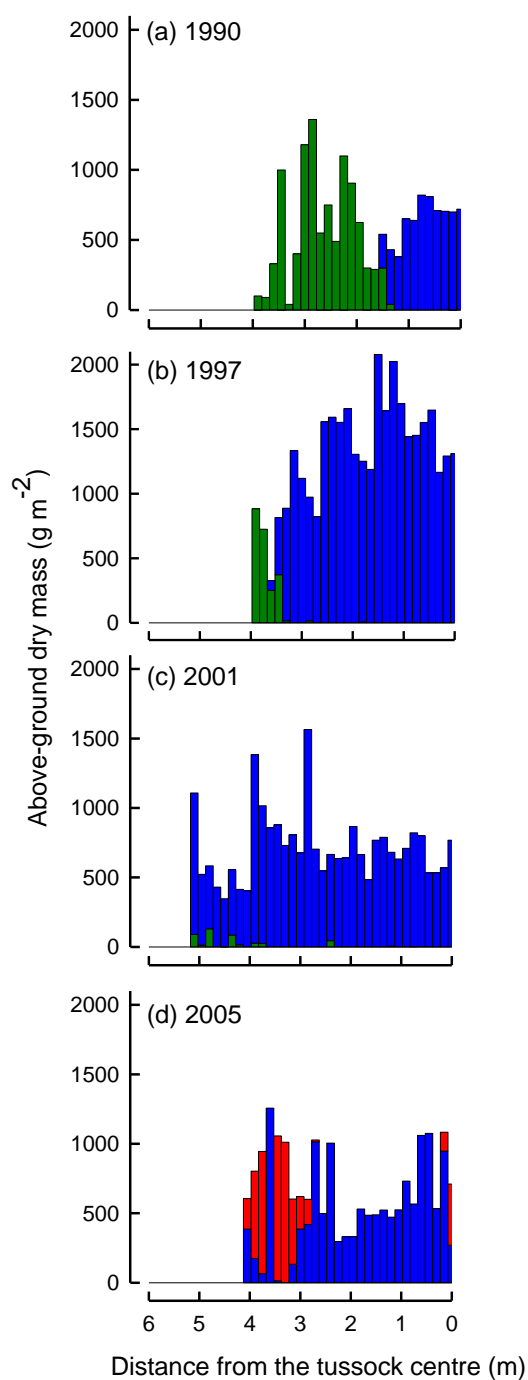


FIGURE 7 Stacked bar histogram showing the distribution of above-ground dry mass in a radial transect from one representative, permanently marked tussock in a well-drained intertidal lagoon (Don Claudio) at Odiel Marshes (Southwest Iberian Peninsula) that was colonised by *Atriplex portulacoides*. (a) 1990, (b) 1997, (c) 2001 and (d) 2005. *Spartina maritima* (green); *Sarcocornia perennis* (blue); *Atriplex portulacoides* (red).

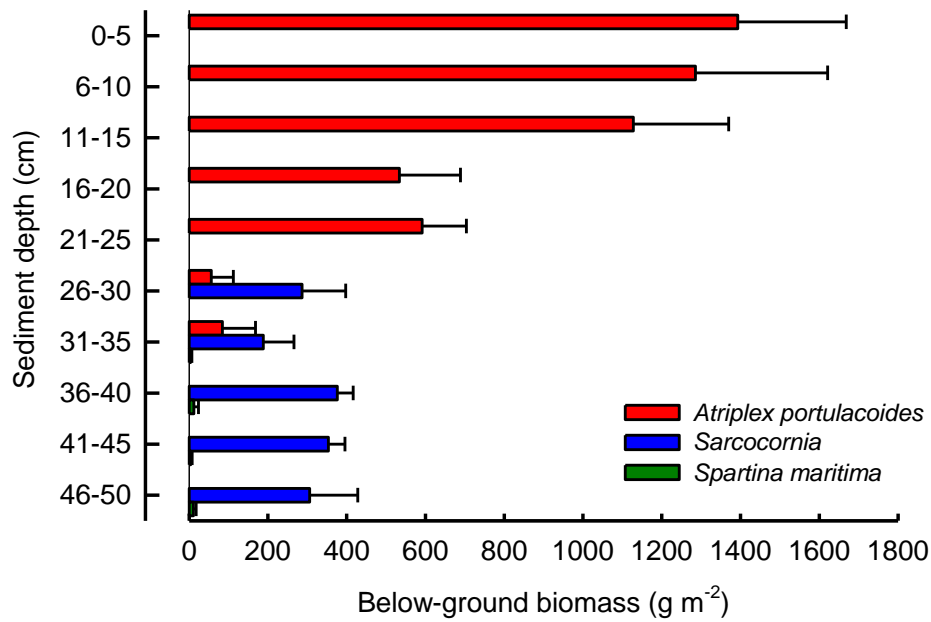


FIGURE 8 Depth profile of the below-ground dry mass of three perennial plant taxa under the canopy of *Atriplex portulacoides* on tussocks in a well-drained intertidal lagoon at Odiel Marshes (Southwest Iberian Peninsula) in April 2005. Values are means \pm SE of 5 tussocks.

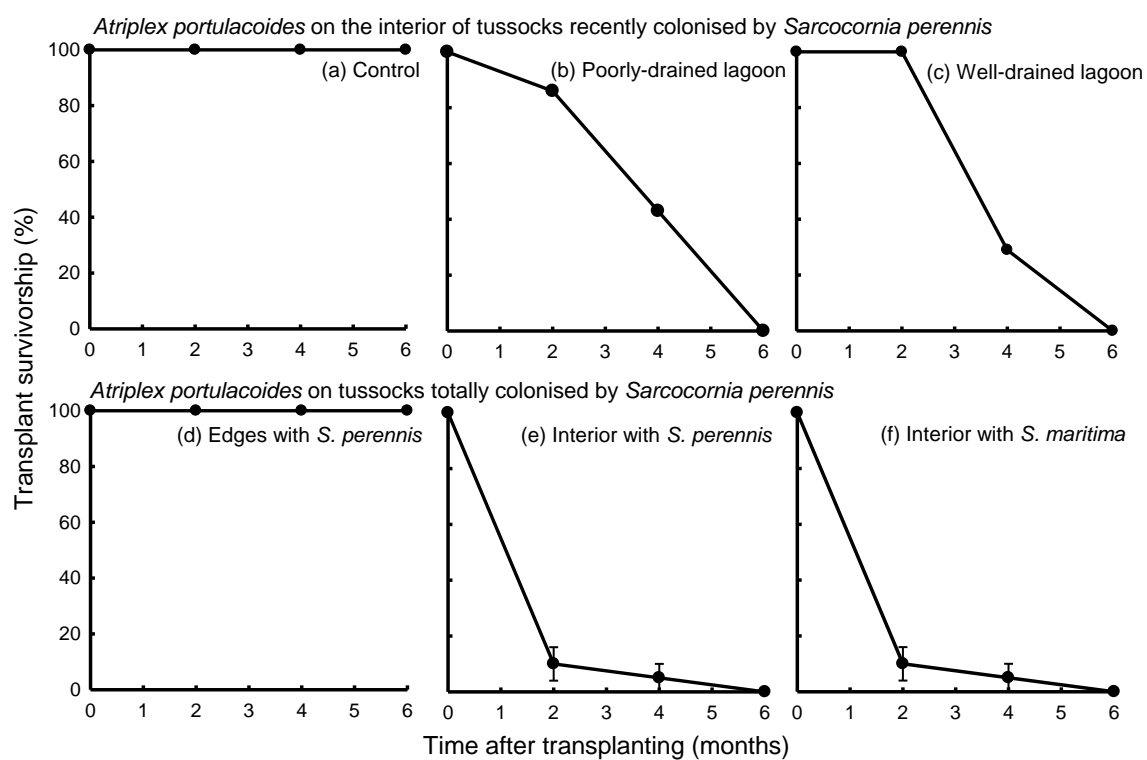


FIGURE 9 Survival of seedlings of *Atriplex portulacoides* after transplantation to different drainage regimes.

Transplants to tussocks in poorly and well drained lagoons: (a) control, (b) poorly drained (Ludovico), (c) well-drained (El Manto) ($n = 7$ tussocks, with single transplants per tussock). Transplants to different zones of tussocks in a well drained lagoon (Don Claudio): (d) tussock edges dominated by *S. perennis* (e), interior areas dominated by *S. perennis* and (f) interior areas dominated by *Spartina maritima*. Values are means \pm SE ($n = 4$ tussocks, with 5 transplants per tussock).