ORIGINAL ARTICLE

Disentangling elevation, annual flooding regime and salinity as hydrochemical determinants of halophyte distribution in non-tidal saltmarsh

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Running title: Hydrochemical determinants of halophyte distribution in non-tidal saltmarsh

- **Background and Aims** Hydrological disconnection, especially in a Mediterranean climate, creates coastal saltmarshes with an annual cycle of flooding that are unlike tidally inundated systems. Winter rainfall produces long, continuous hydroperiods, alternating with continuous exposure caused by evaporation in warm, rain-free summers. We aimed to distinguish the effects of elevation, hydroperiod and salinity on annual and perennial halophytes in such a system.
- **Methods** We recorded vegetation and sediment salinity in permanent quadrats on a marsh in the Doñana National Park, Spain, over 7 consecutive years with widely differing rainfall. Elevation was determined from LIDAR data and the duration of the annual hydroperiod from satellite imagery. The independent effects of collaterally varying elevation, hydroperiod and salinity on species distribution were examined using GLMs and hierarchical partitioning.
- **Key Results** Hydroperiod and salinity were both inversely related to elevation but interannual fluctuations in rainfall facilitated discrimination of independent effects of the three collaterally varying factors on halophyte distribution. Perennial distribution was strongly structured by elevation, whereas many annual species were more sensitive to hydroperiod. The independent effects of salinity varied according to individual species' salt tolerance from positive to negative. Thus life-history and, in the case of annuals, phenology were important in determining the relative impact of elevation and hydroperiod.
- **Conclusions** The consequences of elevation for halophyte distribution in seasonally flooded saltmarshes are fundamentally different from those in tidal marshes, because protracted and frequent flooding regimes require different adaptations, and because of the unpredictability of flooding from year-to-year. These differences could explain greater species diversity in non-tidal marshes and the absence of key saltmarsh species prominent in tidal marshes. The vegetation of non-tidal marshes will be particularly susceptible to the more extreme annual cycles of temperature and rainfall predicted for Mediterranean climates.

Key words: coastal marsh, hydroperiod, flooding regime, life-history, marsh embankment, Mediterranean climate, remote sensing, salt tolerance,

INTRODUCTION

Periodic flooding is a defining feature of coastal saltmarshes. Typically, they are tidal and experience frequent, usually semi-diurnal, inundations with seawater (Adam, 1990). Less well-known, however, are non-tidal saltmarshes (Costa *et al*., 2003), especially those with limited hydrological connectivity with the sea (Vélez-Martín *et al*., 2018), where the dominant cycle of inundation is much longer i.e. seasonal rather than semi-diurnal. When tidal influence is attenuated by physical barriers, a Mediterranean climate ensures that flooding is concomitant on autumn and winter rains but then the water levels drop with the relentless evapotranspiration of the virtually rainless summer. Furthermore, the Mediterranean climate is becoming more extreme with global climate change (Cramer *et al*., 2018).

An annual hydrological cycle is likely to create substantially different environmental conditions from a tidally-dominated one, because of the longer periods of continuous flooding and exposure. The zonation of halophytes in tidal marshes is strongly influenced by elevation in the tidal frame (e.g. Zedler *et al*., 1999; Bockelmann *et al*., 2002; Silvestri *et al*., 2005). The frequency and duration of flooding combine to limit oxygen supply to the sediments and create gradients in their redox status (Armstrong *et al.,* 1985; Castillo *et al.,* 2000; Anastasiou and Brooks, 2003). However, the consequences of elevation under a seasonal flooding regime are less well understood. Long periods of continuous flooding will be associated with long periods of sediment anoxia, over a range of elevations. Long-term submergence of plant leaves and shoots will also limit oxygen transport to their underground organs. Consequently, tolerance to the duration of reducing conditions may be more important than to the average values of redox potential experienced (Pezeshki and DeLaune, 2012). Conversely, long periods of continuous exposure may result in drought, and evapotranspiration might be expected to lead to long-term changes in salinity that also depend on elevation. Salinity and flooding are recognised as the main selection pressures on saltmarsh plants (Colmer and Flowers, 2008; Flowers and Colmer, 2008) and both of these factors would be subject to the effects of inter-annual fluctuations in rainfall.

We hypothesised that the main determinants of halophyte distribution on a non-tidal marsh would be elevation, hydroperiod and salinity, and that effects would be different on annual and perennial species. Elevation is spatially variable but invariant with time, whereas hydroperiod and salinity will vary from year to year with the weather. These factors will inevitably show collateral variation that obscures understanding of their relative importance. However, the inter-annual variation in hydroperiod and salinity at any particular elevation provides a means of distinguishing the independent effects of these variables on halophyte species by using the technique of hierarchical partitioning (Chevan and Sutherland, 1991). This approach has proved successful in disentangling the effects on plant distribution of similar complexes of environmental variables (e.g. Davy *et al.*, 2011; Lambert and Davy, 2011).

The saltmarshes of Doñana National Park (south-west Spain) are largely isolated from tidal influence by embankments and dune ridges (Vélez-Martín *et al.*, 2018). Because they occupy shallow clay basins, rainfall in their catchment area causes flooding and surface run-off, whereas evapotranspiration in summer can leave the soil surfaces dry and cracked, with efflorescing salts. Their vegetation consists of a matrix of relatively a few perennial halophytic species, interspersed with numerous annuals, distributed across a varying topography with hummocks and depressions. Bare ground is frequent and the vegetation is sparse, suggesting that species interactions would be less important than abiotic factors in determining species distribution (cf. Pennings and Callaway, 1992).

Our overall aim was to seek explanations for the distributions of halophytes in this annually flooded Mediterranean saltmarsh. The specific objectives were: (1) to characterize the spatial variation in elevation; (2) to examine annual variations in hydroperiod and salinity at different elevations; (3) to investigate the abundance of halophytes in permanent quadrats over the range of elevations; (4) to distinguish the independent effects of elevation, hydroperiod and salinity in determining the distribution of both annual and perennial species.

MATERIALS AND METHODS

Study site

The Doñana National Park supports c. 25,000 ha of saltmarshes in the estuary of the River Guadalquivir. Although these marshes functioned formerly as the floodplain of the river, agricultural land-claim in the mid-20th century necessitated the construction of embankments, which largely eliminated tidal influence and modified the capacity of the system for storing flood water. Since then, rainfall has been the principal source of water and the primary driver of the flooding cycle throughout most of the Doñana marshes (Díaz-Delgado *et al*., 2006). The Mediterranean climate is strongly seasonal. The hot summers are reliably dry, with virtually no rainfall, but rain at other times can be very variable from year to year. Average annual rainfall is 549 mm, with an average daily temperature of 4.6 °C in January and 32.6 °C in July. The adjacent open coast has semidiurnal tides with a mean spring tidal range of 2.97 m, representing 0.40 - 3.37 m above Spanish Hydrographic Zero (SHZ). Mean sea level is +1.85 m relative to SHZ.

The vegetation consists of a mosaic of halophytic shrubs of the Amaranthaceae (‘chenopods’), more numerous annual species of halophyte, and emergent or submerged aquatic macrophytes in more flooded areas (Rivas-Martínez *et al*., 1980; Marañón *et al*., 1989; García *et al*., 1993; Espinar, 2009). The site is described in more detail by Vélez-Martín *et al*. (2018).

Vegetation sampling

We sampled an area of 3,580 ha near the north-eastern boundary of the Doñana National Park comprising five compartments centred on 37°02´N, 6°18´W. We established 170 permanent sampling locations on a rectilinear grid designed to provide even coverage across the five compartments of the site; locations were arranged in linear groups of three, to be consistent with an adjoining area designated for restoration, but wide spacing between locations (62.5 m within triplets and 1 km between them) would have minimised the possibility of spatial autocorrelation (see Vélez-Martín *et al*., 2018 for further details). We sampled the vegetation in the period June-July from 2004 to 2010, during the dry season, when both plant cover and site accessibility were greatest. For logistic reasons, only four of the compartments were sampled in 2004 and 2005, and in the first year (2004) only the central location of each group of three could be sampled. From 2005 onwards, all locations were sampled and in 2006 it was possible to introduce the fifth compartment into the sampling programme (an additional 9 locations). In consequence, the total number of locations sampled was 54, 161, 170, 170, 170, 170 and 170, for the years 2004, 2005, 2006, 2007, 2008, 2009 and 2010, respectively, giving a total number of vegetation samples for the study of 1,065. At each location, we placed two replicate 2 x 2-m quadrats 10 m apart and recorded the abundance of all plant species and bare ground, using a six-point Braun-Blanquet cover-abundance scale (0-1, 1-5, 5-25, 25-50, 50-75 and 75-100%). Mean scores for the two quadrats were used in statistical analyses.

Environmental measurements

Soil samples were collected from two depths (surface, 0-2 cm) and (sub-surface, 8-10 cm) during the dry season (June-July). For logistic reasons, samples were taken only from the central location of each group of three that were used for vegetational analysis (hence at 1 km spacing). For the reasons described above, there was some variation in number from year to year: 8, 18, 18, 19, 19 and 19 for the years 2004, 2006, 2007, 2008, 2009 and 2010, respectively, giving a total of 101 for each depth for the study. No samples could be taken in 2005. Each sample comprised three bulked replicate subsamples of c. 100 ml taken immediately adjacent to the vegetation quadrats and c. 1 m apart. Soil was air-dried under laboratory conditions, crushed and sieved to <2 mm. Electrical conductivity (EC) was measured in 1:1 (by volume) soil-water mixtures after equilibration over-night, using a Crison Basic 30 conductivity meter (Crison Instruments S.A., Spain).

Surface elevation for each plant sampling location was obtained from LIDAR data (precision >0.5 m horizontally and >0.15 m vertically). The flight was commissioned for the whole Doñana marsh by the Confederación Hidrográfica del Guadalquivir in September 2002, when there was no standing water and errors due to vegetation were minimized by the large fraction of bare ground (37%). A raster file with a pixel size of 2 x 2 m, provided by the Estación Biológica de Doñana, was processed using Arcgis 10.0 (ESRI®ArcMap™ 10.0). LIDAR data were ground-truthed at numerous permanent sampling points using a high-resolution (±2 cm) differential GPS (Leica 1200).

Remote sensing was used to determine the duration and extent of surface flooding. We examined successive false-colour images (250-m pixel size) from MODIS (Moderate Resolution Imaging Spectroradiometer) aboard Aqua (EOS PM) satellites. These were compared with LANDSAT imagery from a narrower span of dates but with a higher precision (30-m pixel size) from the Landsat images online server (LAST-EBD, CSIC; Díaz-Delgado *et al.*, 2016). False colour compositions of both datasets indicated flooded areas. For each plant sampling location, the annual period of inundation (hydroperiod) was estimated, assuming that inundation was continuous between consecutive images (Díaz-Delgado *et al.*, 2010). Inundated areas were eventually ground-truthed by field observation.

Data analysis

Correlation between environmental variables was assessed using Spearman's rank correlation. Differences between surface and subsurface electrical conductivities were tested with Friedman test. Univariate analysis and correlation analyses were performed using SPSS 21.0 (IBM Corporation, 2012).

Statistical modelling was carried out using R 3.5.2 (R Core Team, 2018). Potential temporal autocorrelation of species abundance between sampling years was examined using the *gls* function of the R package *nlme*. Autocorrelation was not detected. Generalized linear models were used to examine the relationship between environmental variables (elevation, hydroperiod and EC at the two depths) on the cover of each plant species and bare ground. Models with Gaussian errors were fitted using appropriate transformations to give approximately symmetric distributions. Percentage cover of bare ground was square-root transformed, percentage cover of species was log(x+1)-transformed and the independent variables were transformed to log or square root. The significance of the whole model was tested by comparing with an intercept-only null model. Then the independent additive effects of elevation, hydroperiod and EC (at the two depths) on the cover of each plant species and bare ground were quantified using hierarchical partitioning, implemented with the R package *hier.part* (Walsh and MacNally 2007). Significant effects were identified on the basis of an upper 0.95 confidence limit by their Z-score (1.65) generated by the *rand.hp* function. To visualise the interacting effects of elevation and soil salinity on plant occurrence and percentage cover (arcsine transformed), we constructed generalised additive models using the R package *mgcv* (Wood, 2006), setting the maximum complexity of smoothed terms to three effective degrees of freedom.

RESULTS

Environmental variables

The overall range of elevation of the sampling points was 1.17 m (1.08 - 2.25 m above SHZ), with most of the sites at elevations of between 1.2 and 2.2 m (FIG. 1a). There were large variations in hydroperiod from year to year at these sampling points (FIG. 1b), depending largely on changing rainfall. The mean hydroperiod at the lowest elevations extended to 250 days year^{-1} of continuous inundation (FIG. 2a). Hydroperiod decreased linearly with increasing elevation to *c*. 50 days year^{-1} at an elevation of 1.7 m, but showed little further decrease above this elevation. The inter-annual variation in hydroperiod at any elevation introduced much more noise into this relationship (FIG. 2b) but there is still a highly significant negative correlation between hydroperiod and elevation ($r_s = -0.573$, $n = 1197$, $P < 0.01$).

Similarly, there was a significant inverse relationship between elevation and mean annual sediment salinity, expressed as electrical conductivity (EC), at both sampling depths (FIG. 2c, e). In surface samples there was a rapid decline in conductivity up to an elevation of c. 1.5 m but little further change above that, whereas in the deeper samples, there was a continuous decline. Again, including the inter-annual variation in conductivity introduced more noise into both of these relationships (FIG. 2d, f) but there were still highly significant negative correlations between salinity and elevation (surface, $r_s = -0.671$, $n = 101$, $P < 0.001$; sub-surface, $r_s = -0.464$, $n = 101$, $P < 0.001$). Surface and sub-surface conductivities were also themselves strongly correlated ($r_s = 0.704$, $n = 101$, $P < 0.01$). Mean surface values (10.18 mS/cm) were slightly higher than the deeper (9.35 mS/cm) ones (Friedman test: $\chi^2 = 9.51$, $P < 0.01$) but surface conductivities showed a greater range with elevation.

Plant species abundance

The individual effects of local elevation, annual hydroperiod and EC at both depths on the cover of the perennial species and bare ground, over whole sampling period, are shown in FIG. 3. The five species clearly occupied successively lower ranges of elevation: *Suaeda vera* was distributed overwhelmingly at the highest elevations; *Arthrocnemum macrostachyum* had a broad range, avoiding high and low extremes of elevation; *Juncus subulatus* and *Bolboschoenus maritimus* had distributions successively biased to lower elevations, and *Schoenoplectus litoralis* occupied only the lowest elevations. The area of bare ground was greatest at low elevation and decreased continuously to very low values at the highest elevations. The responses of these species to hydroperiod were broadly the inverse of those to elevation, although they were rather less distinct. *S. vera* was only found under the shorter hydroperiods (<150 days). *A. macrostachyum*, *J. subulatus*, *B. maritimus* and *S. litoralis* all had broad ranges that were, however, successively biased towards longer hydroperiods. The distribution of bare ground was very clearly the inverse of that of elevation. The perennial species also showed distinct responses in cover to EC. *A. macrostachyum* and *J. subulatus* were found over a broad range of EC, including the most saline areas. *S. vera* was only marginally less broad in its tolerance. The two helophytes, *B. maritimus* and *S. litoralis* were opposite in their distributions, the former at predominantly lower EC values and the latter only at the highest ones. The area of bare ground increased with EC, closely following the trend of hydroperiod. The distributional responses of plant species to EC at the two sampling depths were broadly similar, but were more marked in the case of the generally more extreme surface conductivities (FIG. 3).

It was clear that elevation and EC can be combined to show clear niche separation between these dominant perennial species, whether in terms of their cover or their probability of occurrence, and this was substantiated by the General Additive Models (FIG. 4). Both occurrence and cover of *S. vera* were strongly associated with a combination of high elevation and low subsurface salinity, whereas *S. litoralis* favoured the opposite combination of low elevation and high salinity. *B. maritimus*, on the other hand, was restricted to areas of both low elevation and low salinity; *A. macrostachyum* was associated with high elevation and *J. subulatus* with low elevation but their distributions were weakly differentiated by EC.

Distributional responses to the four environmental variables for the nine most abundant annual species are presented in FIG. 5. Again, species tended to occupy distinct ranges of the environmental gradients. *Lolium rigidum* and *Plantago lanceolata* favoured high elevation, shorter hydroperiod and low EC. *Medicago polymorpha*, *Leontodon longirostris*, *Plantago coronopus*, *Beta macrocarpa* and *Spergularia nicaeensis* tended to occupy a broad mid-range of elevation but nevertheless had distributions strongly biased to shorter hydroperiods; they were all also tolerant of a broad range of EC. *Damasonium alisma*, on the other hand, favoured low elevation with mid-range hydroperiods and a broad range of EC. Although it had low overall mean cover, *Salicornia ramosissima* had a very striking distribution, being found only at the lowest elevations and highest EC, but with a remarkably broad tolerance of hydroperiod.

Hierarchical partitioning of environmental effects

Hierarchical partitioning provided estimates of the independent contribution of each environmental variable to the cover of bare ground and 24 of the commonest individual species (Table 1). All the generalized linear models on which it is based were significant ($P < 0.05$). Among perennials, the total variance explained by the four variables ranged from 52% for *Arthrocnemum macrostachyum* to 7% for *Juncus subulatus*. There were similar differences among the annuals e.g. *Leontodon longirostris* and *Hordeum marinum* at >30% variance explained and *Bromus lanceolatus* or *Chamaemelum mixtum* at 6% . Elevation, rather than hydroperiod was overwhelmingly more important in explaining the abundance of the perennial species, although *A. macrostachyum* combined a large positive influence of elevation with a smaller negative one of hydroperiod. All but *J. subulatus* were also significantly influenced by EC, *S. litoralis* positively and *B. maritimus* negatively; *A. macrostachyum* was unusual in showing a significant adverse effect by surface EC and a positive one of sub-surface EC.

In contrast, hydroperiod rather than elevation was the strongest overall determinant of the cover of annual species, especially *Beta macrocarpa*, *Chamaemelum mixtum*, *Damasonium alisma*, *Leontodon longirostris*, *Lythrum tribracteatum*, *Medicago polymorpha*, *Parapholis pycnantha*, *Plantago coronopus* and *Spergularia nicaeensis*. Most were negatively influenced by hydroperiod but the aquatics *D. alisma* and *L. tribracteatum* showed the opposite trend. Certain species (*Bromus lanceolatus*, *Hordeum marinum*, *Juncus bufonius*, *Lolium rigidum* and *Plantago lanceolata*), however, were mainly influenced by elevation, although it was a significant subsidiary influence on many other species. Surface EC was also a significant determinant of the cover of many annuals, mostly having a strong negative effect. Nevertheless, the only significant effect found for *Salicornia* was the positive one of surface EC, which accounted for 68% of the variation in that model. Sub-surface EC was much less important for the annuals, although *Coronopus squamatus, Rumex dentatus* and *Spergularia nicaeensis* were significantly positively associated with it and *Bromus lanceolatus*, *Phalaris minor* and *Plantago lanceolata* negatively associated. The poorer association between EC and cover by annuals than with cover by perennials may be due in part to the sampling time, when annual populations would have been in decline.

All four environmental variables were significant determinants of the cover of bare ground. Elevation was the greatest negative influence, whereas EC (at both depths) was the greatest positive one. Hydroperiod, nevertheless, had a significant positive effect on the distribution of bare ground, independent of the effect of elevation.

DISCUSSION

Our results show that the hydrochemical environment of the Doñana non-tidal saltmarshes varies in a complex way, both in time and space, with collateral variation between soil salinity and flooding. There has been little previous work on such European systems (García *et al*., 1993; González-Alcaraz *et al*., 2014) but spatial and temporal variations of salinity and waterlogging determine plant distribution and limit crop production over large areas of the Australian drylands (see Bennett *et al*., 2009). We consistently recorded greater soil salinity at lower elevations, particularly in summers following longer hydroperiods. This trend is in general agreement with the situation in Australian saltlands, where salinity increased as the water table became shallower (Barrett-Lennard *et al*., 2013). At Doñana it suggests that the salt capital locked-up in this system is largely a legacy of historically greater tidal connectivity and that salt is recycled locally between high and low ground, through alternating leaching and evaporation (Cook *et al*., 2009). In tidal marshes, however, the highest salinities tend to be at higher elevations in summer, when evapotranspiration exceeds precipitation during successive spring tidal cycles (e.g. Jefferies *et al*., 1979). The usual relationship between annual hydroperiod and elevation (Davy *et al*., 2011) was confounded at Doñana by the large inter-annual differences in winter rainfall.

It was clear that species distributions in the Doñana non-tidal saltmarshes were substantially structured by the interaction of flooding and salinity. This is also the case in Australian drylands, where the distribution of species can be largely accounted for with a matrix of their tolerances to these two factors (Bennett *et al*., 2009; Barrett-Lennard *et al*., 2013). In fact, where more than one species is present, a range of naturalized and native species can be employed as indicators of the agricultural potential of theses salt-affected lands (Bennett and Barrett-Lennard, 2013). As in the zonation of tidal marshes, the distribution of individual species in our study was primarily structured by elevation. There was a clear, general elevational sequence of perennial species from permanent pools to hummocks: *Schoenoplectus litoralis* < *Bolboshoenus maritimus* < *Juncus subulatus* < *Arthrocnemum macrostachyum* < *Suaeda vera* – corresponding to an inverse sequence with annual hydroperiod length. In an experimental study, Barrett-Lennard *et al.* (2013) were able to relate the survival and growth of Australian perennial species to depth to the water table and soil salinity, with the most important factor being the presence of shallow groundwater in summer. A similar elevational zonation of our most abundant annuals was nearly as distinct: *Salicornia ramosissima* < *Damasonium alisma* < *Spergularia nicaeensis* < *Beta macrocarpa* < *Plantago coronopus* < *Leontodon longirostris* < *Medicago polymorpha* < *Plantago lanceolata* < *Lolium rigidum*. These elevational sequences were generally consonant with elevational or flooding tolerances reported from other brackish or saline marshes (e.g. Rogel *et al*., 2000; Curcó *et al*., 2002; Silvestri *et al*., 2005; Watt *et al*., 2007). Bare ground is a feature of the relatively sparse vegetation of these saltmarshes and it is not surprising that lower elevation, longer hydroperiods and higher salinities, all potentially adverse for plants, favoured bare ground.

One of our key objectives was to discriminate independent effects of collaterally varying factors on plant distribution by the use of hierarchical partitioning (Davy *et al*., 2011; Mossman *et al*., 2020). The inter-annual variation across the extended time-span of this study was crucial in uncovering these independent effects. Because there was no temporal autocorrelation in our time series, the different extents of rainfall-driven flooding over seven years provided envelopes of variation for flooding and salinity at any particular elevation. A striking finding was that many species were influenced independently by elevation and hydroperiod, albeit to different extents. This would be unlikely in a tidal system (Davy *et al.* 2011; Mossman *et al*., 2020) because increasing daily exposure and drainage allows greater diffusion of oxygen into the pore spaces. In contrast, with seasonal hydroperiods plants at all elevations would be exposed to anoxic conditions within a few days of inundation and so responses of species would depend more on how long they could tolerate anoxia rather than the mean intensity of hypoxia experienced at a particular elevation. Annuals were more likely to be sensitive to the independent effect of hydroperiod, because preceding winter rainfall would have modulated the underlying effects of elevation on their ability to become established and complete their life cycle. In contrast, perennials would have persisted through repeated cycles in water level, the average effect of which would be less distinguishable from that of elevation.

In perennials, negative independent responses to elevation can be regarded as indicators of adaptation to flooding. Perennial emergent helophytes (such as *Bolboschoenus maritimus* and *Schoenoplectus litoralis*) would have been able to aerate underground organs from the atmosphere via internal airspaces (aerenchyma), and *B. maritimus* is able to survive and maintain growth under strict experimental anaerobiosis (Barclay and Crawford, 1982) or when completely submerged (Clevering *et al.*, 1995). The positive responses to elevation of *A. macrostachyum* and *S. vera* corresponds with them inhabiting the drier areas of a entire Mediterranean semiarid saline watershed (González-Alcaraz *et al.*, 2014). Most annuals were probably influenced negatively by hydroperiod because they were more likely to be submerged at a critical stage in their life history. Seeds of *Damasonium alisma* will only germinate if submerged (Birkinshaw, 1994), which may explain its strong positive response to hydroperiod. Exceptionally, *Lolium rigidum* and *Juncus bufonius* responded substantially to elevation rather than hydroperiod. As both were restricted to the upper parts of the elevational range it is possible that annual establishment occurred after flooding had receded every year and thus appeared to be little affected by it. Above an elevation of 1.60 m hydroperiod changed relatively little.

The significant independent effects of soil salinity were generally smaller than those of elevation or hydroperiod. All of these species are salt-tolerant to a degree but most were more or less negatively associated with sediment salinity; a striking exception was the strict annual halophyte *Salicornia ramosissima* (Davy *et al*., 2001), whose only significant influence was a positive one of salinity. Although *Arthrocnemum macrostachyum* is undoubtedly an extreme halophyte (Redondo-Gómez *et al*., 2010) and it was positively associated with subsurface salinity, elevation was the stronger independent influence on its distribution. Notwithstanding the strong correlation between salinities at the two soil depths, hierarchical partitioning discerned important differences between their effects. Annuals exhibited greater independent responses to the surface salinity (0-2 cm), whereas perennials responded more to the deeper salinity (8-10 cm). According to Clemente *et al*. (1998) the root systems of these annuals are most abundant in the top 5 cm, whereas the rooting depths of the perennials are all much greater. In addition, we measured much higher salinities in the surface layer than deeper, which agrees with the description by Clemente *et al*. (1998) of a silty surface crust, containing precipitated salts.

The investigation of saltmarshes with annual rather than daily cycles of flooding provides a novel perspective on the factors determining the distribution of coastal halophytes. It confirms the over-riding importance of elevation but reveals considerable differences in the mechanisms responsible for its effects. The Doñana marshes support a much wider range of species than their tidal counterparts (cf. Castellanos *et al*., 1994; Castillo *et al*., 2000; Figueroa *et al*., 2003). Many of these are annuals able to exploit the temporal heterogeneity of the elevated, brackish areas. The predictable flooding regime of tidal upper marshes does not afford such opportunities. Also, the salinities we report are generally lower than those of seawater, with little evidence of hypersalinity. However, some important coastal halophytes (e.g. *Salicornia ramosissima, A. macrostachyum, S. vera*) were well represented at elevations that are consistent with their distribution in tidal marshes. Equally interesting are halophytes that are typically dominant on tidal marshes and absent in our study: notably *Spartina maritima* of the lower marshes and *Atriplex portulacoides* of mid- to higher marshes. *S. maritima* is characteristic of consistently flooded, low-redox sites (Castellanos *et al.*, 1994) and presumably would not survive the long summer exposure, whereas *Atriplex* is highly sensitive to reducing conditions and would not survive prolonged inundation (Mossman *et al.*, 2020). This highlights the distinction between consistently hypoxic conditions and sustained episodes of anoxia in structuring the vegetation on saltmarshes. The different roles of these two aspects of flooding tolerance, similar to frequency and duration of flooding in the more predictable tidal systems (Eleuterius and Eleuterius, 1979), would clearly reward further investigation. In addition, the Mediterranean climate is becoming warmer and drier, and is projected to become more extreme (Cramer *et al.*, 2018). Manifold threats to coastal systems are likely to arise from future climate change (e.g. Hanley *et al.*, 2019). Improved understanding of the hydrochemical processes underlying the composition and structure of the vegetation of non-tidal marshes in general, and the internationally important Doñana National Park (Vélez-Martín *et al.*, 2018) in particular, and will be valuable in informing their future conservation and restoration.

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LITERATURE CITED

Adam, P. 1990. *Saltmarsh Ecology*. Cambridge, UK: Cambridge University Press.

Anastasiou, C. J., Brooks, J. R. 2003. Effects of soil pH, redox potential, and elevation on survival of *Spartina patens* planted at a west Central Florida salt marsh restoration site. *Wetlands*, **23**: 845-859.

Armstrong, W., Wright, E. J., Lythe, S., Gaynard, T. J. 1985. Plant zonation and the effects of the spring-neap tidal cycle on soil aeration in a Humber salt marsh. *The Journal of Ecology,* **73**: 323-339.

Barclay, A. M., Crawford, R. M. M. 1982. Plant growth and survival under strict anaerobiosis. *Journal of Experimental Botany*, **33**: 541-549.

Barrett-Lennard E. G., Bennett S. J., Altman M. 2013. Survival and growth of perennial halophytes on saltland in a Mediterranean environment is affected by depth to watertable in summer as well as subsoil salinity. *Crop and Pasture Science*, **64**: 123-136.

Bennett, S.J., Barrett-Lennard, E.G. 2013. Predictions of watertable depth and soil salinity levels for land capability assessment using site indicator species. *Crop and Pasture Science*, **64**: 285-294.

Bennett, S.J., Barrett-Lennard, E.G., Colmer, T.D. 2009. Salinity and waterlogging as constraints to saltland pasture production: A review. *Agriculture, Ecosystems and Environment*, **129**: 349-360.

Birkinshaw, C.R. 1994. Aspects of the ecology and conservation of *Damasonium alisma* Miller in Western Europe. *Watsonia*, **20**: 33-39.

Bockelmann, A. C., Bakker, J. P., Neuhaus, R., Lage, J. 2002. The relation between vegetation zonation, elevation and inundation frequency in a Wadden Sea salt marsh. *Aquatic Botany*, **73**: 211-221.

Castellanos, E. M., Figueroa, M. E., Davy, A. J. 1994. Nucleation and facilitation in saltmarsh succession: Interactions between *Spartina maritima* and *Arthrocnemum perenne*. *Journal of Ecology*, **82**: 239-248.

Castillo, J. M., Fernández-Baco, L., Castellanos, E. M., Luque, C. J., Figueroa, M. E., Davy, A. J. 2000. Lower limits of *Spartina densiflora* and *S. maritima* in a Mediterranean salt marsh determined by different ecophysiological tolerances. *Journal of Ecology*, **88**: 801-812.

Chevan, A., Sutherland, M. 1991. Hierarchical partitioning. *The American Statistician*, **45**: 90-96.

Clemente, L., García, L. V., Siljeström, P. 1998. *Suelos del Parque Nacional de Doñana*. Madrid, Spain: Ministerio de Medio Ambiente.

Clevering, O. A., van Vierssen, W., Blom, C. W. P. M. 1995. Growth, photosynthesis and carbohydrate utilization in submerged *Scirpus maritimus* L. during spring growth. *New Phytologist*, **130**: 105-116.

Colmer, T. D., Flowers, T. J. 2008. Flooding tolerance in halophytes. *New Phytologist*, **179**: 964-974.

Cook, H. F., Bonnett, S. A., Pons, L. J. 2009. Wetland and floodplain soils: their characteristics, management and future. In *The Wetlands Handbook* (eds E. Maltby, T. Barker), pp. 382-416. Wiley-Blackwell. doi:10.1002/9781444315813.ch18

Costa, C.S.B, Marangoni, J.C., Azevedo, A.M.G. 2003. Plant zonation in irregularly flooded salt marshes: relative importance of stress tolerance and biological interactions. *Journal of Ecology*, **91**: 951-965.

Cramer, W., Guiot, J., Fader, M. *et al.* 2018. Climate change and interconnected risks to sustainable development in the Mediterranean. *Nature Climate Change,* **8**: 972-980.

Curcó, A., Ibàñez, C., Day, J. W., Prat, N. 2002. Net primary production and decomposition of salt marshes of the Ebre Delta (Catalonia, Spain). *Estuaries*, **25**: 309-324.

Davy, A. J., Bishop, G. F., Costa, C. S. B. 2001. *Salicornia* L. (*Salicornia pusilla* J. Woods, *S. ramosissima* J. Woods, *S. europaea* L., *S. obscura* P.W. Ball & Tutin, *S. nitens* P.W. Ball & Tutin, *S. fragilis* P.W. Ball & Tutin and *S. dolichostachya* Moss). *Journal of Ecology*, **89**: 681-707.

Davy, A. J., Brown, M. J., Mossman, H. L., Grant, A. 2011. Colonization of a newly developing salt marsh: disentangling independent effects of elevation and redox potential on halophytes. *Journal of Ecology*, **99**: 1350-1357.

Díaz-Delgado, R., Bustamante, J., Pacios, F., Aragonés, D. 2006. Hydroperiod of Doñana marshes: Natural or anthropic origin of inundation regime. In *Proceedings of the 1st Global Wetland Symposium* (pp. 19-20), Frascati, Italy: ESA & Ramsar Convention.

Díaz-Delgado, R., Aragonés, D., Ameztoy, I., Bustamante, J. 2010. Monitoring marsh dynamics through remote sensing. *Conservation Monitoring in Freshwater Habitats:*

A Practical Guide and Case Studies (eds C. Hurford, M. Schneider & I. Cowx), pp. 375-386. Dordrecht, The Netherlands: Springer.

Díaz-Delgado, R., Aragonés, D., Afán, I., Bustamante, J. 2016. Long-term monitoring of the flooding regime and hydroperiod of Doñana marshes with Landsat time series (1974–2014). *Remote Sensing*, **8**: Article Number: 775. DOI: 10.3390/rs8090775 775.

Eleuterius, L. N., Eleuterius, C. K. 1979. Tidal levels and salt marsh zonation. *Bulletin of Marine Science*, **29**: 394-400.

Espinar J. L. 2009. 1410 Pastizales salinos mediterráneos (Juncetalia maritimi). In: Bases ecológicas preliminares para la conservación de los tipos de hábitat de interés comunitario en España. Madrid, Spain: Ministerio de Medio Ambiente, y Medio Rural y Marino.

Figueroa, M. E., Castillo, J. M., Redondo, S., Luque, T., Castellanos, E. M., Nieva, F. J., Luque, C. J., Rubio-Casal A. E., Davy A. J. 2003. Facilitated invasion by hybridization of *Sarcocornia* species in a salt-marsh succession. *Journal of Ecology*, **91**: 616-626.

Flowers, T., Colmer, T. 2008. Salinity tolerance in halophytes. *The New Phytologist*, **179**: 945-963.

García, L. V., Marañón, T., Moreno, A., Clemente, L. 1993. Above-ground biomass and species richness in a Mediterranean salt marsh. *Journal of Vegetation Science*, **4**: 417-424.

González-Alcaraz, M. N., Jiménez-Cárceles, F. J., Álvarez, Y., Álvarez-Rogel, J. 2014. Gradients of soil salinity and moisture, and plant distribution, in a Mediterranean semiarid saline watershed: a model of soil–plant relationships for contributing to the management. *Catena*, **115**: 150-158.

Hanley, M.E., Bouma, T.J., Mossman, H.L. 2019. The gathering storm: optimizing management of coastal ecosystems in the face of a climate-driven threat. *Annals of Botany*, https://doi.org/10.1093/aob/mcz204

IBM Corp. 2012. IBM SPSS Statistics for Windows, Version 21.0. Armonk, New York: IBM Corp.

Jefferies, R. L., Davy, A. J., Rudmik, T. 1979. The growth strategies of coastal halophytes. In: *Ecological Processes in Coastal Environments* (Eds R.L. Jefferies & A.J. Davy), pp. 243-268. Oxford, UK: Blackwell Scientific Publications.

Lambert, S. J., Davy, A. J. 2011. Water quality as a threat to aquatic plants: discriminating between the effects of nitrate, phosphate, boron and heavy metals on charophytes. *New Phytologist*, **189**: 1051-1059.

Marañón, T., García, L. V., Murillo, J. M., Clemente, L. 1989. Las marismas del Guadalquivir, reserva biogenética de plantas tolerantes a la salinidad. *Anales de Edafología y Agrobiología*, **48**: 725-740.

Mossman, H. L., Grant, A., Davy, A. J. 2020. Manipulating saltmarsh microtopography modulates the effects of elevation on sediment redox potential and halophyte distribution. *Journal of Ecology*, **108**: 94-106.

Pennings, S. C., Callaway, R. M. 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. *Ecology*, **73**: 681-690.

Pezeshki, S. R., DeLaune, R. D. 2012. Soil oxidation-reduction in wetlands and its impact on plant functioning. *Biology*, **1**: 196-221.

R Core Team 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. URL: http://www.R-project.org/

Redondo-Gómez, S., Mateos-Naranjo, E., Figueroa, M. E., Davy, A. J. 2010. Salt stimulation of growth and photosynthesis in an extreme halophyte, *Arthrocnemum macrostachyum*. *Plant Biology*, **12**: 79-87.

Rivas-Martínez, S., Costa, M., Castroviejo, S., Valdés, E. 1980. Vegetación de Doñana (Huelva, España). *Lazaroa*, **2**: 5-189.

Rogel, J. A., Ariza, F. A., Silla, R. O. 2000. Soil salinity and moisture gradients and plant zonation in Mediterranean salt marshes of Southeast Spain. *Wetlands*, **20**: 357-372.

Silvestri, S., Defina, A., Marani, M. 2005. Tidal regime, salinity and salt marsh plant zonation. *Estuarine, Coastal and Shelf Science*, **62**: 119-130.

Vélez-Martín, A., Davy, A. J., Luque, C. J., Castellanos, E. M. 2018. Reference conditions for restoration of heterogeneous Mediterranean wetland are best defined by multiple, hydrologically diverse sites. *Restoration Ecology*, **26**: 145-155.

Walsh, C., MacNally, R. 2007. *Hierarchical Partitioning*. R project for statistical computing. URL: http://cran.r-project.org/.

Watt, S. C. L., García-Berthou, E., Vilar, L. 2007. The influence of water level and salinity on plant assemblages of a seasonally flooded Mediterranean wetland. *Plant Ecology*, **189**: 71-85.

Wood, S. N. 2006. *Generalized Additive Models: An Introduction with R*. London, UK: Chapman and Hall.

Zedler, J., Callaway, J., Desmond, J., Vivian-Smith, G., Williams, G. D., Sullivan, G., Brewster, A. E., Bradshaw, B. K. 1999. Californian salt-marsh vegetation: an improved model of spatial pattern. *Ecosystems*, **2**: 19-35.

Table 1. Coefficients (SE) of generalized linear models for the environmental variables (elevation, hydroperiod and salinity at two soil depths) are indicated for all the response variables (cover of bare ground, five perennial and 19 annual species). Independent effects (Ind Eff %) were calculated by hierarchical partitioning. Total variance explained (overall R^2) is derived from generalized linear models using all of the variables.

	Elevation		Hydroperiod		EC 0-2		EC 8-10		Total variance explained (%)
	Coefficient	Ind Eff (%)	Coefficient	Ind Eff (%)	Coefficient	Ind Eff (%)	Coefficient	Ind Eff (%)	
Bare ground	-11.59 (4.31)**	**30.1**	0.0791 (0.0481)	**12.2**	1.2234 (0.9037)	**26.6**	0.0474 (0.0132)***	**31.0**	55.4
Perennial species:									
Arthrocnemum macrostachyum	4.451 (0.938)***	**50.1**	-0.0084 (0.0105)	**13.9**	-0.6459 (0.1966)**	**26.7**	0.0099 (0.0029)***	**9.4**	52.3
Bolboschoenus maritimus	-3.217 (0.802)***	**41.2**	-0.0180 (0.0089)*	8.0	-0.2512 (0.1681)	**15.4**	-0.0064 (0.0024)**	**35.4**	17.1
Juncus subulatus	-2.729 (0.981)**	**56.4**	-0.0074 (0.0109)	5.2	-0.4589 (0.2054)*	20.6	0.0046 (0.0030)	17.8	7.0
Schoenoplectus litoralis	-0.4806 (0.6816)	**28.5**	0.0070 (0.0076)	**17.5**	0.2398 (0.1428)†	**40.7**	0.0001 (0.0021)	13.4	14.1
Suaeda vera	2.300 (0.864)**	**52.8**	-0.0029 (0.0096)	13.3	0.1498 (0.1810)	14.0	-0.0039 (0.0026)	**19.9**	16.4
Annual species:									
Beta macrocarpa	-0.2627 (0.5168)	**9.5**	-0.0315 (0.0058)***	**78.8**	-0.0834 (0.1083)	3.4	0.0031 (0.0016)†	**8.3**	29.5
Bromus lanceolatus	0.7283 (0.5567)	**38.9**	-0.0008 (0.0062)	9.8	0.0117 (0.1166)	20.4	-0.0020 (0.0017)	**30.9**	6.3
Chamaemelum mixtum	-0.2521 (0.7210)	11.7	-0.0189 (0.0080)*	**66.5**	-0.1585 (0.1510)	12.5	0.0026 (0.0022)	9.3	6.2
Coronopus squamatus	-0.8767 (0.4661)†	8.2	-0.0104 (0.0052)*	**18.8**	-0.3688 (0.0976)***	**40.5**	0.0048 (0.0014)**	**32.5**	15.1

Damasonium alisma	-0.8606 (1.0545)	**7.7**	0.0538 (0.0118)***	**51.2**	-0.8328 (0.2209)***	**33.5**	0.0004 (0.0032)	7.6	28.6
Hordeum marinum	3.163 (0.784)***	**53.9**	-0.0198 (0.0087)*	**35.3**	0.3045 (0.1643)†	8.4	0.0011 (0.0024)	2.4	30.1
Juncus bufonius	1.299 (0.755)†	**50.1**	-0.0025 (0.0084)	15.9	-0.1340 (0.1581)	**26.9**	0.0011 (0.0023)	7.1	9.7
Leontodon longirostris	1.395 (0.922)	**27.7**	-0.0458 (0.0103)***	**58.3**	-0.0001 (0.1931)	**9.3**	-0.0017 (0.0028)	4.7	36.3
Lolium rigidum	5.109 (0.927)***	**72.6**	0.0083 (0.0103)	8.5	0.5102 (0.1941)**	**12.2**	-0.0035 (0.0028)	6.7	29.0
Lythrum tribracteatum	-0.496 (0.777)	7.6	0.0258 (0.0087)**	**42.8**	-0.4550 (0.1627)**	**38.9**	-0.0001 (0.0024)	10.7	15.3
Medicago polymorpha	0.748 (0.950)	**19.4**	-0.0498 (0.0105)***	**69.6**	-0.1302 (0.1979)	6.1	0.0046 (0.0029)	4.9	31.0
Parapholis pycnantha	0.470 (0.842)	**19.2**	-0.0281 (0.0094)**	**60.9**	-0.1570 (0.1764)	8.2	0.0047 (0.0026)†	11.7	16.0
Phalaris minor	1.214 (0.850)	**35.3**	-0.0142 (0.0095)	**26.9**	-0.0140 (0.1781)	**18.4**	-0.0033 (0.0026)	**19.4**	17.2
Plantago coronopus	1.462 (0.979)	**28.0**	-0.0442 (0.0109)***	**62.5**	-0.0227 (0.2050)	**7.1**	0.0019 (0.0030)	2.3	29.7
Plantago lanceolata	2.911 (0.825)***	**51.6**	-0.0122 (0.0092)	**20.8**	0.1899 (0.1728)	**12.5**	-0.0045 (0.0025)†	**15.1**	31.5
Polypogon maritimus ssp. *maritimus*	0.288 (1.050)	24.2	-0.0156 (0.0117)	**29.7**	-0.3716 (0.2199)†	**38.7**	0.0023 (0.0032)	7.5	9.0
Rumex dentatus ssp. *halacsyi*	-0.569 (0.833)	10.6	-0.0164 (0.0093)†	**27.0**	-0.5225 (0.1745)**	**45.0**	0.0059 (0.0025)*	**17.5**	12.4
Salicornia ramosissima	0.249 (0.412)	12.5	0.0018 (0.0046)	5.5	0.2302 (0.0863)**	**67.9**	-0.0005 (0.0013)	14.0	9.3
Spergularia nicaeensis	-1.659 (0.556)**	**11.5**	-0.0323 (0.0062)***	**57.9**	-0.3296 (0.1165)**	**10.6**	0.0054 (0.0017)**	**20.0**	27.4

Significant coefficients are represented by $^{\dagger}p < 0.1$; $*p < 0.05$; $**p < 0.01$; $***p < 0.001$. Significant independent effects from hierarchical partitioning are shown in bold.

LEGENDS TO FIGURES

FIG. 1 (a) The distribution of elevation (relative to Spanish Hydrographic zero) of 170 permanent sample points on a grid covering the Doñana non-tidal salt marsh; (b) boxplot showing variation in hydroperiod from year to year (2004-2010) at the 170 sample points (different letters indicate significant differences between years in Mann-Whitney tests, $P<0.05$).

FIG. 2 The relationships between elevation and (a) mean hydroperiod per sample point ($n = 170$); and (b) hydroperiod in all the sample points for every year ($n = 1190$); and (c) mean electrical conductivity (EC(1:1)) in surface per sample point ($n = 19$); and (d) electrical conductivity in surface in all the sample points for every year ($n = 101$); and (e) mean electrical conductivity in subsurface per sample point ($n = 19$); and (f) electrical conductivity in subsurface in all the sample points for every year ($n = 101$).

FIG. 3 The distribution of abundance of perennial species and bare ground in relation to (from left to right): elevation, hydroperiod, surface salinity (EC(1:1) 0-2 cm) and subsurface salinity (EC(1:1) 8-10 cm). Cover values are means. $n = 1065$ for elevation and hydroperiod; $n = 101$ for salinity measurements.

FIG. 4 Contour lines showing the relationship between subsurface salinity (EC(1:1) 8-10 cm) and elevation and (a) the probability of occurrence and (b) the percentage cover (arcsine transformed) of perennial species (*Suaeda vera*, *Arthrocnemum macrostachyum*, *Juncus subulatus*, *Bolboschoenus maritimus* and *Schoenoplectus litoralis*). Contours show the predicted probability from generalised additive models. Darker colours indicate higher occurrence or cover. Species are ordered as in Fig. 3.

FIG. 5 The distribution of abundance of annual species in relation to (from left to right): elevation, hydroperiod, surface salinity (EC(1:1) 0-2 cm) and subsurface salinity (EC(1:1) 8-10) cm. Cover values are means. *n* = 1065 for elevation and hydroperiod; *n* = 101 for salinity measurements.

Fig. 1

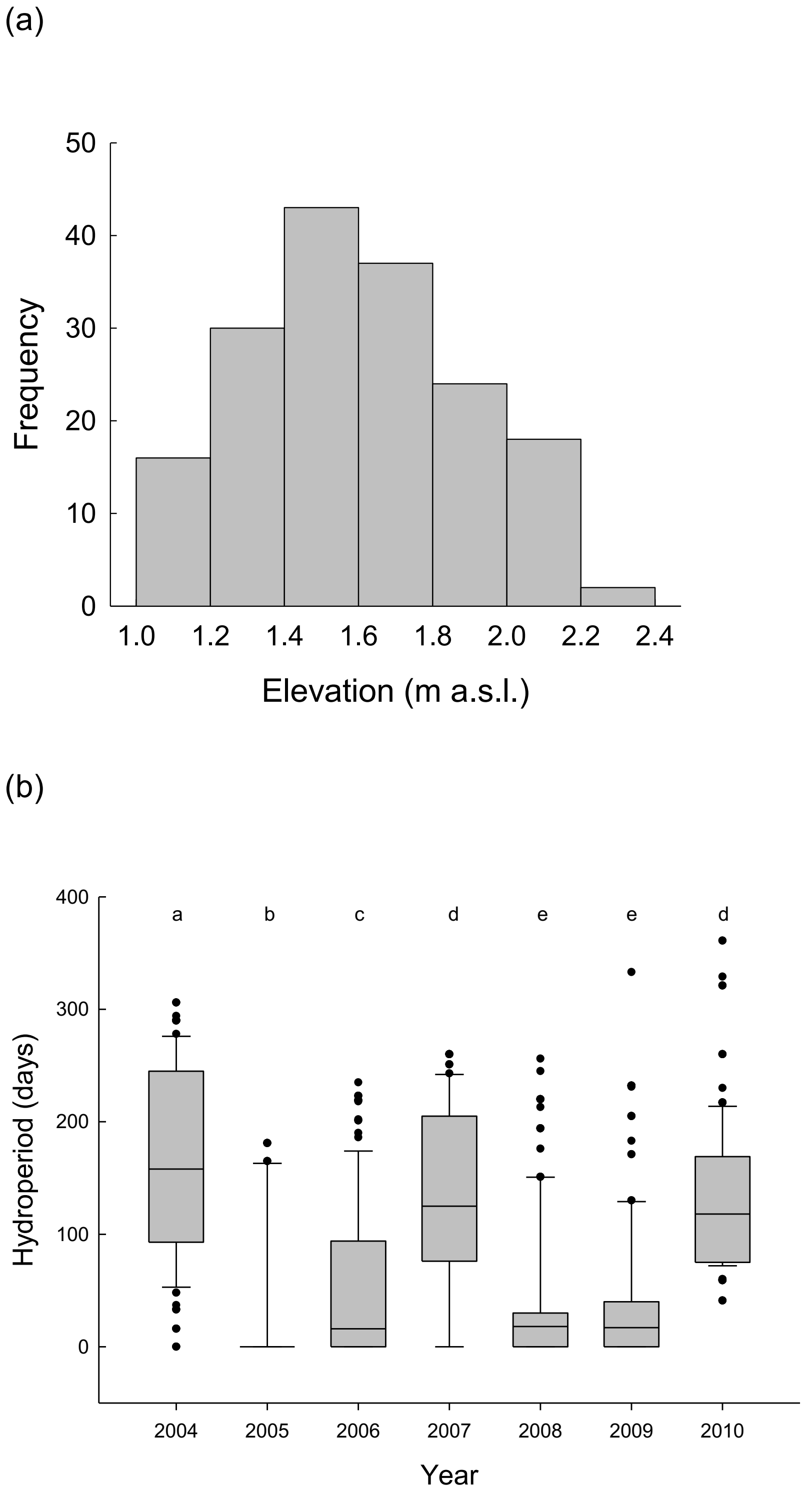

(a)
Frequency
0
10
20
30
40
50
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
Elevation (m a.s.l.)
(b)
Hydroperiod (days)
0
100
200
300
400
a
b
c
d
e
e
d
2004
2005
2006
2007
2008
2009
2010
Year

Fig. 2

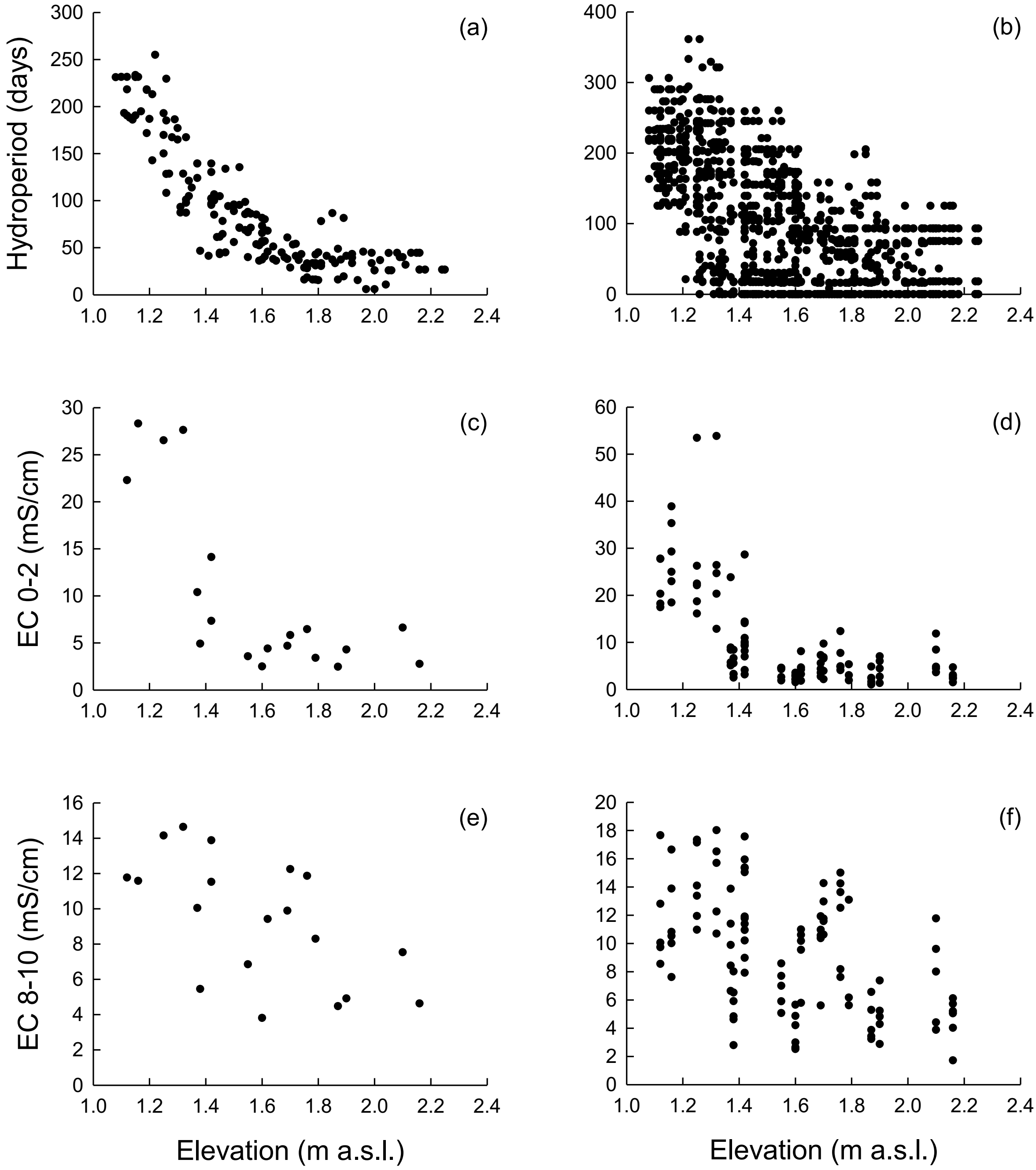

(a)
(b)
(c)
(d)
(e)
(f)
Hydroperiod (days)
EC 0-2 (mS/cm)
EC 8-10 (mS/cm)
Elevation (m a.s.l.)
Elevation (m a.s.l.)
0
50
100
150
200
250
300
0
100
200
300
400
0
5
10
15
20
25
30
0
10
20
30
40
50
60
0
2
4
6
8
10
12
14
16
0
2
4
6
8
10
12
14
16
18
20
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4

Fig. 3

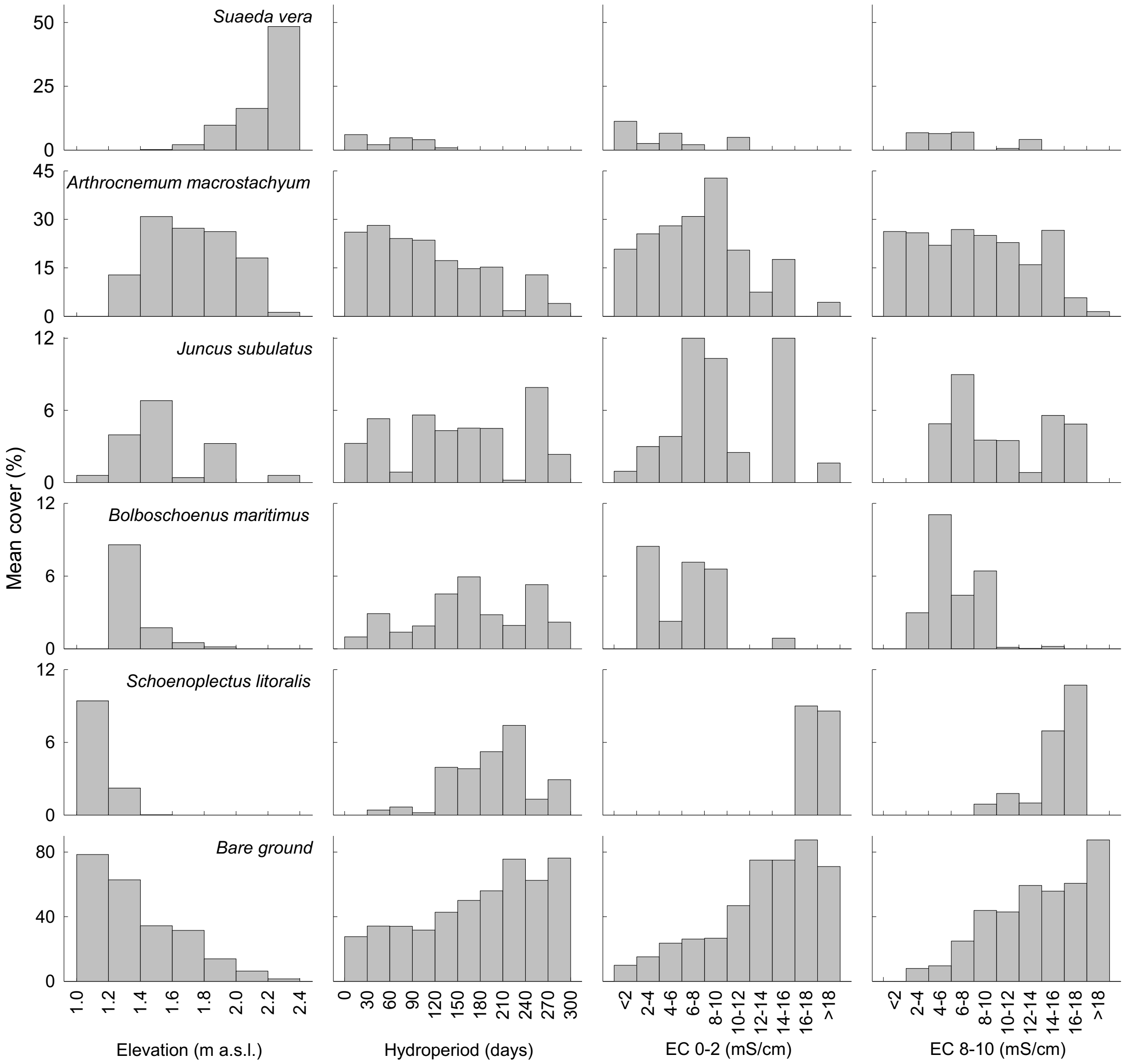

Suaeda vera
Arthrocnemum macrostachyum
Juncus subulatus
Bolboschoenus maritimus
Schoenoplectus litoralis
Bare ground
Mean cover (%)
50
25
0
45
30
15
0
12
6
0
12
6
0
12
6
0
80
40
0
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
Elevation (m a.s.l.)
0
30
60
90
120
150
180
210
240
270
300
Hydroperiod (days)
<2
2-4
4-6
6-8
8-10
10-12
12-14
14-16
16-18
>18
EC 0-2 (mS/cm)
EC 8-10 (mS/cm)

Fig. 4

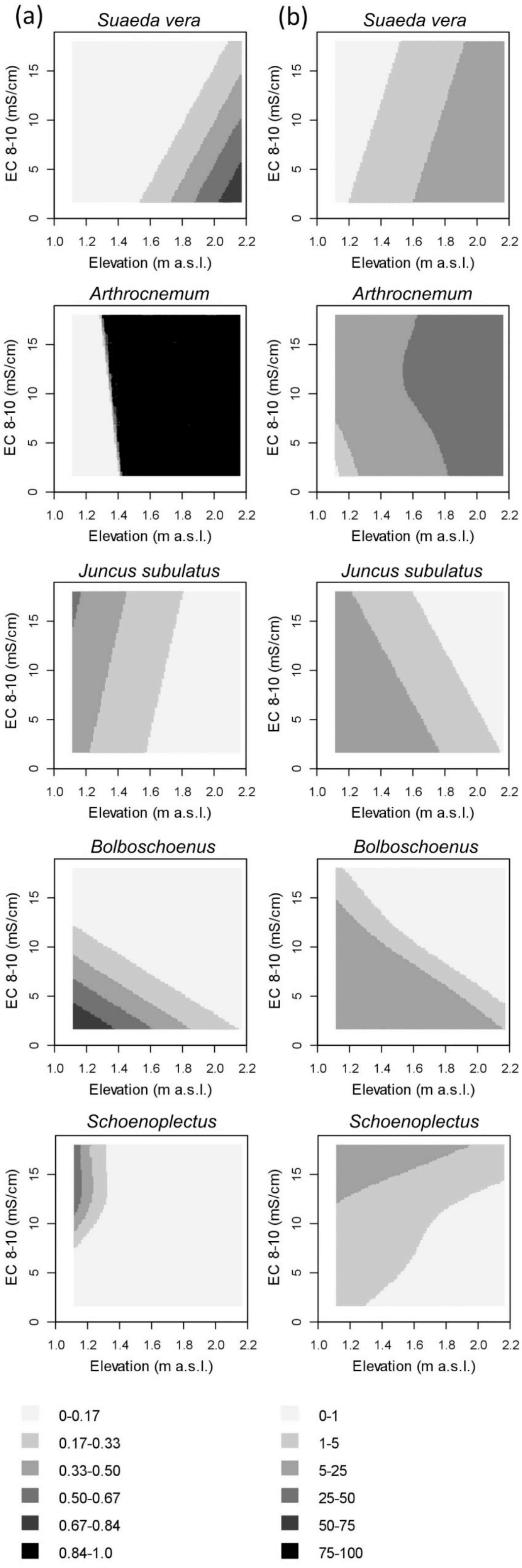
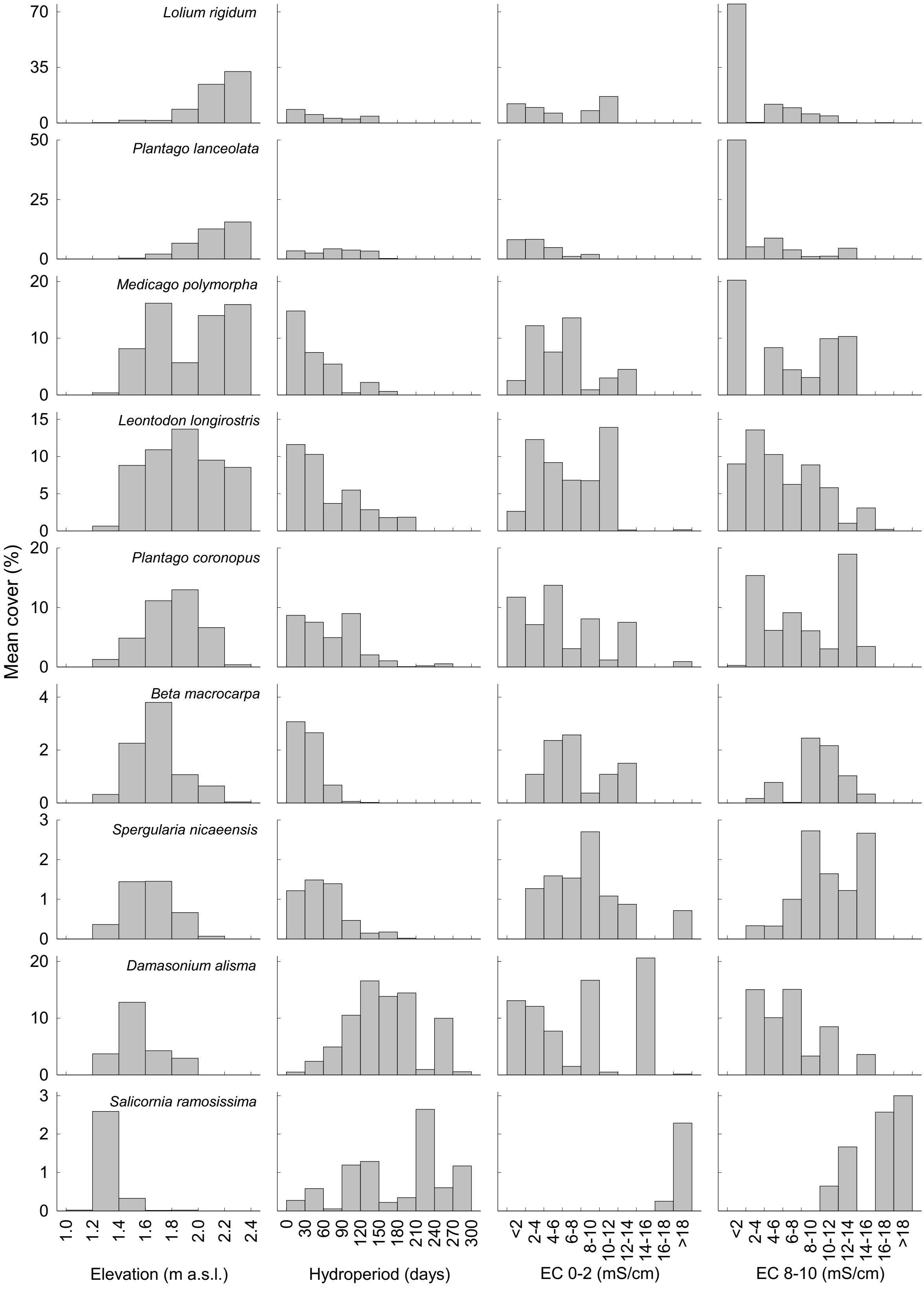

(a)
(b)
Suaeda vera
Arthrocnemum
Juncus subulatus
Bolboschoenus
Schoenoplectus
EC 8-10 (mS/cm)
0
5
10
15
Elevation (m a.s.l.)
1.0
1.2
1.4
1.6
1.8
2.0
2.2
0-0.17
0.17-0.33
0.33-0.50
0.50-0.67
0.67-0.84
0.84-1.0
0-1
1-5
5-25
25-50
50-75
75-100

Fig. 5


Lolium rigidum
Plantago lanceolata
Medicago polymorpha
Leontodon longirostris
Plantago coronopus
Beta macrocarpa
Spergularia nicaeensis
Damasonium alisma
Salicornia ramosissima
Mean cover (%)
70
35
0
50
25
0
20
10
0
15
10
5
0
20
10
0
4
2
0
3
2
1
0
20
10
0
3
2
1
0
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
0
30
60
90
120
150
180
210
240
270
300
<2
2-4
4-6
6-8
8-10
10-12
12-14
14-16
16-18
>18
<2
2-4
4-6
6-8
8-10
10-12
12-14
14-16
16-18
>18
Elevation (m a.s.l.)
Hydroperiod (days)
EC 0-2 (mS/cm)
EC 8-10 (mS/cm)