

SEED STORAGE CONDITIONS CHANGE THE GERMINATION PATTERN OF CLONAL GROWTH PLANTS IN MEDITERRANEAN SALT MARSHES¹

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The effect of salinity level and extended exposure to different salinity and flooding conditions on germination patterns of three salt-marsh clonal growth plants (*Juncus subulatus*, *Scirpus litoralis*, and *S. maritimus*) was studied. Seed exposure to extended flooding and saline conditions significantly affected the outcome of the germination process in a different, though predictable, way for each species, after favorable conditions for germination were restored. Tolerance of the germination process was related to the average salinity level measured during the growth/germination season at sites where established individuals of each species dominated the species cover. No relationship was found between salinity tolerance of the germination process and seed response to extended exposure to flooding and salinity conditions. The salinity response was significantly related to the conditions prevailing in the habitats of the respective species during the unfavorable (nongrowth/nongermination) season. Our results indicate that changes in salinity and hydrology while seeds are dormant affect the outcome of the seed-bank response, even when conditions at germination are identical. Because these environmental-history-dependent responses differentially affect seed germination, seedling density, and probably sexual recruitment in the studied and related species, these influences should be considered for wetland restoration and management.

Key words: Doñana; dormancy control; environmental stress; helophyte; *Juncus*; Mediterranean; *Scirpus*; species zonation.

Germination traits of species are considered to be under strong selective pressures, and germination syndromes are widely accepted as adaptive at the species level (reviewed in Schütz, 2000). In highly seasonal climates, a critical role of seed dormancy regulation mechanisms is in determining the timing of germination (Grime et al., 1981; Schütz, 2000) because the optimum onset of germination of the plants may greatly increase the likelihood of seedling survival (Silvertown and Lovett-Doust, 1993; Baskin and Baskin, 1998).

Traditionally, studies on the regulation of primary dormancy have focused mainly on the effects of light and temperature (see Baskin and Baskin, 1998). Only a few papers have reported effects of salinity (mainly in annual halophyte species; Woodell, 1995; Kieffer and Ungar, 1997) or flooding (e.g., wet stratification effects in perennial wetland species; Clevering, 1995) on seed primary dormancy.

The effects of extended exposure to salinity on seed-bank response—Although the effect of salinity during the germination period is known to be one of the main factors affecting the events of sexual recruitment in Mediterranean salt marshes (Ungar, 1978, 1982, 1996; Ungar and Riehl, 1980; Shumway and Bertness, 1992; Noe and Zedler, 2001a; Noe, 2002), only some studies have shown (mainly for annual species) that in such fluctuating environments, the seed response during germination depends not only on the salinity values during the process of germination itself, but also on the levels and changes

of salinity at the site where the seeds are deposited (i.e., the seed bank) (Woodell, 1985; Keiffer and Ungar, 1997).

In many cases, the periods preceding exposure to high saline concentrations stimulate germination to proceed when environmental salinity declines (Ungar, 1978, 1982; Keiffer and Ungar, 1997; Rubio et al., 2002). This type of response has been related to the need to take advantage of the periods with ideal conditions for establishment (i.e., “windows of germination,” Noe and Zedler, 2001b; or “windows of opportunity,” Eriksson and Fröberg, 1996).

The annual fluctuations in salinity and the duration of flooding are factors that may provide seeds with accurate signals about the potential success in establishing seedlings and could be an important system of regulation. Such mechanisms may be crucial when the survival of the population depends on successive events of sexual recruitment from a seed bank (i.e., in populations of annual species). For perennial species with clonal growth that colonize Mediterranean marshes, there is no information on how germination patterns are affected by the period before a seed's exposure to salinity.

The effect may not be as pivotal as it is for annual species, because in this case the role of the seed bank and the events of sexual recruitment are less critical in ensuring the maintenance of the populations in the short term (Shumway and Bertness, 1992). Therefore, mechanisms that contribute to the persistence of seed banks might be more highly developed in wetland annuals than in wetland perennials (Schütz, 1997). Nonetheless, the events of sexual regeneration provide many advantages for the populations (reviewed in Stearns, 1987).

In this work, we analyze experimentally the germination patterns in three species of clonal growth plants—*Juncus subulatus* Forsskal, *Scirpus maritimus* L., and *Scirpus litoralis* Scharader. Seeds were exposed to (1) different conditions of salinity during the germination process and (2) different periods of extended exposure to salinity and flooding before germination. The consequences of these exposures on seed germination were then examined.

¹ Manuscript received 26 August 2004; revision accepted 7 April 2005.

The authors thank J. M. Espinar and E. Gutiérrez for field and laboratory assistance. T. Marañón made useful suggestions for planning germination experiments. Financial support from the Spanish Ministry of the Environment (MMA, project 05/99), and the Junta de Andalucía (research group #4086) enabled us to carry out the present work.

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The main aims are to understand (1) how these key environmental factors (acting on the seed bank) affect the germination patterns of the studied species, and (2) if eventual differences in species' seed response may be related to the different environmental conditions experienced by seed banks in the field, in sites where perennial cover is dominated by established individuals of the different species.

MATERIALS AND METHODS

Study site and species—The three plant species studied, *Juncus subulatus* Forsskal, *Scirpus maritimus* L. [or *Bolboschoenus maritimus* (L.) Palla sensu Flora of North America, 2002], and *Scirpus litoralis* Scharader, are rhizomatous emergent macrophytes and are the major components of the perennial vegetation in the temporary marshes within Doñana National Park. The Doñana salt marsh is a senescent marsh with a Mediterranean climate located in southwest Spain (37° N 6° W) and is, in practicality, isolated from tidal influence; the lower zones are subject to seasonal flooding under the effect of precipitation and storm discharge of some streams and behave as a floodplain. A marked seasonality in water availability clearly differentiates a dry season (June–October) and a wet one (November–April).

Juncus subulatus inhabits shallow brackish waters in coastal areas of the Mediterranean and Irano-Turacic regions (Valdes et al., 1987). *Scirpus litoralis* Scharader and *Scirpus maritimus* L. (Cyperaceae) are more widely distributed in shallow brackish water bodies of temperate regions (Valdes et al., 1987).

In all three species, the tuber sprouts after the start of the wet season (autumn). The shoot grows up the water column, emerging in autumn (*J. subulatus*) or winter (*Scirpus* spp.), fruits through the spring, and dies in the dry season (summer).

Previous studies (García et al., 1993; Espinar et al., 2002) have shown that these geophytes become dominant in different zones of the microtopographic gradient, with *J. subulatus* occupying the highest parts, which are flooded to a lesser depth and for a shorter time, while *S. litoralis* colonizes the lowest areas and *S. maritimus* occupies intermediate areas. In these habitats, salinity tends to increase with elevation during the wet season, but the reverse may be true during the dry season (Marañón et al., 1989; Clemente et al., 1998). In the study area, the species have an abundant and persistent seed bank with seeds distributed at different soil depths (J. L. Espinar et al., unpublished manuscript).

Seed collection and pretreatment—Ten populations of each of the studied species were selected at random in the southern part of the marshes of Doñana National Park. From each population, the inflorescences were collected at random from 60 shoots separated from each other by at least 10 m. Achenes of *Scirpus* spp. (hereafter seeds) and seeds of each species were separated from the spikes and mixed to produce a homogeneous sample representative of the study area. The seeds were stored in darkness at 4°C, in order to stimulate germination (Clevering, 1995).

Saline solutions used in the experiments were prepared by adding different amounts of sea salt (dried to 110°C for 24 h) to demineralized water to produce the range of salinity observed in the field during the growth season (<1–30 decisiemens per m, dS · m⁻¹). Seven different solutions (0 to 20 g · L⁻¹) were used, with electrical conductivities (EC) of 0, 1, 2, 4, 8, 16, and 32 dS · m⁻¹.

In the extended-exposure experiment, seeds were placed in tightly closed flasks containing a different saline solution for 1, 3, 6, or 12 mo. During the exposure period, the flasks were stored in the dark at 4°C. A null (dry) pretreatment was also included in the experiment by directly germinating dry-stratified seeds of the three species, without pre-exposing them to any solution.

Germination experiments—In the “salinity tolerance experiment,” four 25-seed replicates of each species were placed in Petri dishes containing a disc of Whatman (Whatman plc, Brentford, Middlesex, UK) no. 1 filter paper and 20 mL of one of the seven solutions. In the case of *S. litoralis*, a significant proportion of seeds germinate only if they are submerged (J. L. Espinar

et al., unpublished data). Therefore, the seeds were kept continuously submerged, in precipitation flasks of 250 mL. A total of 2100 seeds in 83 dishes (or flasks) were used in this experiment (100 seeds × 7 salinity levels × 3 spp.).

In the “extended-exposure experiment” (once the selected exposure time had elapsed), seeds were removed from the pretreatment solution, rinsed with distilled water, and placed in Petri dishes containing a disc of Whatman no. 1 filter paper and 20 mL of demineralized water (or, in the case of *S. litoralis*, in flasks of 250 mL). A total of 8400 seeds in 336 dishes and flasks were used in this experiment (100 seeds × 7 salinity levels × 4 pre-exposure times × 3 spp.).

In both experiments, dishes and flasks were placed on trays in an incubator, with a 12-h/12-h light–dark photoperiod and a photon flux of 200 μmol photons · m⁻² and temperature cycles of 25°C/10°C. Every two d, the number of seeds germinated in each dish/flask was counted to obtain, after 30 d, the total percentage germination.

Habitat data—Data on the habitat (flooding depth and duration, water salinity) of established individuals of the three studied species were gathered at 49 sites during the wet season (near the location of the highest flooding–lowest salinity points) in three yr (1996, 1997, and 2001). Data for surface soil (0–5 cm) salinity and elevation (a proxy for the inverse of the flooding period length) were also obtained at 24 sites that were dominated by one of the three studied species, after shoots of established individuals were dead (summer). Soil saturation extracts were prepared according to standard methods, and their electrical conductivity was measured using a high-salinity probe. Soluble salts content (in g · L⁻¹) of the soil extracts was obtained by summation of the contributions of the main anions and cations (Rhoades, 1996).

Data analysis—The relationships between seed germination (i.e., the proportion of seeds germinating in each Petri dish) and the values of the predictors (salinity level and exposure time) were modeled for each species using a generalized linear model (GLM) with binomial error and a logit link function. In the extended-exposure experiment, the values of both predictors were log-transformed prior to modeling.

Both direct (linear and quadratic) and indirect (first-order interaction) effects were considered as potentially explanatory. Akaike's information criterion (AIC) was used as a guide to select the best models (i.e., those being more parsimonious and with a better fit, minimizing the AIC values). These were finally selected after checking for overdispersion, residual patterns, and possible artifacts derived from extreme values.

Equality of the mean values of the measured environmental variables (flooding, salinity, elevation) in sites dominated by each of the three studied species was tested using a one-way ANOVA. Assumptions of normality (normality plots), homocedasticity (Brown-Forsythe test) were checked prior to the parametric ANOVA (Zar, 1999). When the ANOVA null hypothesis was rejected, post hoc comparisons were performed using the Tukey unequal-*N* test. Observed and simulated “species dominance maps” (see results) were compared using a two-way MANOVA.

Significance was fixed at the 0.05 level throughout the study. In order to minimize the probability of “false positives” because of repeated testing (García, 2004), a sequential Bonferroni procedure (Holm, 1979) was used. All data analyses were performed using the Statistica software package (Statsoft, 2001).

RESULTS

Salinity effect on seed germination—According to the fitted models explaining the change in seed germination on day 30 as a function of salinity level (Table 1) and the average seed germination for each species obtained in each salinity treatment, together with a representation of the fitted logistic models (Fig. 1), seeds of *J. subulatus* are the most salt tolerant (*S*₅₀ of about 33 dS · m⁻¹), while *S. maritimus* and *S. litoralis*

TABLE 1. Effect of salinity (S , $\text{dS} \cdot \text{m}^{-1}$) on seed germination (on day 30) for the three species studied. Data have been modeled using a generalized linear model with binomial error and logit link, and linear (S) and quadratic (S^2) effects. Values of Akaike's information criterion (AIC) and of the overall significance of the fitted models, together with coefficient estimates, standard errors, and significance are shown for each species.

Species	Whole model		Effect	Salinity (S)			
	AIC	P		Coefficient	SE	Wald's χ^2	P
<i>Juncus subulatus</i>	228.9	0.000	S^2	-0.0043	0.0004	97.89	0.0000
<i>Scirpus maritimus</i>	742.0	0.000	S^2	-0.0103	0.0015	47.00	0.0000
<i>Scirpus littoralis</i>	545.9	0.000	S^2	-0.0151	0.0035	18.78	0.0000

seeds have a much lower, similar, tolerance (S_{50} of about 10 and 8 $\text{dS} \cdot \text{m}^{-1}$, respectively).

Effect of extended exposure to different saline environments—The fitted models (Table 2) and the trend surfaces derived from the fitted models (Fig. 2) significantly explain the observed seed germination for the three studied species, as a function of the time of exposure to flooding and salinity of the storage solution, after transfer for 30 days to a nonsaline environment having suitable light and temperature conditions for seed germination.

In all species studied, the length of the pretreatment had a direct, significant effect on seed germination. In both *J. subulatus* and *S. maritimus*, seed storage in a flooding environment significantly decreased germination when seeds were transferred to favorable conditions (Table 2). However, while germination of *S. maritimus* seeds decreased monotonically at a low rate, those of *J. subulatus* decrease at a very high rate at the short exposures (Fig. 2A). Increasing salinity of the storage solution produced a small (marginally significant) increase in seed germination in the case of *J. subulatus*, but significantly decreased germination of *S. maritimus* seeds (Table 2). For both species, seed germination under favorable conditions may be predicted by considering only the independent effect of each predictor (i.e., the interaction effect was nonsignificant).

In *Scirpus littoralis*, seed response to changes in the exposure time and salinity level of the storage solution seems to be somewhat more complex (Table 2, Fig. 2B). For short exposures to flooding, germination tended to decrease as the salinity of the storage solution increased, while for longer exposures, germination was stimulated as salinity increased (Table 2, Fig. 2C).

When results of the null-exposure treatment (i.e., dry stratified seeds) are analyzed together with those of the flooding nonsaline one (Table 3), a new insight is obtained into the

differential effects of only time of exposure to flooding (without salinity) on seed germination in the three species studied. In seeds of both *Scirpus* species, germination peaked after a short period (30 days) of exposure to flooding, and then tended to decrease (at a different rate in the two species) as exposure time increased. In contrast, *J. subulatus* seed germination peaked in the null-exposure treatment and decreased steeply as the duration of exposure to flooding increased (Fig. 3).

Using the models in Tables 2 and 3 to make predictions of species germination for different hydrology and salinity exposures (in the range 30–365 d), and for the whole range of exposure durations (0–360 d) in a nonsaline environment illustrates which species may have the maximum response in different areas of the flooding duration–salinity plane studied (Fig. 4). According to these estimates, *J. subulatus* would be the most-responsive species in the short-exposure range (<30 days), except in nonsaline (<1 $\text{dS} \cdot \text{m}^{-1}$) habitats. *Scirpus maritimus* would have the maximum germination in most of the remaining flooding duration–salinity plane, except for regions having extreme values of both predictors, in which *S. littoralis* would prevail. As salinity increased, *S. littoralis* would tend to be the most-responsive species at exposure durations ranges in which *S. maritimus* dominated at lower salinities.

Species habitats—During the growth season, sites dominated by *J. subulatus* were significantly more saline than those dominated by *Scirpus* species, although no significant differences in average salinity level and flooding duration were found between sites dominated by either of the two studied *Scirpus* species (Table 4).

At the time of dehiscence (dry season), the amount of soluble salts accumulated in the surface soil at sites inhabited by *S. littoralis* significantly exceeded that measured both at sites with a predominance of *J. subulatus* and at sites dominated by *S. maritimus* (Table 4).

TABLE 2. Effect of flooding duration (E) and salinity level (S) on seed germination. Data were modeled using a generalized linear model with binomial error and logit link, and log-transformed predictors. Linear (E , S), quadratic (E^2 , S^2) and interaction ($S \times E$) effects of exposure duration (E) and salinity (S) have been considered.

Species	Whole model		Factors			
	AIC	P	Effects	Coefficient	Wald's χ^2	P
<i>Juncus subulatus</i>	3489.7	0.000	E	-5.326	94.2	0.000
			E^2	0.526	81.9	0.000
			S	0.078	4.7	0.030
<i>Scirpus maritimus</i>	3129.5*	0.000	E	-0.248	27.2	0.000
			S	-0.108	8.3	0.004
<i>Scirpus littoralis</i>	3697.6	0.000	E	-2.093	16.1	0.000
			E^2	0.191	11.9	0.001
			S	-0.481	6.7	0.010
			$S \times E$	0.107	7.9	0.005

* One less treatment.

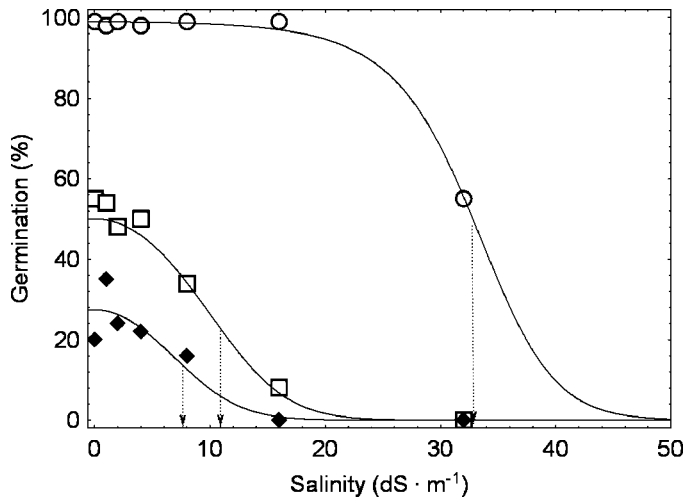


Fig. 1. Fitted logistic models (see Table 1) relating seed germination at day 30 to salinity for the three species studied. Points (circle: *Juncus subulatus*; square: *Scirpus littoralis*; triangle: *S. maritimus*) represent the mean of four replicates. Arrows indicate the estimated salinity level that reduces germination by 50% (S_{50}) in each species.

Germination response and distribution patterns—When field data on species habitat (Table 4) were related to predictions from models fitted to data derived from the laboratory experiments (Table 1, Fig. 1), several patterns emerged. First, salinity tolerance of the germination process ranked in the same way as the average salinity level measured in species habitats during the growth (wet) season (Fig. 5). Both germination tolerance to laboratory saline treatments and average habitat salinity during the growth season were significantly higher for *J. subulatus* than for the two *Scirpus* species. Second, no relationship was found between salinity tolerance of the germination process and (1) seed-bank response to extended exposure to salinity or (2) average salinity levels of species’ habitats after dehiscence. In fact, seeds of the species which showed the lowest average tolerance to salinity during the germination process (*S. littoralis*) were the most exposed in the field to extreme saline environments after dehiscence (i.e., during the nongrowth season; Table 1), and the most responsive, after long exposures to wet and highly saline treatments, when transferred to a favorable nonsaline environment (see Fig. 4). Third, applying the models fitted to laboratory data across the whole flooding duration/salinity plane for each species, a “dominance in germination” map could be obtained. This map resembles the one representing the cover dominance of the three studied species across the plane defined by the reciprocal of relative site elevation (a proxy for the length of seed-bank exposure to flooding/moisture at the site, because in the study area, flooding period is closely related to maximum water depth; Fig. 6) and topsoil salinity during the dry (nongrowth) season (Fig. 7). Both modeled and observed “dominance maps” were related in a statistically significant way (Fig. 8).

DISCUSSION

Effect of salinity on germination—In numerous works, an increase in salinity during germination causes a decrease in germination (Ungar, 1996, 1998; Noe and Zedler, 2000; Rubio et al., 2002; Espinar et al., 2004). The results obtained in the present work support this finding.

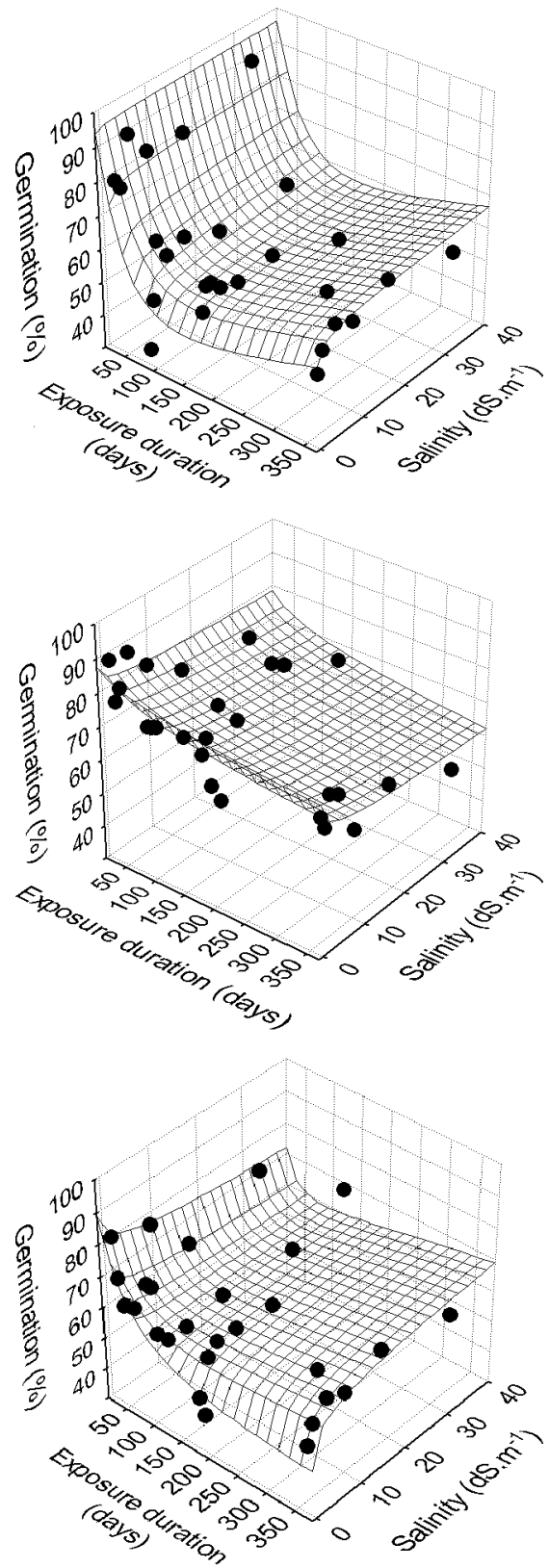


Fig. 2. Trend surfaces derived from the logistic models fitted to species germination data (upper: *Juncus subulatus*; middle: *Scirpus maritimus*; lower: *S. littoralis*), using exposure duration and salinity level as explanatory variables. Points (filled circles) represent the mean of four replicates.

TABLE 3. Effect of flooding duration in nonsaline environment on seed germination for the three species studied. Data were modeled using a generalized linear model with binomial error and logit link, and log-transformed predictors.

Species	Whole model		Effect	Salinity (S)			
	AIC	P		Coefficient	SE	Wald's χ^2	P
<i>Juncus subulatus</i>	545.5	0.000	E	-2.690	1.031	6.8	0.0091
			E ²	0.252	0.111	5.1	0.0234
<i>Scirpus maritimus</i>	562.2	0.000	E	0.896	0.188	22.7	0.0000
			E ²	-0.137	0.033	17.6	0.0000
<i>Scirpus litoralis</i>	601.8	0.000	E	1.564	0.183	73.0	0.0000
			E ²	-0.234	0.030	58.9	0.0000

Note: E = exposure duration.

During germination, the three species present different ranges of tolerance to salinity. *Juncus subulatus* is the most tolerant, its response practically not varying up to 16 dS · m⁻¹. The *Scirpus* species are much less tolerant; their germination fell sharply from 2 dS · m⁻¹, and germination was nearly completely inhibited from 8 dS · m⁻¹.

Similarities have been detected between the salinity values at which germination is higher and the salinity levels of the populations established during the growth season (for each of the three species), although some authors have suggested that in general the range of tolerance for each species during the germination stage is lower than the range of tolerance for the established individual (Poljakoff-Mayber et al., 1994; Ungar, 1995).

Dormancy conditions and germination patterns—We have not found any relationship between salinity tolerance for germination and tolerance to extended exposure to salinity. The results lead to conclusions similar to those reached by Keiffer and Ungar (1997) for annual plants: in the studied species, seed tolerance to salinity during germination is more related to the environmental conditions at the time of germination in natural habitats, while seed-bank response to extended salinity exposure is closely related to the environmental conditions during the seed dormancy period.

However, beside the effect of duration of flooding, Table 3 and Fig. 3 show that there are two other main patterns: first, the seeds of *J. subulatus* do not present primary dormancy and

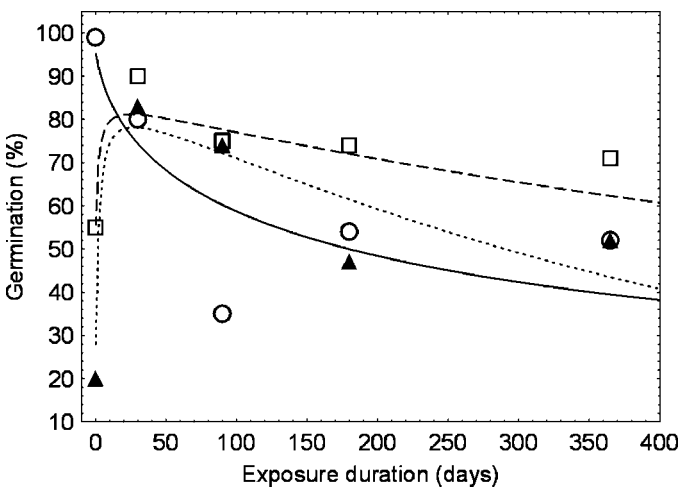


Fig. 3. Effect of flooding duration in nonsaline environment on seed germination for the three species studied. Both fitted models (lines) and observed (mean of four replicates) values are shown.

germinate at a very high percentage without the need for flooding. For this species, prolonged exposure to flooding markedly decreased germination.

In contrast, the *Scirpus* species present primary dormancy, and the seeds that are not exposed to wet conditions have very low germination, which increased considerably after a month of flooding (especially in the case of *S. litoralis*, which increased from 20 to 80% germination), but fell progressively after two mo of flooding (Fig. 3).

During the established individuals' "no-growth" season, the prevailing environmental conditions of the seed bank significantly affected the seed response during the germination process, once the ideal conditions were reestablished.

Although all these results are rather similar to those obtained by Keiffer and Ungar (1997) for different species (most of them annuals or biennials), in the present study, the duration that the seeds were flooded was a significant factor, explaining a considerable part of the variance obtained in the response during the experiment.

Could germination patterns help to explain zonation?—

We have found that the average relative position of a species germination dominance on a simulated environmental (flooding duration and salinity) plane significantly matches the observed average relative position, on a similar plane, of the same species cover dominance in the field, as is shown in Fig.

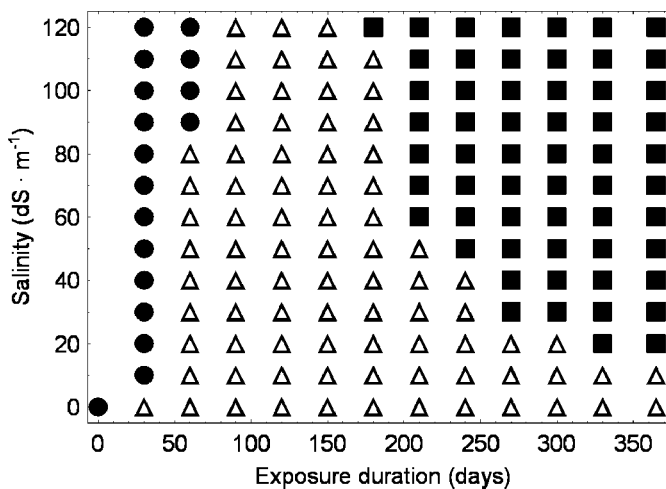


Fig. 4. Predicted distribution of germination maxima in the flooding duration/salinity plane. Symbols (circle: *Juncus subulatus*; square: *Scirpus litoralis*; triangle: *S. maritimus*) indicate the species having the maximum germination (after being placed in favorable conditions for 30 d) for each combination of exposure duration and salinity.

TABLE 4. Flooding/salinity data (mean ± SE) gathered from the three species habitats during the growth (N = 49) and dry (N = 24) seasons. Soil salinity was measured as the electrical conductivity (S) of soil saturation extracts. Means having the same letter were considered as not significantly different, after applying Tukey unequal-N post hoc test.

Habitat feature	<i>J. subulatus</i>	<i>S. maritimus</i>	<i>S. litoralis</i>
Flooding period (weeks)	19.2 ^a ± 0.4	26.6 ^b ± 0.6	28.3 ^b ± 0.6
Water salinity (growth season, dS · m ⁻¹)	5.4 ^a ± 0.3	3.4 ^b ± 0.2	3.1 ^b ± 0.2
Soil salinity (dry season, dS · m ⁻¹)	49.2 ^a ± 11.6	32.5 ^a ± 5.7	90.7 ^b ± 14
(g · L ⁻¹)	37.2 ^a ± 7.7	23.9 ^a ± 4.4	74.3 ^b ± 13

8, when salinity data corresponding to the nongrowth season were used. In fact, sites with dominance of any of the studied species and the end of the growth season are more easily separated using the environmental (salinity) data from the nongrowth season than using the data gathered during the germination/growth season.

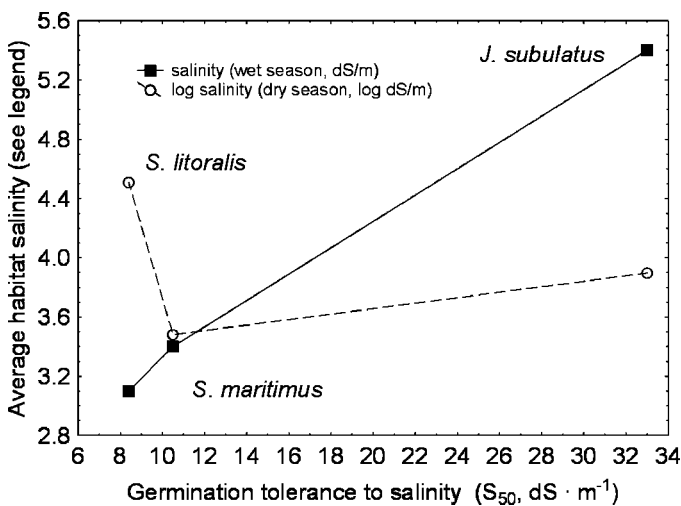


Fig. 5. Relationship between salinity tolerance of the germination process (S₅₀) and the average salinity values in water during the growth season (squares) or in soils during the dry season (circles), in habitats dominated by established individuals of each of the three species studied.

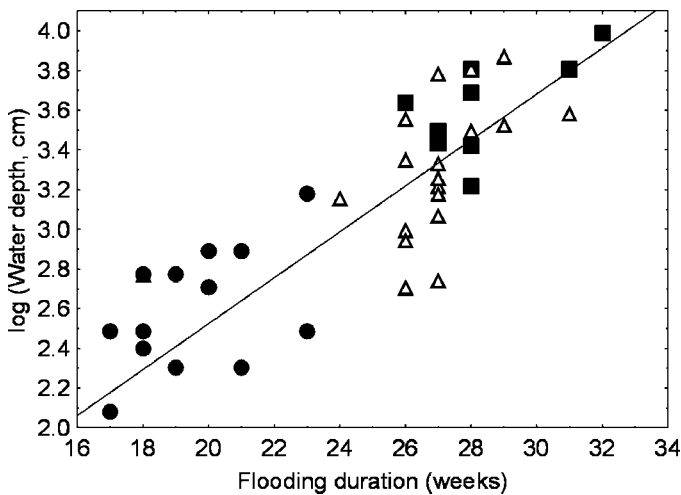


Fig. 6. Relationship between water depth (in cm, log scale) and water persistence (in weeks) at 40 sites having different dominant species. Symbols correspond to the dominant species (circle: *Juncus subulatus*; square: *Scirpus litoralis*; triangle: *S. maritimus*).

The seed storage conditions (flooding duration and salinity level during dormancy) seem to play a fundamental role in determining the seed response when germination conditions become ideal. The way in which particular environmental factors affect the seed bank during the period of dormancy could help to explain, at least at the establishment stage, the distribution patterns of the three species. Thus, the “environmental history” (salinity, flooding) of each site would decisively influence the outcome of the germination process, independently of the direct effect that these factors may have during the germination process itself.

Other important factors have been implicated in salt marsh plant zonation: facilitation (Bertnes and Callaway, 1994; Callaway, 1994; Castellanos et al., 1994), competition and its relative effect in areas with different physical stresses (Pennings and Callaway, 1992; Emery et al., 2001; Penning et al., 2003; Caitlin et al., 2004), and herbivory (Gough and Grace, 1998; Silliman and Zieman, 2001). But the results obtained in this work indicate that, at least in the studied species, salinity and flooding jointly exercise another type of population control, acting on the seed bank (as well as on the germination process), thereby constituting control mechanisms coupled with annual fluctuations in two very important environmental variables.

As indicated by Seabloom et al. (2001), in very dynamic environments the composition of the community results from

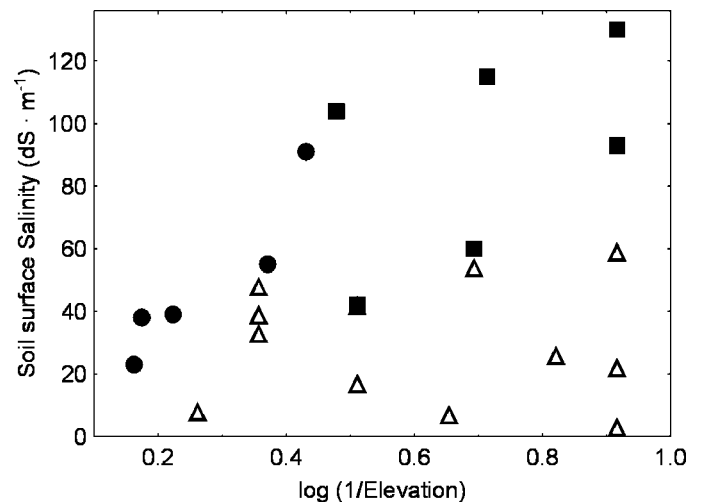


Fig. 7. Distribution of dominance among established individuals of the three studied species, across the soil-salinity/flooding plane during the nongrowth season. Soil salinity is given as the electrical conductivity (in dS · m⁻¹) of the surface soil (0–5 cm) saturation extract. Elevation was expressed in meters before log calculation. Log (1/elevation) is used as a proxy for the duration of the flooding (see Fig. 6). Symbols correspond to the dominant species at each site (circle: *Juncus subulatus*; square: *Scirpus litoralis*; triangle: *S. maritimus*).

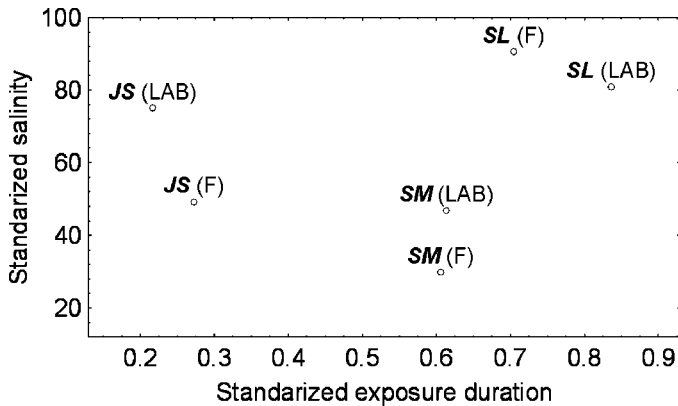


Fig. 8. Projection of the average location of species (JS, SM, and SL) dominance on a standardized exposure/salinity plane. Data are shown for both field conditions of the established individuals (F) and the simulated germination maxima (LAB) of the three species (JS, *Juncus subulatus*; SL, *Scirpus litoralis*; SM, *S. maritimus*). Field and lab-simulated exposure and duration axes were standardized—to compare the relative species positions on a common plane—by matching the minimum values of the two scales and by stretching the log-transformed laboratory-simulated exposure values, to match the range of the corresponding log-transformed field values axis. The salinity axis was not changed, because the laboratory-simulated and the field conductivity ranges were the same. When a two-way MANOVA was applied—using standardized exposure duration/salinity data as dependent variables, and species identity and nature of the species dominance data (germination-laboratory or established individuals-field) as independent factors—a highly significant segregation of species dominance across the exposure/salinity plane was found (Wilks lambda = 0.25, $F = 11.4$, $P < 10^{-5}$), while no significant differences were found between the average location of species dominance in field and laboratory data (Wilks lambda = 0.98, $F = 0.21$, $P = 0.82$).

the balance between the current environmental conditions and historical processes involved in the establishment of the species. The seed bank in the soil seems to integrate with, and respond to, the corpus of information regarding the abiotic characteristics most limiting for seedling survival (salinity and time of flooding).

Implications for management and ecological restoration—

Given the high degree of fit between the germination of these species and the values of salinity and flooding (during both germination and seed dormancy), it is probable that certain variations in the medium that modify the two environmental factors (or certain actions of ecological restoration that alter soil salinity or the duration of flooding) first affect the processes related to sexual regeneration of the populations, mainly by cumulative effects on the seed bank. Although the perennial nature of the species does not make annual recruitment of new individuals “essential” for population maintenance, sustained environmental changes can age the population, making the processes of regeneration exclusively asexual, with consequent implications for the populations (reviewed in Stearns, 1987). This factor has to be taken into account in the management and restoration of Mediterranean wetlands that may alter the hydrology and salinity regimen; activities that have no apparent effect on the established individual but may affect its seed bank.

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