

Seed bank dynamics of the annual halophyte *Salicornia ramosissima*: towards a sustainable exploitation of its wild populations

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Abstract

Halophytes are able to survive in the high salted areas of the world, and have been recognized as sources of bioactive metabolites. There is a need to design sustainable strategies for the use of wild populations of halophytic species in order to avoid irrational gathering. Seed banks are essential for resilience and regeneration in salty ecosystems. We sampled annual seed production, aerial and soil seed banks and seed dynamics for a year in four wild populations of the annual halophyte *Salicornia ramosissima* growing in salt pans, in order to develop sustainable management practices for the use of its populations. The seed production of *S. ramosissima* depended mainly on plant density rather than on the number of seeds produced by each individual plant. In three of the four study populations, most of the annual seed production was exported out of the salt pans (> 79%) and only between 14–20% was accumulated in the initial aerial and soil seed banks. These initial seed banks were highly depleted during the year until the next fruiting period, when they accumulated less than 1% of the annual seed production (from 19 to 15302 seed m⁻²). *Salicornia ramosissima* established a persistent soil seed bank in two of the four locations. Annual seed production would be key for the preservation of those *S. ramosissima* populations that do not establish persistent soil seed banks. In view of our results, each population of *S. ramosissima* should be studied independently to design population-specific management plans.

Introduction

Salt-tolerant plants (halophytes) have been traditionally used as healthy and functional foods and medicines for human and animals (Marinoni et al. 2019; EINaker et al. 2020). More recently, various halophyte species have been recognized as sources of bioactive primary and secondary metabolites of pharmacological, cosmetic, bio-fuel and nutraceutical interest (Debez et al. 2017, Petropoulos et al. 2018; Faustino et al. 2019).

Salt stress negatively affects soil fertility, causing land degradation. In fact, drought and soil salinity are the main factors responsible for crop yield reduction in the present scenario of climate change and sea level rise (Alae-Carew et al. 2020). Nevertheless, halophytes are able to survive in the high salted areas of the world inhabited by an ever-growing number of people (Fita et al. 2015). In this context, halophyte cultivation would seem to be cheaper than other commercial crops, and can yield industrial value, remediate nutrient-rich effluents from aquaculture, and rehabilitate lands through soil desalination (Custodio et al. 2017; Nikalje et al. 2018). Besides 'saline agriculture', wild populations of halophytes can be exploited as sources of 'wild food', but very few studies have analyzed the key ecological aspects of halophytes in the development of sustainable management practices (Godfray et al. 2010). Most studies have focused on analyzing the traditional uses of wild halophyte populations by local people and their bioactive properties (Pereira et al. 2020). Since people have become aware of the potential of some halophytes as part of a healthy diet, their natural growth sites are now threatened in some locations (Nae-Kyu and Lee, 2012). Thus, there is a need to design sustainable strategies for the use of wild populations of halophytic species in order to avoid irrational gathering and genetic erosion threats.

Halophytes colonize saline environments, such as salt marshes, where soil salinity determines plant distribution, as high salinity conditions affect seed survival and germination (Ungar 1987). Salinity reduces germination and stimulates dormancy in halophyte seeds (Pujol et al. 2000). Some plant species survive in unfavorable environmental conditions in saline environments by building on persistent seed banks (> 1 year). Other plant species have transient seed banks (< 1 year) as the result of high and rapid germination and/or because their seeds quickly die in the soil (Walck et al. 2007; Parsons 2012). The reserves of mature viable seeds in the form of seed banks can be repositories of genetic information located on the plants (aerial seed bank) and in the soil (soil seed bank) (Roberts 1981). Germination from halophyte seed banks occurs mainly during germination windows, when soil salinity decreases after rainfalls (Gul and Weber 2001; Noe and Zedler 2001). So, seed banks are essential for resilience, secondary succession and regeneration in salty ecosystems (Honnay et al. 2007). Seed banks may be especially important for the long-term preservation of annual halophytes that may be absent in the above-ground vegetation and present in the seed bank waiting for favorable conditions (Egan and Ungar 2000).

Amaranthaceae (formerly known as Chenopodiaceae) is one of the most represented families of halophytes, with many species that are well known as plants of pharmacological and nutraceutical interest (Lefevre and Riviere 2020). Specifically, the species of the genus *Salicornia* L. have a broad geographical distribution and are among the most frequent halophytes with pharmacological and culinary uses. An array of functional nutrients has been detected in *Salicornia* species, justifying its usage as a 'sea vegetable' (Patel 2016). *Salicornia ramosissima* J. Woods is an annual extremophile halophyte that presents apparently leafless, succulent and articulated stems (Valdés, 1987). *Salicornia ramosissima* colonizes European and North African salt marshes occurring in a whole range of salt marsh habitats, such as saltpans, where it germinates during winter-spring and dies off during autumn-winter (Davy et al. 2001). *Salicornia ramosissima* plants are fit for human consumption (Lima et al. 2020) and are useful for the ecological restoration of saline areas (Santos et al. 2017). The germination of this annual halophyte decreases at salinities higher than 0.2 M NaCl and is rapidly activated after salinity release (Rubio-Casal et al. 2003; Muñoz-Rodríguez et al. 2017). Although seed banks play a significant role in the optimum development of *S. ramosissima* populations (Egan and Ungar 1999; Silva et al. 2007; van Regteren et al. 2019), no study has analyzed in detail the aerial and soil seed banks of any *Salicornia* species and their seasonal dynamics.

Our main goal was to analyze *S. ramosissima* seed bank size and dynamics to help to design sustainable exploitation strategies of wild populations. We hypothesized that annual seed production of *S. ramosissima* would be very high, contributing to the establishment of large and permanent soil seed banks in each population. To test this hypothesis, we sampled annual seed production, aerial and soil seed banks and seed dynamics for a year in different populations of *S. ramosissima* colonizing saltpans. Based on our results, we propose sustainable management practices for the use of wild populations of *Salicornia* as biomass sources.

Materials And Methods

Study area

The present study was carried out in tidal marshes in the Odiel Marshes Natural Park (37°12'32.3" N, 6°58'01.5" W, Gulf of Cádiz, Southwest Iberian Peninsula) (Online Resource 1 – Fig. S1). Mean tidal range is 2.10 m and mean spring tidal range is 2.97 m in the Odiel Marshes. The semidiurnal tides can lead to hypersalinity in some mature marshes (Castellanos et al. 1994). The Odiel Marshes are subjected to a Mediterranean climate with Atlantic influence. Mean temperatures are + 17–24 °C, and annual precipitation is 250–850 mm with 75–85 days of rain during the autumn and winter months, and a 4–5 month dry period from approximately June – September (AEMET, 2018), when potential evapotranspiration exceeds precipitation.

Saltpans are frequent in salt marshes in a Mediterranean climate. They are depressed areas with high salinity concentrations located at high salt marsh zones, where hypersalinity excludes colonization by most plant species (Rubio-Casal et al., 2001). Saltpans are the main habitat of *S. ramosissima* together with low marshes (Rubio-Casal et al. 2001; Contreras-Cruzado et al. 2017). We studied four populations of *Salicornia ramosissima* colonizing four different saltpans: Population 1 (P1) was located at a pond of an abandoned salt mine with no drainage to tidal channels, where *S. ramosissima* colonized the periphery of a central unvegetated mud flat, just below the halophilous scrubby vegetation growing on the pond's containment dams (37°15'41.6" N, 6°58'35.54" W); Population 2 (P2) (37°13'39.63" N, 6°57'46.52" W) and Population 3 (P3) (37°13'34.74" N, 6°57'50.54" W) were colonizing the sediments surrounding the bare central areas of saltpans inundated during spring high tides. The halophilous scrub vegetation occupied higher elevations than *S. ramosissima* in the saltpans; Population 4 (P4) was located along drainage channels in a saltpan with dense scrub vegetation (37°13'33.09" N, 6°57'52.87" W) (Fig. S1). Three zones were differentiated in each study location to analyze the dispersal of *S. ramosissima* seeds within saltpans: 1) unvegetated sediments at the lowest elevations of the saltpan; 2) sediments colonized by monospecific communities of *S. ramosissima*; and 3) sediments colonized by halophilous scrubs, such as *Arthrocnemum machrostachyum* (Moric.) C. Koch, *Limoniastrum monopetalum* (L.) Boiss. and *Atriplex halimus* L., at the highest elevations of the saltpans (Online Resource 2, Fig. S2). Plants species were identified following Valdés et al. (1987).

Sedimentary environment

We collected three sediment samples in each of the three zones of the four study saltpans in October 2017. Sediment samples were collected randomly using stainless steel cores of 50 mm diameter and 50 mm height. Samples were placed in hermetically closed polyethylene bags and stored at – 5 °C until analysis in the laboratory. Sediment electrical conductivity was used as a measure of soil salinity (Richards 1974). From each sample, a mix of 10 ml of sediment and distilled water (1:1, v:v) was homogenized, and the conductivity measured in the unfiltered supernatant with a conductivity meter (Crison Instruments 5064, Hach Lange, Barcelona, Spain). Sediment pH was measured in the same unfiltered supernatant used for conductivity, using a pH meter (Crison 25, Hach Lange, Barcelona, Spain)

(Nieva et al. 2001). Sediment water content was gravimetrically determined using samples of 30 g of sediment (Contreras-Cruzado et al. 2017). Sediment organic matter content was determined by the loss-on-ignition method. Organic matter content was calculated as the proportion of weight lost compared to the weight of the dry sample before incineration (Gavlak et al. 2005).

Annual seed production

Live plant density at the end of the flowering period of *S. ramosissima*, when the vast majority of the plants had ripened fruits, was recorded by counting the total number of live plants in 10 randomly-chosen plots (20 x 20 cm) inside the *S. ramosissima* zone in each population at the same time that sediment samples were collected in P1, P2 and P3, and in November 2017 in delayed P4; withered plants from the previous flowering period were not counted. Seed production per plant was recorded for 30 randomly-collected plants in each population. The production of seeds per plant was calculated in the laboratory using two methods. For small plants (with less than 50 seeds), we counted all their seeds under optical microscope. For large plants (with more than 50 seeds), we separated all the branches from the principal axis and weighed them. Then, three randomly-chosen branches were weighed individually and their total number of seeds counted under optical microscope. The seed production per plant was calculated as the product between the quotient of seeds per weighed unit and the total weight of the braches for each plant. Annual seed production per plot was calculated as the product between plant density and seed production per plant. Finally, we calculated mean annual seed production per square meter in each population.

Aerial seed bank

The aerial seed bank, or storage of seeds on the plants after seed dispersal, was studied at two moments. The initial aerial seed bank included seeds retained by current year plants, and it was recorded just after current seed dispersal in November 2017 for P1, P2 and P3, and in December 2017 for P4. The remnant aerial seed bank included seeds retained by plants just before the seed dispersal of the next flowering period, and it was recorded in October 2018 for each population (Fig. 1). In both cases, we calculated the number of seeds retained per plant following the same methodology reported previously for annual seed production. The initial aerial seed bank was calculated using the density of live plants, and the remnant aerial seed bank was obtained using the density of withered plants from the previous flowering period that still remained in the population (Fig. 1).

Soil seed bank

The soil seed bank was studied at two moments: the initial soil seed bank, just after current seed dispersal (recorded in October 2017 for P1, P2 and P3, and in November 2017 for P4), and the remnant soil seed bank, just before the seed dispersal of the next flowering period (recorded in October 2018 for each population) (Fig. 1). In each sampling, we randomly took 10 sediment samples per zone (unvegetated, *S. ramosissima* and scrub zones) at the four study saltpans using stainless steel cores of 50 mm diameter and 50 mm height. Sediment samples were placed in polyethylene bags, hermetically

sealed and transported to the laboratory for analysis. In the laboratory, the sediment samples were frozen until analyzed. Dry sediment samples were sieved through a 0.4 mm-light sieve to separate the seeds from sediments, and the material retained on the sieve was examined under a magnifying glass (Polo-Ávila et al. 2019).

Seed dynamics

We calculated the percentage of the annual seed production incorporated into initial aerial and soil seed banks at the *S. ramosissima* zone, into the soil seed bank in adjacent vegetation zones and dispersed out of the study salt pans. The annual loss of aerial and soil seed banks was calculated as a percentage of seeds in the initial seed banks not present in the remnant seed banks (Fig. 1).

Data analysis

Data were analyzed using Statistica 8.0 (StatSoft INC., USA). Deviations from the arithmetic means were calculated as standard error (SE). Significant differences were considered when $p < 0.05$. Data series or their transformations (using $\log(x + 1)$, $1/(x + 1)$ or \sqrt{x} functions) were tested for homogeneity of variance and normality with the Levene test and the Kolmogorov Smirnov test, respectively. Data series were compared between populations or vegetation zones using a one-way ANOVA and Tukey's test as *post hoc* analysis. When transformed data series did not show a normal distribution or homogeneity of variance, they were analyzed using the Kruskal-Wallis (H) and Mann-Whitney U tests with population or vegetation zones as grouping factors. The non-parametric Spearman correlation coefficient (ρ) was used to analyze the relationships between annual seed production and seed bank characteristics.

Results

Sedimentary environment

P1 showed the highest electrical conductivity, at 70% higher than that recorded for P4 ($F_{3,11} = 33.415$, $p < 0.0001$) (Fig. 2A). By contrast, sediment pH reached its highest value in P4, and its lowest value in P2 and P3 ($H_{3,36} = 25.04$, $p < 0.0001$; U-test, $P < 0.05$) (Fig. 2B). There were no significant differences for sediment water or organic matter content between populations (water content: $F_{3,11} = 1.258$, $p = 0.352$; Organic matter content: $H_{3,12} = 5.760$, $P = 0.124$) (Fig. 2C,D).

Annual seed production

Live plant densities ranged from 330 ± 47 plants m^{-2} for P3 to 3610 ± 1018 for P4 ($H_{3,40} = 18.46$, $p < 0.0005$; U-test, $P < 0.05$) (Fig. 3A). Seed production per live plant did not show significant interpopulation differences ($H_{3,120} = 3.72$, $p = 0.293$) (Fig. 3B). Annual seed production ranged from 48743 ± 6937 seed m^{-2} for P3 to 2179383 ± 614577 seed m^{-2} for P4 ($H_{3,40} = 24.68$, $p < 0.0001$; U-test, $P < 0.05$) (Fig. 3C).

Aerial seed bank

The number of seeds retained by each *Salicornia* plant just after current dispersal was lower for P2 (7 ± 3 seed plant⁻¹) than for the other 3 populations (c. 50 seed plant⁻¹) ($H_{3,120} = 24.56$, $p < 0.0001$; U-test, $P < 0.05$) (Fig. 3B). The initial aerial seed bank varied between 2848 ± 700 seed m⁻² for P2 and 298645 ± 84217 seed m⁻² for P4 ($H_{3,40} = 30.07$, $p < 0.0001$; U-test, $P < 0.05$) (Fig. 3C), increasing together with the density of the live plants ($\rho = +0.738$, $p < 0.0001$, $n = 40$) and their annual seed production ($\rho = +0.678$, $p < 0.0001$, $n = 40$).

The density of remnant dead plants from the previous year was lowest for P2 and P3 (c. 400 plant m⁻²) and highest for P4 (1570 ± 533 plant m⁻²) ($H_{3,40} = 8.54$, $p < 0.05$; U-test, $P < 0.05$) (Fig. 3A). Seeds retained by these dead plants were lower than 0.1 seed plant⁻¹ for P1 and P3, and reached its maximum (9.75 ± 3.23 seed plant⁻¹) in P4 ($H_{3,120} = 39.50$, $p < 0.0001$; U-test, $P < 0.05$) (Fig. 3B). The remnant aerial seed bank changed from c. 25 seed m⁻² for P1 and P3 to 15302 ± 5196 seed m⁻² for P4 ($H_{3,40} = 29.14$, $p < 0.0001$; U-test, $P < 0.05$) (Fig. 3C), increasing together with the density of the remnant plants ($\rho = +0.639$, $p < 0.0001$, $n = 40$).

Soil seed bank

The initial soil seed bank in *S. ramosissima* zones was similar for each population ($H_{3,120} = 1.98$, $p = 0.577$), whereas the remnant soil seed bank tended to be higher at P1 and P2 (c. 350 seed m⁻²) than at P3 and P4, where no seed was recorded ($H_{3,120} = 7.53$, $p = 0.057$) (Fig. 4). In the four study salt pans, the initial soil seed bank was highest in the zone colonized by *S. ramosissima*, but while it was significantly different to that reached in the two other zones for P2 and P4, it was similar to that in the adjacent soils colonized by halophyllous scrubs for P1 and P3 (P1, $H_{2,30} = 11.21$, $p < 0.005$; P2, $H_{2,30} = 20.16$, $p < 0.0001$; P3, $H_{2,30} = 8.75$, $p < 0.05$; P4, $H_{2,30} = 19.72$, $p < 0.0001$) (Fig. 4). In contrast, the remnant soil seed bank was similar in each vegetation zone at every study salt pan, always lower than 500 seed m⁻² (Kruskal-Wallis test, $P > 0.05$) (Fig. 4).

Seed dynamics

The percentage of the annual seed production retained in the initial aerial seed bank ranged from 2.91% for P2 to 75.93% for P3. The seeds accumulated in the initial soil seed bank varied from 0.36% for P4 to 17.10% for P2. Less than 1.00% of the annual seed production was dispersed from *S. ramosissima* zones to other zones in the study salt pans for each population. Predation and dispersal out of the salt pans were between 18.60% (P3) and 85.93% (P4) of the annual seed production (Fig. 5).

The percentage of the initial aerial seed bank predated and dispersed from the plants throughout the year ranged from c. 71.84% for P2 and P4 to c. 99.87% for P1 and P3 ($H_{3,40} = 19.8$, $p < 0.0001$; U-test, $P < 0.05$). Thus, the percentage of seeds retained in the remnant aerial seed bank was always lower than 0.10% of the annual seed production, ranging from 19 to 15302374 seeds m⁻² (Figs. 3 and 5). The percentage of seeds depleted from the initial soil seed bank during the year ranged from c. 92.55% for P1 and P2 to

100% for P3 and P4 ($H_{3,40} = 8.2$, $p = 0.043$; U-test, $P < 0.05$; U-test, $P < 0.05$). These percentages corresponded to less than 0.35% of the annual seed production for each population, varying from 0 to 407 seeds m^{-2} (Figs. 4 and 5).

Discussion

Our results show that the seed production of the annual halophyte *S. ramosissima* depends mainly on plant density rather than on the number of seeds produced by each individual plant. In three of the four study populations, most of the annual seed production was exported out of the saltpans ($> 79\%$), and only between 14–20% was accumulated in the initial aerial and soil seed banks. These initial seed banks were highly depleted during the year until the next fruiting period, when they accumulated less than 1% of the annual seed production (from 19 to 15302 seed m^{-2}). In fact, *S. ramosissima* established a persistent soil seed bank in only two of the four populations. In this context, annual seed production would be key for the preservation of those *S. ramosissima* populations that do not establish persistent soil seed banks.

We recorded high annual seed production (> 48000 seed m^{-2}) for *S. ramosissima* growing in the harsh environmental conditions of saltpans marked by high sediment salinities (16–63 ppt). High salinity induces *S. ramosissima* seed dormancy without affecting seed viability (Rubio-Casal et al. 2003; Muñoz-Rodríguez et al. 2017). According to Davy et al. (2001), plant density varies greatly among *Salicornia* populations, regulated by a combination of density-dependent seed production and density-independent seedling mortality due to high levels of morphological phenotypic plasticity. In our study, annual seed production increased with the density of individual plants regardless of the seed production per individual plant, which was similar for each population. In fact, the highest seed production per individual plant (604 seeds $plant^{-1}$) was obtained for the population with the highest plant densities (3610 mature plants m^{-2}), and the lowest salinity (P4), resulting 2179383 ± 614577 seeds m^{-2} . This was probably due to the low plant densities recorded in our populations in relation to other studies that have reported close to 30000 mature plants m^{-2} (Davy et al. 2001).

The seed dynamic changed markedly between *Salicornia* populations. For example, between 14.1 and 80.5% of the annual seed production (19603–306539 seeds m^{-2}) was stored in aerial and soil seed banks. The initial aerial seed bank was larger than the initial soil seed bank in three of the four study populations, accumulating more than 2800 seeds m^{-2} in each population. Aerial seed banks help seed dispersal over time, and may protect seeds from being predated in the soil (Santini and Martorell 2013) and from unfavorable soil conditions such as high salinities (El-Keblawy and Bhatt 2015). Between 71.8–99.8% of the initial aerial seed bank was dispersed or predated during the first year, whereas the initial soil seed bank was totally depleted in two of the four study populations. The remnant aerial seed bank also increased together with the density of plants, storing between 19 and 15302 seeds m^{-2} in different populations. Thus, between 19.5–85.9% of annual seed production was predated and exported out of *Salicornia* populations just after seed dispersal. *Salicornia ramosissima* shows a short-distance dispersal strategy since its seeds have hooker hairs that help them to anchor to sediments and vegetation (Polo-

Ávila et al. 2019). *Salicornia* seeds disperse mostly on the soil surface since they float for less than one day (Huiskes et al. 1995). Genetic analyses have shown a strong tendency to inbreeding as a result of a lack of seed immigration from outside *Salicornia* populations (Davy et al. 2001). These previous observations together with our results, which show that less than 0.9% of the annual seed production was dispersed from *Salicornia* populations to adjacent zones in each study saltpan, suggest that predation would be more important than seed exportation in study populations.

Polo-Ávila et al. (2019) stated that *S. ramosissima* establishes persistent seed banks, but we recorded that the soil seed bank was drastically reduced, even totally depleted, during the first year after seed dispersal. This result is in line with Jefferies et al. (1981), who recorded the depletion of the seed bank of *Salicornia europaea* L. in the middle of the first summer following dispersal. The depletion of *S. ramosissima* seeds from its soil seed bank may be related to its high and fast germination during favorable conditions (Parson 2012), and to seed predation recorded in different *Salicornia* species (Davy et al. 2001). Under the Mediterranean climate, soil salts are washed during autumn and winter rainfalls, which interrupts dormancy and favors germination (Vleeshouwers et al. 1995). Tessier et al. (2000) recorded the absence of a persistent seed bank for the annual species *Suaeda maritima* (L.) Dumort. due to very high germination during low salinity periods. The transitory condition of the soil seed bank for some *S. ramosissima* populations recorded in our study is in accordance with previous studies on different *Salicornia* species (Philipupillai and Ungar 1984; Thompson et al. 1997; Wolters et al. 2002; Rubio-Casal et al. 2003).

Conclusions

In view of our results, each wild population of *S. ramosissima* should be studied independently to design population-specific management plans for sustainable exploitation. For example, the establishment of a large persistent soil seed bank on some populations enables the collection of high percentages of adult plants (c. 70–95% of the total population; 233–415 plants m⁻²), ensuring the formation of an initial soil seed bank with double the number of seeds than the recorded number of mature plants. In contrast, plant collection should be limited to 9% of the mature plants (c. 308 plants m⁻²) in other populations to achieve the same goal. In any case, more than 230 plants m⁻² could be extracted from each study population, ensuring the formation of an initial soil seed bank with double the number of seeds than the recorded number of mature plants (Online Resource 3, Table S1). In addition, reintroduction experiments by sowing *S. ramosissima* seeds should be carried out in parallel with studies on the sustainable harvesting of *S. ramosissima* in order to create new populations and reinforce currently existing populations, as reported for *S. europaea* (Nae-Kyu and Lee 2012).

Declarations

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Ethics approval - Not applicable.

Consent to participate All authors participated in this manuscript.

Consent for publication All authors revised the manuscript critically and approved the final manuscript for publication.

Availability of data The *data* that support the findings of this study are *available on request* from the *corresponding author*.

Code availability - Not applicable.

Authors' contributions AP, AFMR and JMC conceived and designed the study. AP, AF, MDII, FJJN and AFMR collected samples. Plant and soil analyses were carried out by AP, AF, MDII, FJJN. AP, AFMR and JMC conducted the statistical analyses. AP, AFMR and JMC wrote the manuscript.

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Figures

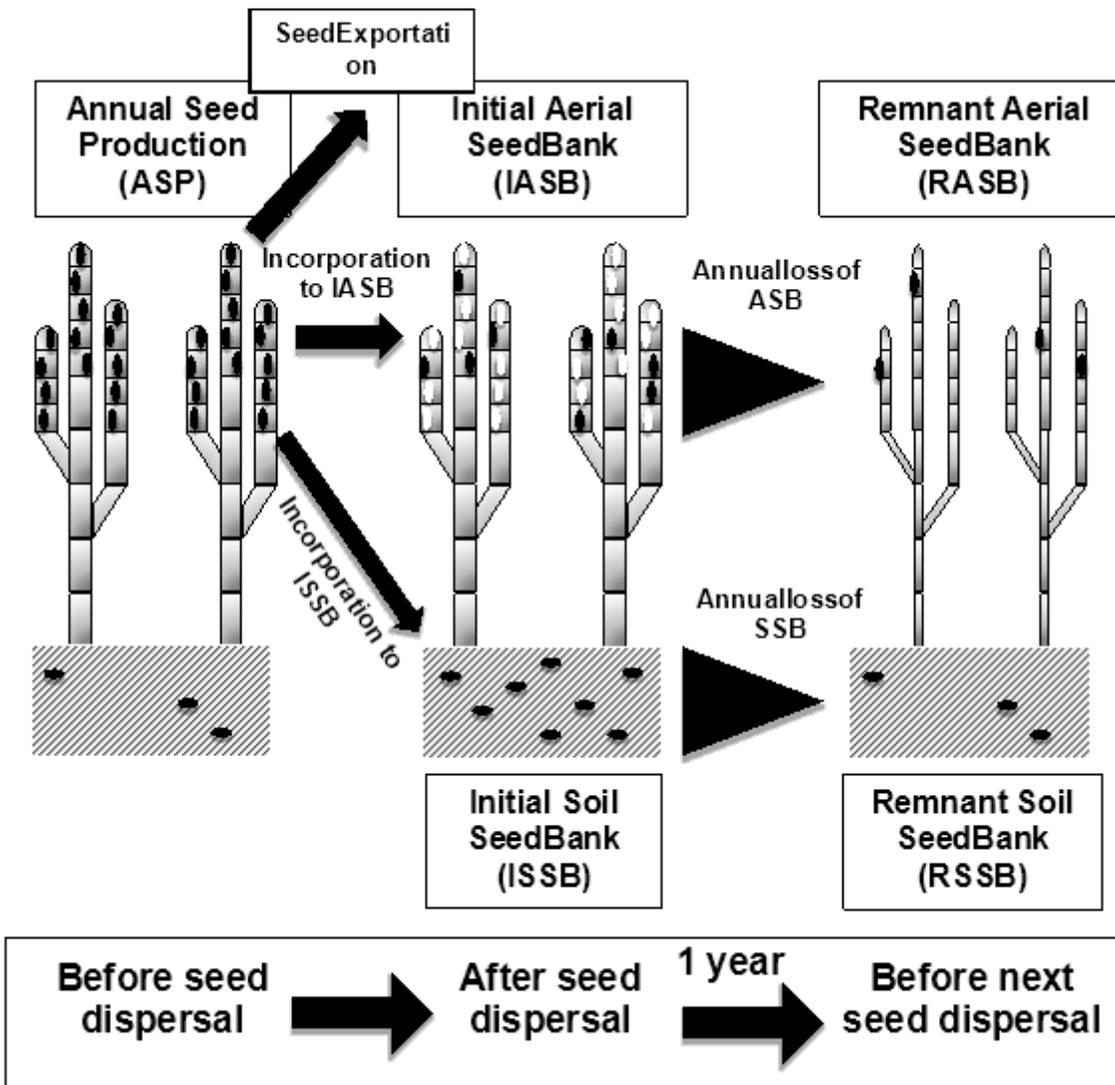


Figure 1

Schematic representation of the dynamics of seed production in *Salicornia ramosissima*, and of aerial and soil seed banks from the moment before seed dispersal to the same moment of the next flowering period

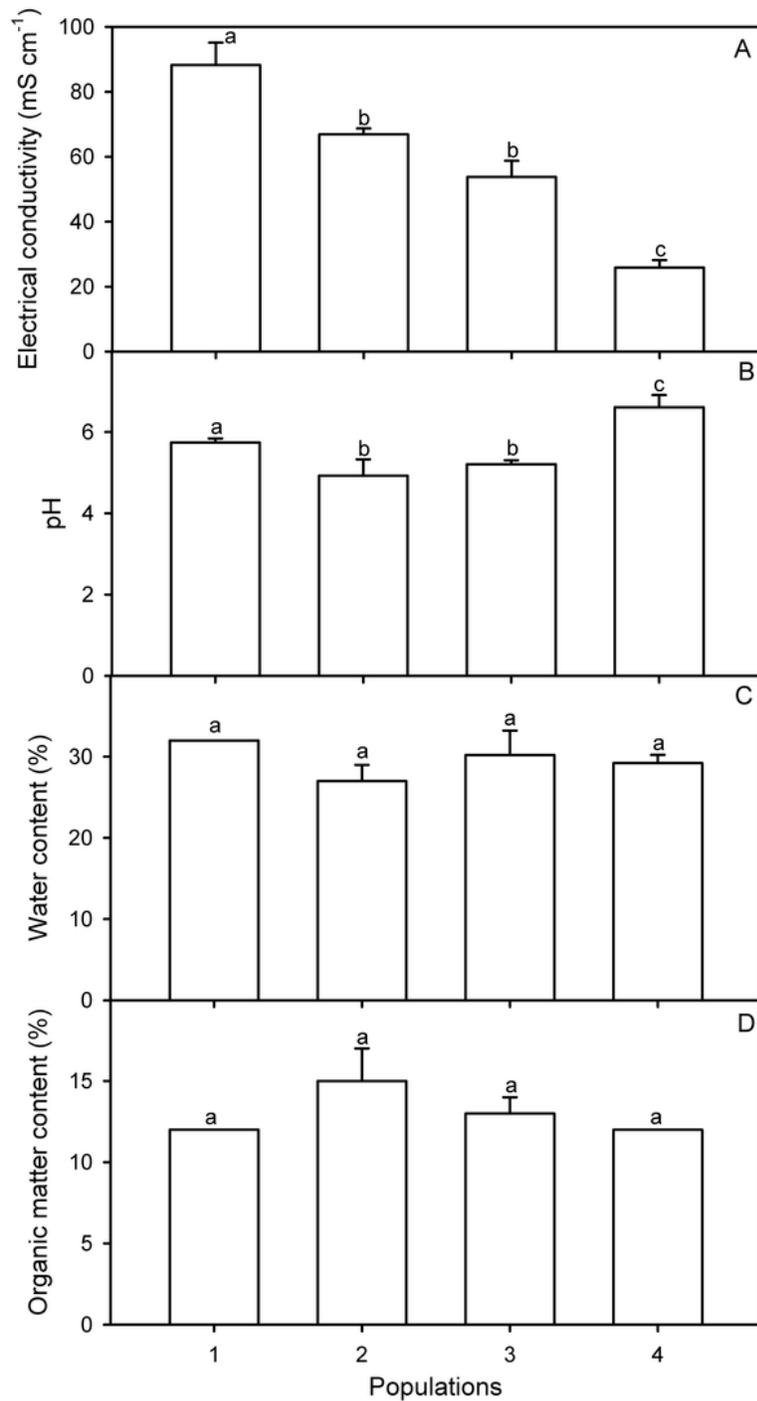


Figure 2

Sediment electrical conductivity (A), pH (B), water content (C), and organic matter content (D) in four *Salicornia ramosissima* populations colonizing salt pans in the Odiel Marshes (Southwest Iberian Peninsula). Different letters indicate significant differences between populations (Tukey test or Mann-Whitney test, $p < 0.05$). Data are mean \pm SE ($n = 3$)

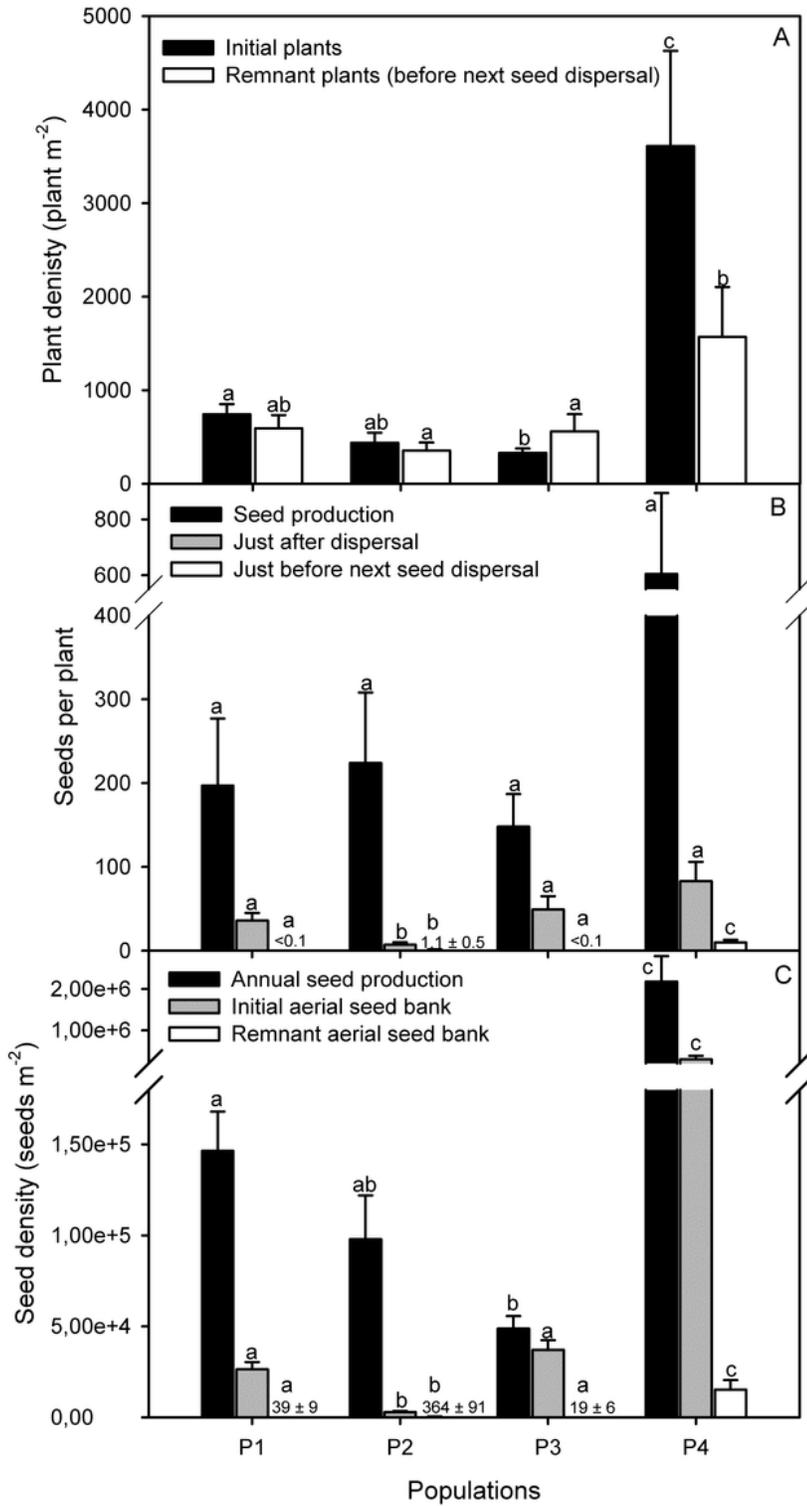


Figure 3

Plant density (A), seed production and number of seeds per plant (B), and annual seed production and aerial seed banks just after seed dispersal and just before next seed dispersal for four populations of *Salicornia ramosissima* (P1-4) colonizing salt pans in the Odiel Marshes (Southwest Iberian Peninsula). Different letters indicate significant differences between populations for the same trait (Mann-Whitney test, $p < 0.05$). Data are mean \pm SE ($n = 10$)

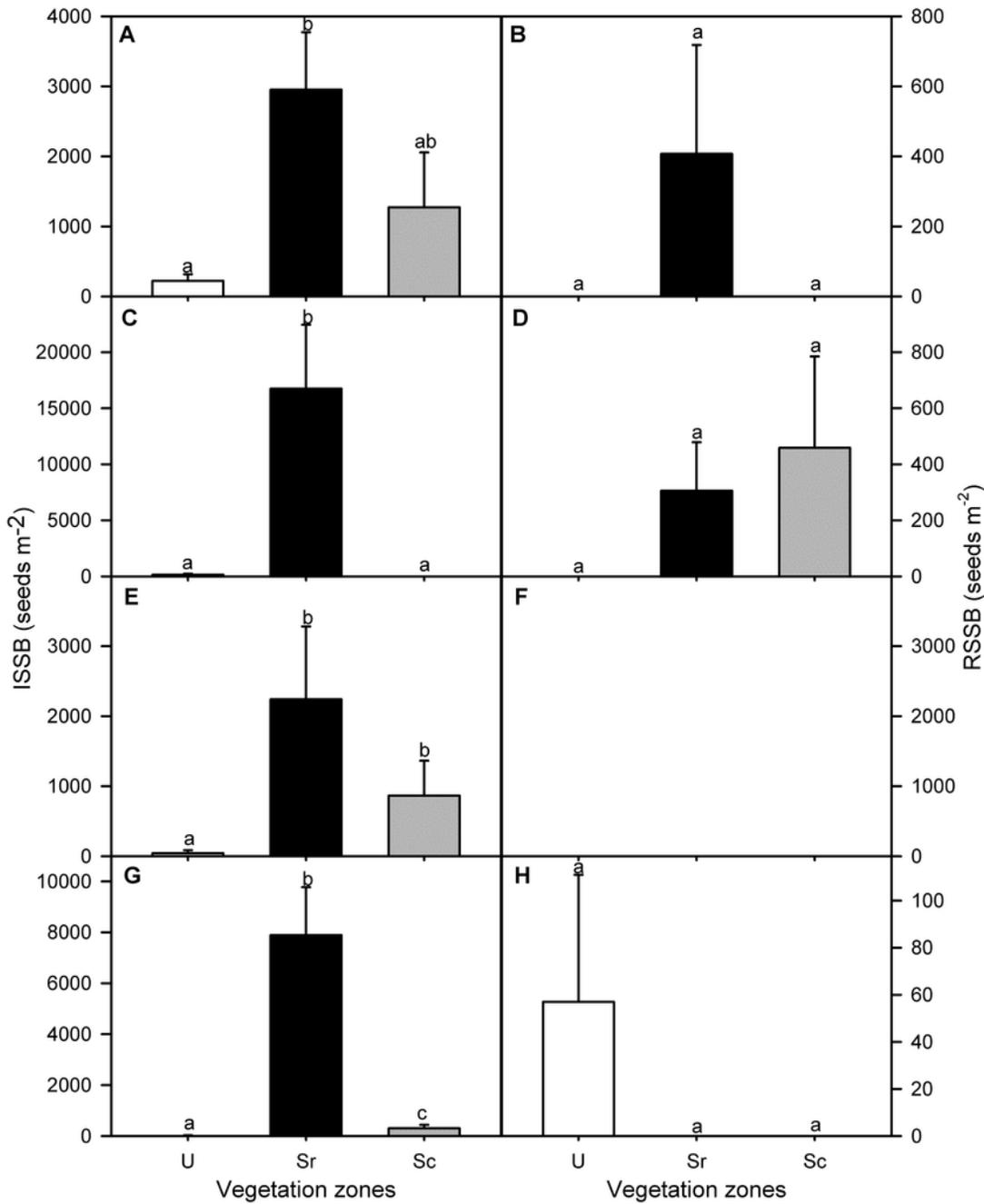


Figure 4

Initial soil seed bank (ISSB) and remnant soil seed bank (RSSB) densities in three vegetation zones (U, unvegetated (white columns); Sr, *S. ramosissima* (black columns); Sc, scrubs (grey columns)) for four *Salicornia ramosissima* populations (P1 (A, B), P2 (C, D), P3 (E, F), P4 (G, H)) growing in saltpans in the Odiel Marshes (Southwest Iberian Peninsula). Different letters indicate significant differences between vegetation zones (Mann-Whitney test, $p < 0.05$). Data are mean + SE ($n = 10$)

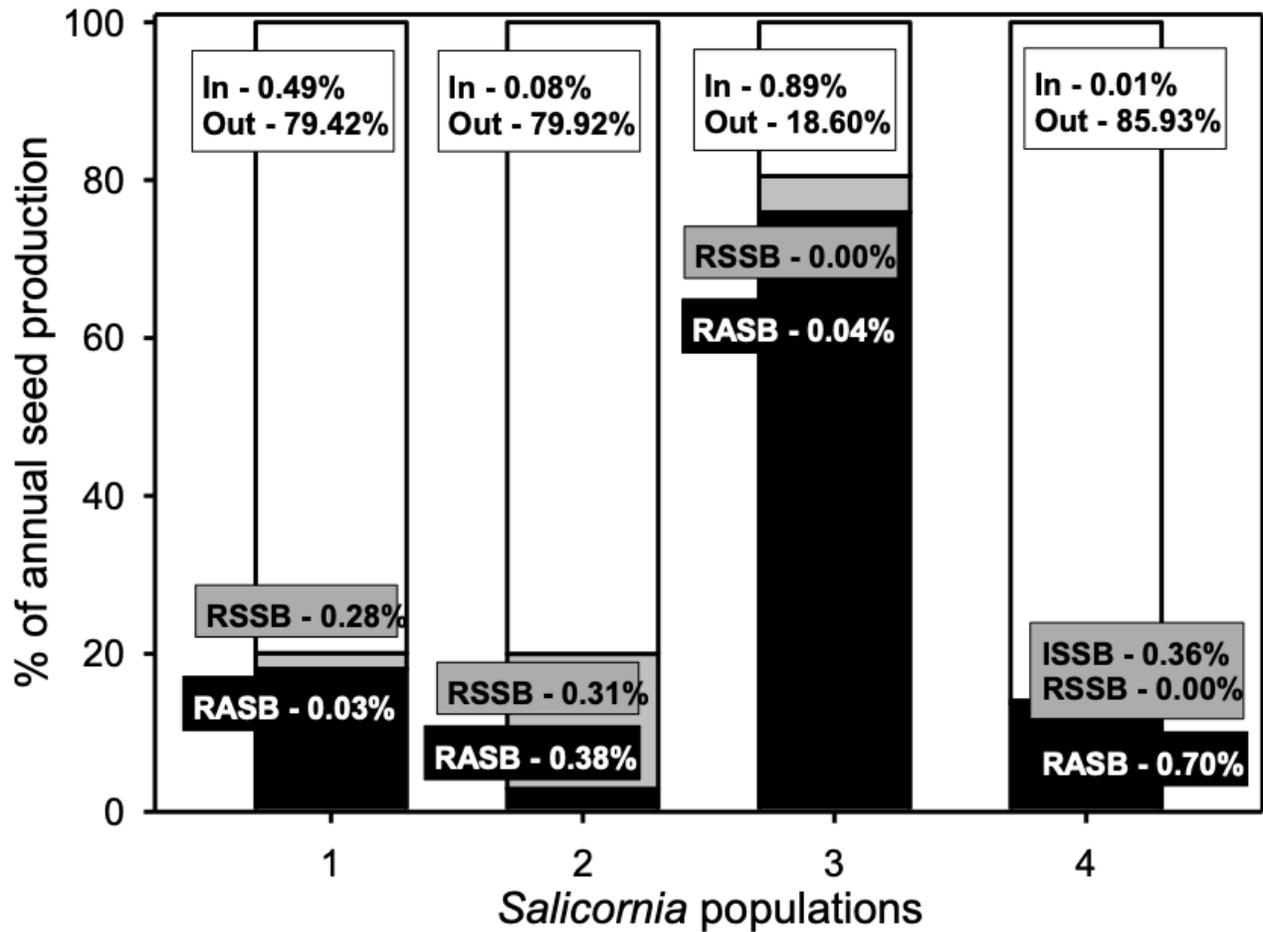


Figure 5

Percentages of annual seed production accumulated in the initial aerial seed bank (black), remnant aerial seed bank (RASB), initial subterranean seed bank (ISSB; grey), remnant soil seed bank (RSSB), total exported (white), exported within salt pans (In), and predated and exported out of salt pans (Out) from four populations of *Salicornia ramosissima* (P1-4) in the Odiel Marshes (Southwest Iberian Peninsula). Data are mean (n = 10)

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