



## Temporal and spatial patterns of airborne pollen dispersal in six salt marsh halophytes



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### ARTICLE INFO

#### Article history:

Received 23 July 2021

Received in revised form 31 March 2022

Accepted 5 April 2022

Available online 12 April 2022

#### Keywords:

Air temperature

Airborne pollen

Aeropalynology

Chenopodiaceae

*Sarcocornia fruticosa*

Wind speed

### ABSTRACT

Pollination is a key process in the life cycle of most plant species, but very little is known about airborne pollen dispersal in salt marsh anemophilous halophytes. We analyzed the temporal and spatial dynamics of airborne pollen dispersal, using portable volumetric pollen traps, for six anemophilous Chenopodiaceae halophytic species in tidal salt marshes. In addition, we studied the effects of air temperature and wind speed on airborne pollen dispersal. Our study shows high levels of temporal and spatial constraint on airborne pollen dispersal. We recorded the lowest airborne pollen concentrations at air temperatures lower than 22 °C and wind speeds higher than 6 m s<sup>-1</sup>. These environmental conditions set up a narrow temporal pollination window during morning hours. We also recorded severe spatial limitation for pollen dispersal in three of the six halophytes studied, which presented airborne pollen concentrations that were 9 to 53 times smaller only 5 m away from source populations than within those populations. These results show that even related species colonizing the same ecosystem may show contrasted airborne pollen spatial dispersal dynamics that depend on several environmental factors. This should be taken into account for estimates of vegetation composition based on pollen production in aerobiological and paleopalynological studies. The restricted airborne pollen dispersal recorded would promote geitonogamy and limit interpopulation genetic exchange to the dispersal of their hydrochorous fruits.

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### 1. Introduction

Pollination is a key process in the life cycle of most plant species. Specifically, wind pollination (anemophily) is a sophisticated dynamic solution to the problem of pollen release, dispersal, and capture widely distributed in many taxa (Ackerman, 2000). Numerous models have tried to estimate airborne pollen dispersal distances (Okubo and Levin, 1989; Bunting and Middleton, 2005; Zhang et al., 2014; Souhar et al., 2020), but such models are often validated by limited field data and offer only highly variable predictions of pollen dispersal distances, since many factors influence airborne pollen dispersal (Li et al., 2019).

Among the multitude of factors that determine the dispersion of airborne pollen, there are several related to the characteristics of the plants themselves. Vertical vegetation structures may limit airborne pollen dispersal by acting as obstacles for winds (Whitehead, 1969; Jackson and Lyford, 1999; Dupont et al., 2006). Plant height is also an important factor for airborne pollen dispersal since the taller the plant, the lower

its rate of pollen sedimentation on the ground (Court-Picon et al., 2005; Ranta et al., 2008). Moreover, the type of flower arrangement influences pollen grain transport by determining the micrometeorology of pollen release (Niklas, 1985; Friedman and Barrett, 2009; Cresswell et al., 2010). In addition, pollen grain shape, size, ornamentation and density determine its gravitational settling velocity, following Stokes' law (Di-Giovanni and Kevan, 1991; Aylor, 2002). According to Stokes' law, pollen deposition depends on its diameter, since the density of pollen protoplasm does not vary much among species and is roughly equal to the density of water (Niklas, 1985). Among atmospheric conditions, high wind speed increases pollen dispersal distances and stamen vibration, a key mechanism of pollen release (Zhang et al., 2016; Timerman et al., 2014; Timerman and Barret, 2021). In contrast, relative air humidity promotes pollen sedimentation (Volkova et al., 2013; Timerman et al., 2014) and may interfere in the processes of anther dehiscence and pollen release that usually occur under dry conditions (Whitehead, 1983; Pacini, 1990). Air temperature also determines pollen release and dispersal by influencing on relative air humidity, pollen moisture and anther dehiscence (Harsant et al., 2013; Wang et al., 2019;

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León-Osper et al., 2020). The combination of all these factors leads to temporal and spatial changes in atmospheric pollen concentrations controlled on diurnal time scales by individual flower maturity and local meteorological conditions, on multi-day scales by weather patterns, and on week-long scales by flowering phenology (Laursen et al., 2007). In addition to the above described bottom-up controls on pollination dynamics, pollen supply may also be controlled by top-down processes such as pollen predation (Bertness and Shumway, 1992).

Tidal salt marshes are valuable ecosystems that provide many ecosystem services (Barbier et al., 2011) and where wind-pollinated species are widely distributed (Friess et al., 2012). Nevertheless, to our knowledge, just one study, by the authors, has recorded airborne pollen grain concentrations specifically in salt marshes. In this previous paper, we recorded pollen production per species and habitat, and airborne pollen concentrations for seven Chenopodiaceae species in tidal salt marshes under Mediterranean climate conditions. We concluded that neither the phenology nor the pollen production had a significant predictor value for airborne pollen concentrations for halophytes such as *S. fruticosa* (L.) A.J. Scott and *Halimione portulacoides* Aellen., in spite of their considerable contribution to landscape pollen production (Fernández-Illescas et al., 2010a). In this context, pollen limitation has been demonstrated for some salt marsh halophytes (Friess et al., 2012), and has been related to an Allee effect (causal relationship between population size/density and mean individual fitness) in different wind-pollinated *Spartina* (cordgrass) species (Davis et al., 2004; Murphy and Johnson, 2015). This work delves into wind pollination in salt marshes by analyzing the temporal and spatial dynamics of airborne pollen dispersal, using portable volumetric pollen traps, for six anemophilous Chenopodiaceae halophytic species. In addition, we studied the effects of air temperature and wind speed on airborne pollen dispersal. We hypothesized that airborne pollen concentration would be higher during morning hours, with increasing air temperatures and moderate wind speeds, and would decrease markedly within short distances from source populations due to high sedimentation rates related to environmental conditions typical of tidal marshes such as high relative air humidity. Our results increase knowledge on the ecology of salt marsh halophytes, and are useful for interpreting aerobiological and paleopalynological results.

## 2. Materials and methods

### 2.1. Studied species

Airborne pollen dispersal was studied in six dominant Chenopodiaceae species distributed along the intertidal gradient: *Atriplex halimus* L., *Salsola vermiculata* L., *Suaeda vera* Forssk. ex J.F. Gmel, *Arthrocnemum macrostachyum* (Moris.) Moris, *S. fruticosa* and *H. portulacoides*. We have already studied pollen production, phenology and relative importance in airborne pollen for these same species (Fernández-Illescas et al., 2010a, 2010b). The six halophyte species studied are scrubs that inhabit middle and high salt marshes (Contreras-Cruzado et al., 2017), and have smooth and spherical pollen grains (Candau, 1987). These species bloom at

different periods of the year, show contrasted inflorescence architectures and their plant communities present dissimilar structures (Fernández-Illescas et al., 2010a) (Table 1; Fig. A1).

### 2.2. Study site

The study was carried out at 2–4 populations for each species in middle and high salt marshes in the Odiel Marshes (Southwest Iberian Peninsula) (Table A1, Fig. 1). The Odiel Marshes are one of the largest areas of salt marsh in the Iberian Peninsula and they are protected as a Natural Reserve of the Biosphere by UNESCO. The study area has a semi-diurnal mesotidal regime, with a tidal range (equinoctial mean) of 2.97 m (Figuerola et al., 2003). The Odiel Marshes are subjected to a Mediterranean climate with Atlantic influence. Annual mean air temperature is 18 °C. Mean monthly temperatures are between +11 °C in January and +25 °C in August. Annual average precipitation is 523 mm, varying between 250 and 850 mm with 75–85 days of rain during the autumn and winter months, and a 4–5 month dry period from approximately June to September. Prevailing winds blow from the southwest at a mean speed of 3 m s<sup>-1</sup> and mean gust speed of 5 m s<sup>-1</sup> (Data series 1984–2010 from Huelva meteorological station (37°16'00"N 06°57'00"W); AEMET, 2022). At low marshes, *Spartina maritima* (Curtis) Fernald usually forms monospecific stands or appears together with *Zostera noltii* Hornem. and *Sarcocornia perennis* (Miller) A.J. Scott ssp. *perennis*. Middle marshes are usually occupied by the alien *Spartina densiflora* Brongn., hybrids of *S. perennis* and *S. fruticosa*, *H. portulacoides*, *Suaeda maritima* (L.) Dumort. and *Salicornia ramosissima* Woods (Figuerola et al., 2003). High marshes are typically colonized by *S. fruticosa*, *A. macrostachyum*, *S. vera*, *A. halimus* and *S. vermiculata* (Contreras-Cruzado et al., 2017).

### 2.3. Airborne pollen dispersal

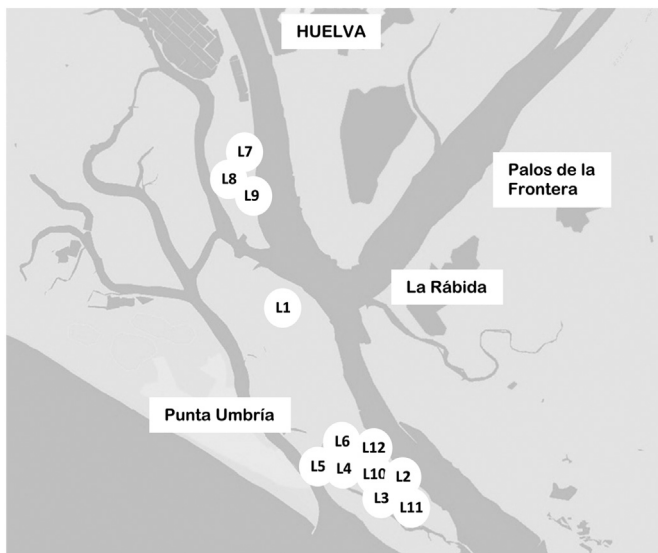
The study was carried out from May to September 2012. To record pollen size, we measured 25 non-collapsed randomly selected pollen grains for each species during the morning. Airborne pollen concentration was recorded using portable volumetric air samplers (personal volumetric air sampler, Burkard Manufacturing Co Ltd., Rickmansworth, England), with an inflow rate of 10 L min<sup>-1</sup>, using white petrolatum as adhesive (Tormo et al., 2010). We took three samples with 9 min of exposition at each position. To study the pollen dispersal dynamic during the day, samples were taken at three intervals: morning (6:00–10:00 solar time), midday (10:00–14:00) and afternoon (14:00–18:00) (Table A1). To study spatial dynamics in pollen dispersal, samples were taken at six positions in each studied population: on the ground surface below the vegetation canopy (position 1), at the height of the inflorescences (position 2), 0.5 m above the inflorescences (position 3), 1 m above the inflorescences (position 4) in the middle of the studied population, at the height of inflorescences at the edge of the population (position 5), and 5 m from the edge in an area free of obstacles in the prevailing wind direction (position 6) (Fig. A2). Pollen sedimentation was studied by comparing pollen concentrations at positions 1 and 2,

**Table 1**

Different factors influencing airborne pollen dispersal of six Chenopodiaceae species in the Odiel Marshes (Southwest Iberian Peninsula): vertical vegetation structure, total vegetation cover, blooming period, inflorescence architecture, pollen size, and wind speed and air temperature recorded during airborne pollen sampling. Different letters indicate significant differences among species (HSD or U-test,  $p < 0.05$ ). Values are mean  $\pm$  SE.

Species	Vegetation structure <sup>1,2</sup>	Vegetation cover (%) <sup>1,2</sup>	Blooming period <sup>1,3</sup>	Inflorescence architecture <sup>4</sup>	Pollen size ( $\mu$ m)	Wind speed (m s <sup>-1</sup> )	Air temperature (°C)
<i>Atriplex halimus</i>	Obstacles of 2.0 m	50	July–August	Panicle-like	19.5 $\pm$ 0.3 <sup>b</sup>	1.8 $\pm$ 0.2 <sup>a</sup>	28.4 $\pm$ 0.3 <sup>a</sup>
<i>Salsola vermiculata</i>	Obstacles of 1.5 m	15	June–November	Panicle-like	22.1 $\pm$ 0.5 <sup>ac</sup>	4.2 $\pm$ 0.3 <sup>b</sup>	23.8 $\pm$ 0.2 <sup>b</sup>
<i>Suaeda vera</i>	Obstacles of 0.5–1.0 m	5	April–May	Solitary	22.0 $\pm$ 0.2 <sup>c</sup>	2.6 $\pm$ 0.2 <sup>a</sup>	24.5 $\pm$ 0.2 <sup>bc</sup>
<i>Arthrocnemum macrostachyum</i>	Obstacles of 0.5–1.0 m	50	May	Spike-like	23.9 $\pm$ 1.5 <sup>a</sup>	2.4 $\pm$ 0.2 <sup>a</sup>	25.1 $\pm$ 0.2 <sup>c</sup>
<i>Sarcocornia fruticosa</i>	No obstacles	> 50	September–October	Spike-like	23.4 $\pm$ 0.5 <sup>ac</sup>	0.9 $\pm$ 0.1 <sup>c</sup>	28.5 $\pm$ 0.2 <sup>a</sup>
<i>Halimione portulacoides</i>	No obstacles	> 50	July–September	Panicle-like	20.2 $\pm$ 0.3 <sup>b</sup>	1.5 $\pm$ 0.1 <sup>a</sup>	28.6 $\pm$ 0.2 <sup>a</sup>

Sources: <sup>1</sup>Fernández-Illescas et al. (2010a); <sup>2</sup>Contreras-Cruzado et al. (2017); <sup>3</sup>Pastor (1987); <sup>4</sup>Castroviejo (1990).



**Fig. 1.** Sampling locations (L1–12) in the Odiel Marshes (Huelva, Southwest Iberian Peninsula). Samples dates and species sampled in each location are listed in Table S1.

vertical pollen dispersal by comparing positions 2, 3 and 4, and horizontal pollen dispersal by comparing positions 2, 5 and 6. As *S. vera* inhabits the same communities as *A. macrostachyum* and they bloomed at the same time, sampling for *S. vera* was done in the most elevated areas where *A. macrostachyum* was less frequent. A total of 522 samples of 90 L of air each were taken.

Samples were mounted on glass with glycerogelatine stained with fuchsin and covered with coverslips. Chenopodiaceae is a stenopalinous family whose species cannot be separated by palynological characters (Muñoz-Rodríguez et al., 2000; Cariñanos et al., 2004), so the analysis was carried out by counting all the Chenopodiaceae pollen grains obtained on the capture surface of each sample (2 mm × 14 mm) under an optical microscope at 40×, and transformed into pollen grains per cubic meter. We counted the collapsed pollen grains in each sample since pollen abortion is a generalized event in some Chenopodiaceae species (Fernández-Illescas et al., 2010c). Aborted pollen grains have no cytoplasm or a sparse cytoplasm that partially occupies the grain, which is itself also smaller (Fernández-Illescas et al., 2010c). Additionally, we recorded the pollen concentrations in *Olea europaea* L., as a passive airborne particle, at the six sampling spatial positions, and at the three time intervals in two days in *A. macrostachyum* and *S. vera* samples. The nearest source of *O. europaea* pollen was far from the sampling sites (> 500 m), enabling us to analyze how environmental conditions were affecting pollen dispersal regardless of the relative position of the source (Muñoz-Rodríguez et al., 2011).

#### 2.4. Meteorological conditions

We recorded air temperature and wind speed in the field, using a thermo-anemometer (AZ8908, AZ Instrument, Taichung City, Taiwan), at the same time as airborne pollen concentration. Wind speed was recorded at positions 2, 5 and 6, and the arithmetic mean of these three positions was calculated to be used in analyses. Air temperature was recorded at position 2.

#### 2.5. Statistical analyses

Statistics were carried out with STATISTICA 8.0 (Statsoft Inc., Tulsa, USA) and SPSS v. 22 (IBM Corp., Armonk, New York). Deviations were calculated as standard errors of the mean (SE). A significance level ( $\alpha$ ) of 0.05 was applied for every analysis. We tested the normality and

homogeneity of the variance of the data series, or of their transformations ( $1/(x+1)$ ,  $\sqrt{x+1}$ ,  $\ln(x+1)$ ,  $\arcsin(x)$ ), using the Kolmogorov–Smirnov test and the Levene test, respectively. The Generalized Linear Model was used to compare airborne pollen concentrations between spatial positions, time intervals, species and their interactions, using air temperature and wind speed as covariant factors. Linear mixed model was applied to compare means of air temperature (with a normal distribution) between species habitats and sampling positions using time intervals as a covariable, using Tukey's Honest Significant Difference (HSD) as a post-hoc test. Kruskal–Wallis test (H) followed by the Mann–Whitney U-test as post-hoc analysis were used to compare means of airborne pollen concentration between positions and time intervals for each species, pollen size among species, and wind speed between species habitats. The Spearman correlation coefficient ( $\rho$ ) was applied to analyze relations between environmental conditions and airborne pollen concentrations.

### 3. Results

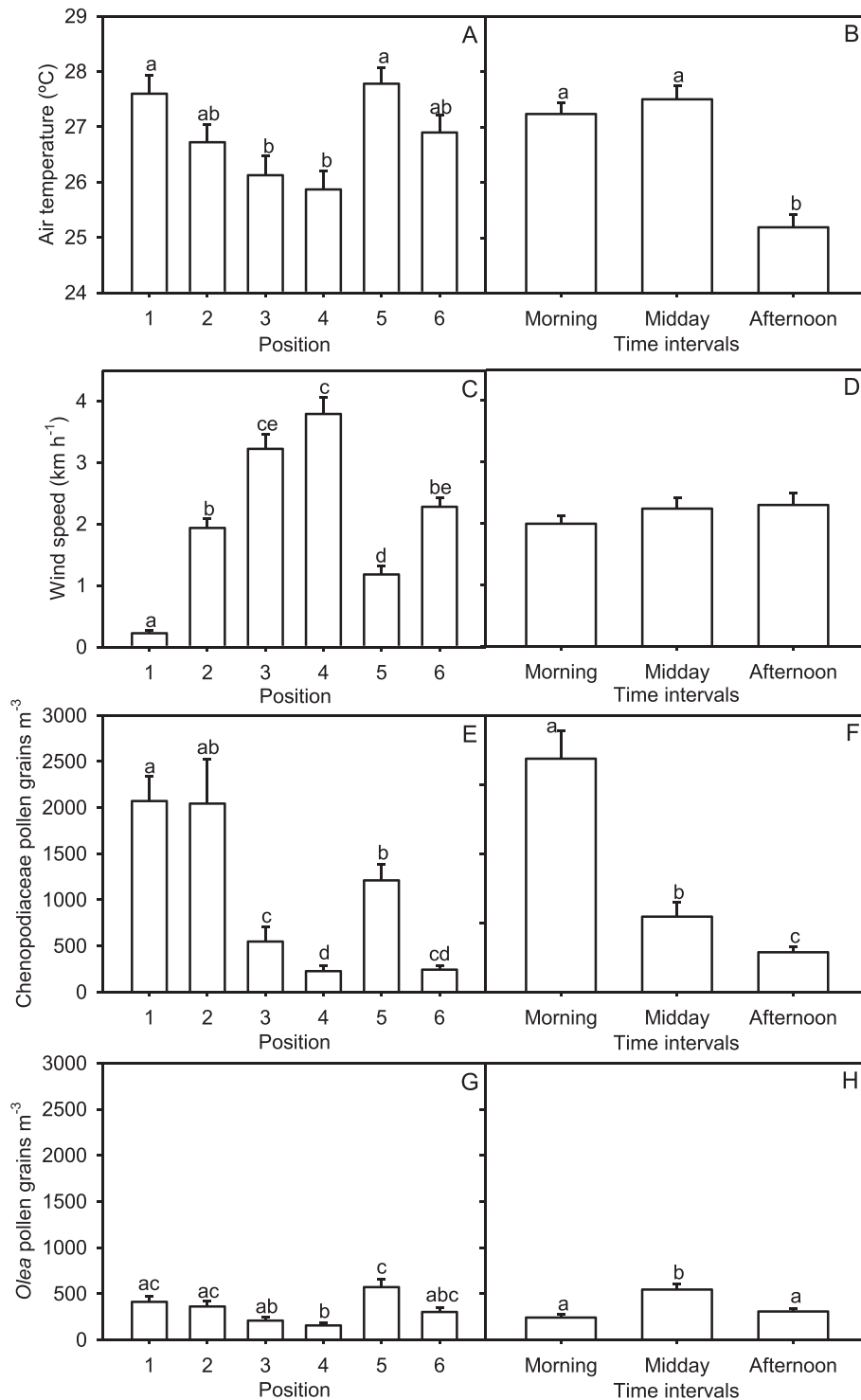
#### 3.1. Meteorological conditions

Air temperature in the field was c. 2 °C higher at positions 1 and 5 than at positions 3 and 4 (Fig. 2A), reaching its highest values during the morning and midday (Fig. 2B). Air temperature was c. 12% higher at *A. halimus*, *S. fruticosa* and *H. portulacoides* sampling dates than at *A. macrostachyum* (Table 1) (Table A2). Moreover, air temperature decreased with increasing wind speed (Spearman correlation test,  $\rho = -0.521$ ,  $n = 513$ ,  $p < 0.0001$ ). On the other hand, wind speed was c. 3.3 km h<sup>-1</sup> higher at positions 3 and 4 than at position 1 (Kruskal–Wallis test:  $H_{5,513} = 9.540$ ,  $p = 0.002$ ) (Fig. 2C), whereas no significant differences were recorded for wind speed between time intervals (Kruskal–Wallis test,  $p > 0.05$ ) (Fig. 2D). Mean wind speed was 77% higher at *S. vermiculata* than at *S. fruticosa* sampling dates, with the other species showing intermediate values (Kruskal–Wallis test,  $H_{5,513} = 86.571$ ,  $p < 0.0001$ ) (Table 1).

#### 3.2. Airborne pollen dispersal

*Arthrocnemum macrostachyum*, *S. fruticosa* and *S. vermiculata* presented pollen grains c. 10% larger than *H. portulacoides* and *A. halimus*, with *S. vera* showing intermediate values (Kruskal–Wallis test,  $H_{5,150} = 73.400$ ,  $p < 0.0001$ ; U-test,  $p < 0.05$ ) (Table 1). In addition, Chenopodiaceae airborne pollen concentration changed significantly between sampling positions, time intervals, species and their interactions, except for the interaction between position and time interval. Additionally, air temperature and wind speed also presented significant predictive power (Table A3). Pollen concentration decreased c. 83% during the day, especially from morning to midday (Fig. 2F). In general, aerial Chenopodiaceae pollen concentration increased together with air temperature ( $\rho = +0.235$ ,  $n = 513$ ,  $p < 0.0001$ ) and decreased with increasing wind speed ( $\rho = -0.319$ ,  $n = 513$ ,  $p < 0.0001$ ) (Fig. 3). As a comparison, the pollen concentration of *O. europaea* reached its maximal at position 5 at midday (Kruskal–Wallis test,  $p < 0.0001$ ), with no significant differences between positions 1, 2, 5 and 6 (Fig. 2G,H).

In general, airborne pollen concentration decreased at greater heights above the marsh surface, and no significant differences in pollen concentration were recorded within halophyte populations. Thus, pollen concentration was 5.25 times higher at positions 1, 2 and 5 than at positions 3, 4 and 6 (Fig. 2E). In this sense, all the studied species showed significant differences in airborne pollen concentration at the different positions (one-way ANOVA,  $p < 0.0001$ ) (Fig. 4). Nevertheless, pollen sedimentation was only recorded within *S. fruticosa* populations, where pollen concentration was c. 8 times higher at position 1 than 2 (HSD test,  $p < 0.05$ ) (Fig. 4). In relation to vertical airborne pollen dispersal, *A. halimus*, *A. macrostachyum* and *S. fruticosa* showed higher pollen concentrations at position 2 than at 4, with position 3



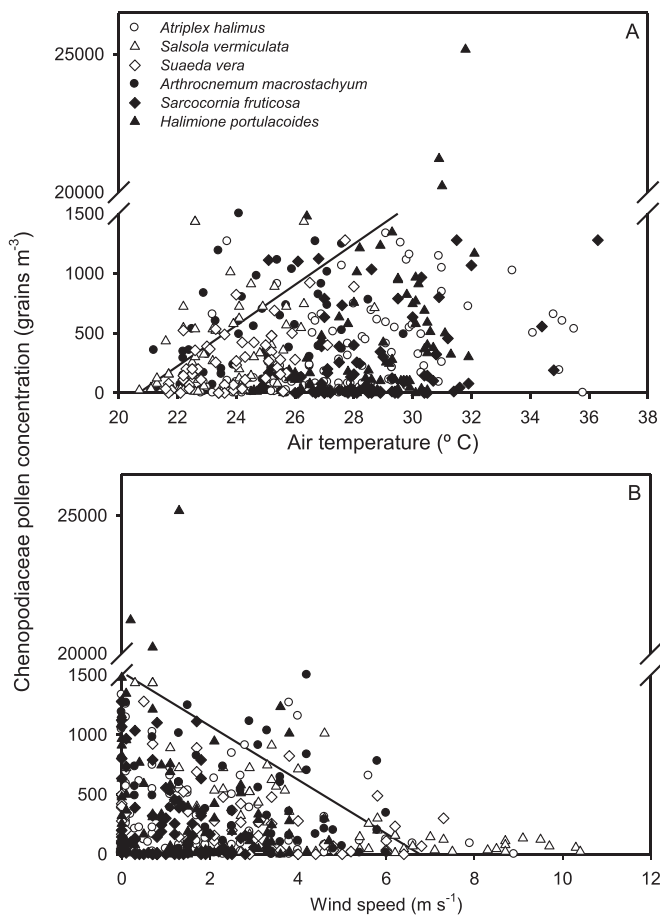
**Fig. 2.** Air temperatures (A, B), wind speed (C, D), Chenopodiaceae airborne pollen concentration for six halophyte species (E, F) and for *Olea europaea* (G, H) at different positions (see Fig. S3) and time intervals in the Odiel Marshes (Southwest Iberian Peninsula). Different letters indicate significant differences between positions or time intervals (HSD test for A, B, E, F, and H; U-test for C, D, and G,  $p < 0.05$ ) ( $N = 513$  for A-F, H;  $N = 144$  for G, H). Values are mean  $\pm$  SE. Sampling positions (Fig. A2): 1, on the ground below the vegetation; 2, at the height of inflorescences; 3, 0.5 m above the inflorescences; 4, 1.0 m above the inflorescences; 5, at the edge of the population; 6, 5.0 m apart from the edge of the population.

showing intermediate values (HSD test,  $p < 0.05$ ) (Fig. 4). In contrast, *S. vermiculata*, *S. vera* and *H. portulacoides* presented higher pollen concentrations at position 2 than at positions 3 and 4 (HSD test,  $p < 0.05$ ) (Fig. 4). Regarding horizontal airborne pollen dispersal, *A. halimus*, *A. macrostachyum*, and *H. portulacoides* showed between 9.0 to 53.8 times higher values at positions 2 and 5 than at position 6 (HSD test,  $p < 0.05$ ) (Fig. 4). In contrast, *S. vermiculata*, *S. vera* and *S. fruticosa* showed

similar pollen concentrations at positions 2, 5 and 6 (HSD test,  $p < 0.05$ ) (Fig. 4).

### 3.3. Collapsed pollen grains

Considering only those samples collected in the morning, the lowest proportion of collapsed pollen grains was recorded at position 2



**Fig. 3.** Relations between airborne pollen concentration, air temperature (A) and wind speed (B) for six Chenopodiaceae halophyte species in the Odiel Marshes (Southwest Iberian Peninsula). Regression equations:  $T^{\circ}C, y = -3523.340 + 170.316x$  ( $p = +0.235$ ,  $n = 513$ ,  $p < 0.0001$ ); Wind speed,  $y = 1524.551 - 225.303x$  ( $p = -0.319$ ,  $n = 513$ ,  $p < 0.0001$ ).

(Kruskal-Wallis test,  $H_{5,240} = 19.042$ ,  $p = 0.002$ ) (Fig. 5A). Moreover, the lowest proportion of collapsed pollen grains was recorded in the morning (Kruskal-Wallis test,  $H_{2,472} = 29.339$ ,  $p < 0.0001$ ) (Fig. 5B). *Arthrocnemum macrostachyum*, *S. fruticosa* and *H. portulacoides* showed c. 50% lower proportion of collapsed airborne pollen grains than *A. halimus*, *S. vermiculata* and *S. vera* (Kruskal-Wallis test,  $H_{5,240} = 47.433$ ,  $p < 0.0001$ ) (Fig. 5C). Finally, the proportion of collapsed pollen grains was independent of air temperature and wind speed (Spearman correlation test,  $p > 0.05$ ).

#### 4. Discussion

Our study shows high levels of temporal and spatial constraint on airborne pollen dispersal of Chenopodiaceae halophyte species in tidal salt marshes. We recorded airborne pollen concentrations c. 90% lower than the recorded maximum concentration at air temperatures lower than 22 °C and wind speeds higher than 6  $m s^{-1}$ . These environmental conditions set up a narrow temporal pollination window during a few morning hours when anther dehiscence occurs, coinciding with high wind speeds and increasing air temperatures that enhance pollen release (Monroy-Colín et al., 2018). Additionally, we also recorded severe spatial limitation for pollen dispersal for three of the six halophytes studied that presented airborne pollen concentrations 9 to 53 times smaller only 5 m away from source populations than within those populations.

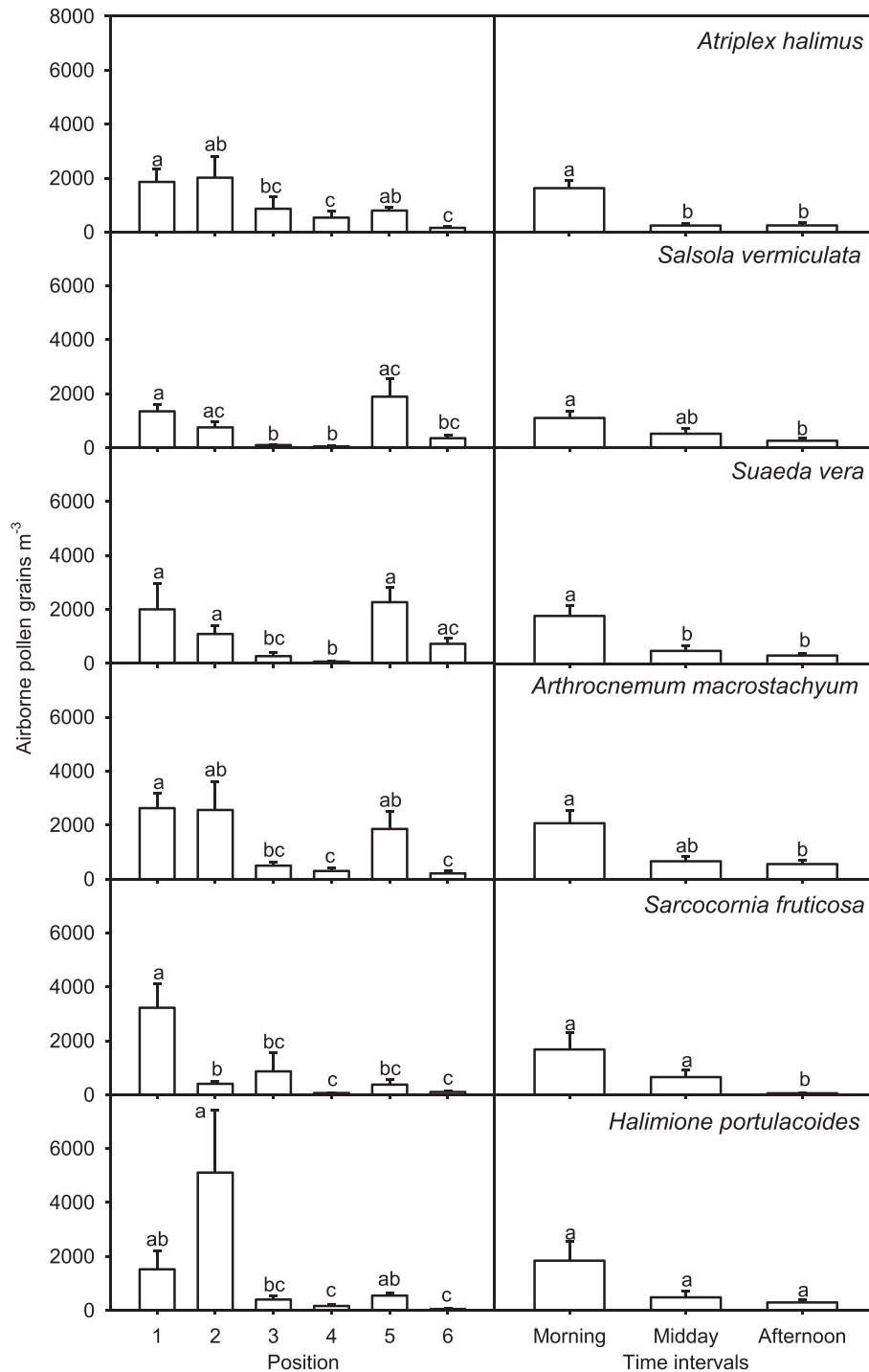
The temporal pattern of Chenopodiaceae airborne pollen dispersal recorded mostly during morning hours did not match that recorded

for *O. europaea*, which reached its maximum concentration around midday, as recorded previously by Alba et al. (2000). In this sense, Muñoz-Rodríguez et al. (2000) also recorded the highest concentration of Chenopodiaceae airborne pollen around midday in grasslands in interior Iberian Peninsula. In addition to the recorded temporal limitation in pollen dispersal, the proportion of collapsed pollen grains was the lowest during the morning and close to the inflorescences, indicating that pollen abortion increased from the moment that pollen grains were dispersed. This temporal pattern of pollen abortion would reinforce the importance of the first morning hours just after pollen release for pollination success.

The recorded dramatic decrease in airborne pollen concentration within a few meters from source populations in *A. macrostachyum*, *A. halimus* and *H. portulacoides* seemed to be related to pollen sedimentation or pollen dilution with distance (Streiff et al., 1999). Evidence of limited local pollen dispersal was also recorded for cordgrass *Spartina alterniflora* Loisel. and its hybrids in salt marshes (Davis et al., 2004; Sloop et al., 2011) and for *Cyperus papyrus* L. in freshwater wetlands (Geremew et al., 2018). We did not find this spatial limitation in airborne pollen dispersal for *S. vermiculata* and *S. vera* that inhabit high marshes with low plant cover (Fernández-Illescas et al., 2010a; Contreras-Cruzado et al., 2017). At these habitats, we recorded the highest wind speed that increases transport of pollen grains to greater distances (Jackson and Lyford, 1999). In this sense, Deng et al. (2006) reported that vegetation zonation in salt marshes was reflected in the pollen rain, however, the more open vegetation types at high marshes tended to be 'overwhelmed' by regional pollen. Interestingly, *S. vermiculata* and *S. vera*, which presented higher horizontal airborne pollen dispersal, showed lower vertical pollen dispersal than the other studied halophytes. This result points to a tradeoff between horizontal and vertical pollen dispersal under limited pollen release conditions. Moreover, the vertical drop in airborne pollen concentration was also recorded for *O. europaea*, which pointed to changing environmental conditions with increasing height above ground, meaning higher wind speed and lower air temperatures (Muñoz-Rodríguez et al., 2000; Cariñanos et al., 2004; Muñoz-Rodríguez et al., 2011). Settling velocities for studied species have ranged from 0.6 to 30  $cm s^{-1}$  (Gómez-Noguez et al., 2017).

*S. fruticosa* was the only species showing higher airborne pollen concentration below than at its canopy level, explaining why Fernández-Illescas et al. (2010a) found that *S. fruticosa* pollen production did not have a significant predictor value for airborne pollen concentrations. The high pollen sedimentation recorded for *S. fruticosa* may be explained by low wind speed during its sampling days, by its relatively large pollen grains, and higher relative air humidity during its autumnal blooming period than during blooming in the other studied species in spring and summer (Fig. A3). In this sense, pollen grains imbibe water, undergo a harmomegatic effect and clump together under high relative air humidity (Volkova et al., 2013; Timerman et al., 2014). Moreover, *S. fruticosa* was the shortest species among those studied, together with *H. portulacoides*, and pollen sedimentation on the ground is higher in short than in tall plants (Court-Picon et al., 2005; Ranta et al., 2008). In the case of *H. portulacoides*, the positive effect of plant height on pollen sedimentation would be compensated by other factors such as presenting panicle-like inflorescences, producing small pollen grains and flowering in a dryer seasonal period (Table 1; Fig. A3). By flowering during autumn, *S. fruticosa* avoids abiotic pollination competition with other coexisting species (Fernández-Illescas et al., 2010a) and its membranous-covered fruits can germinate quickly after dispersal, evading seed predation (Muñoz-Rodríguez et al., 2017).

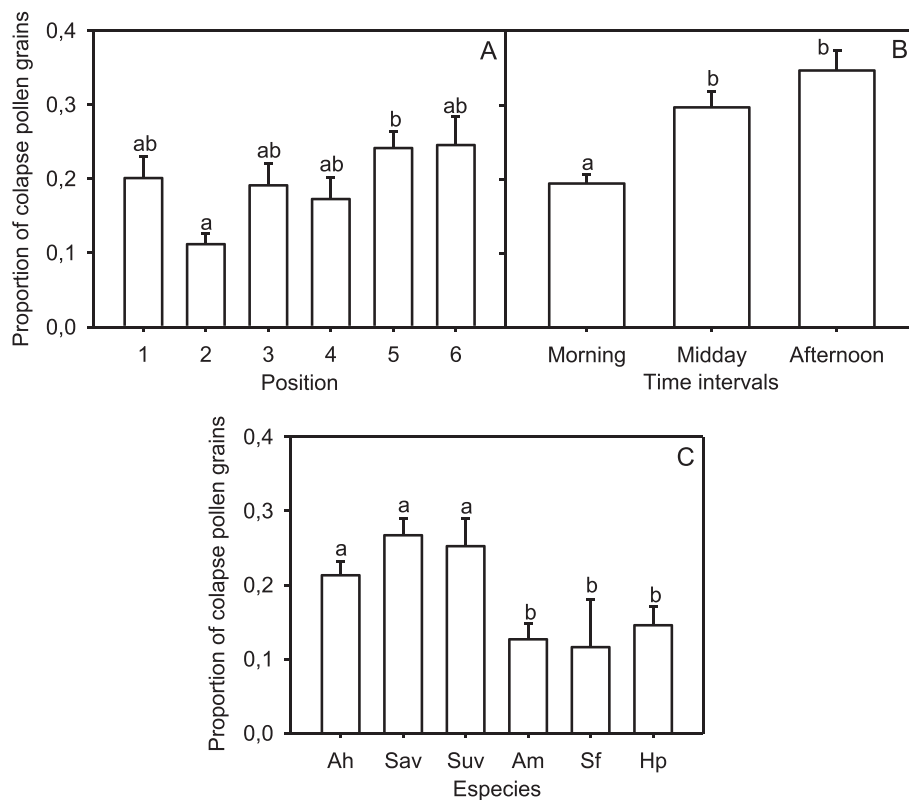
The limited airborne pollen dispersal recorded for the studied Chenopodiaceae halophytes colonizing salt marshes would constrain their interpopulation genetic exchange mostly to the dispersal of their hydrochorous fruits that frequently travel long distances, except for *S. fruticosa* and *H. portulacoides* (Polo-Ávila et al., 2019). In this situation, when pollen is dispersed over a short distance and seeds are widely



**Fig. 4.** Airborne pollen concentration at different positions (see Fig. S3) and time intervals for six Chenopodiaceae halophyte species in the Odiel Marshes (Southwest Iberian Peninsula). Different letters indicate significant differences between means (HSD test for B, C, D, E, F, H, I, K, and L; U-test for A, G, and J,  $p < 0.05$ ) ( $N = 126$  for C, D;  $N = 72$  for A, B, G, H, K, L;  $N = 84$  for I, J;  $n = 87$  for E, F). Values are mean  $\pm$  SE. Sampling positions (Fig. A2): 1, on the ground below the vegetation; 2, at the height of inflorescences; 3, 0.5 m above the inflorescences; 4, 1.0 m above the inflorescences; 5, at the edge of the population; 6, 5.0 m apart from the edge of the population.

dispersed, a weak fine-scale spatial genetic structure would be expected (Resende et al., 2011). Furthermore, according to Baker's Law, the limited airborne pollen dispersal recorded would act as an adaptive pressure towards developing self-compatibility and the ability of spontaneous self-pollination to ensure fruit set when isolated individuals start colonizing new salt marshes (Pannell et al., 2015). In fact, sporophytic self-incompatibility has been described only for a few glycophyte Chenopodiaceae species such as *Beta vulgaris* L. (Lundqvist

et al., 1973). Additionally, limited airborne pollen dispersal would render high levels of geitonogamy, which may be related with the expression of distinct phenotypes within populations (J.M. Castillo, field observation for *S. fruticosa*) and the stabilization of populations with different chromosome numbers, such as the hybrids between *S. perennis* and *S. fruticosa* (Figuerola et al., 2003; Gallego-Tévar et al., 2018). Moreover, our results show that even related species colonizing the same ecosystem show contrasted airborne pollen spatial dispersal dynamics



**Fig. 5.** Proportion of collapsed pollen grains for different (A) positions (see Fig. S3), (B) time intervals and (C) six Chenopodiaceae halophyte species. Different letters indicate significant differences between means (U-test,  $p < 0.05$ ) ( $N = 240$ ). Values are mean  $\pm$  SE. Sampling positions (Fig. A2): 1, on the ground below the vegetation; 2, at the height of inflorescences; 3, 0.5 m above the inflorescences; 4, 1.0 m above the inflorescences; 5, at the edge of the population; 6, 5.0 m apart from the edge of the population. Species: Ah, *Atriplex halimus*; Sav, *Salsola vermiculata*; Suv, *Suaeda vera*; Am, *Arthrocnemum macrostachyum*; Sf, *Sarcocornia fruticosa*; Hp, *Halimione portulacoides*.

that depend on several environmental factors. This can render differences in their representation in air and sedimentary pollen records through pollen filtration and dilution (Bunting, 2008) that should be accounted for in estimates of vegetation composition based on pollen production in aerobiological and paleopalynological studies.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Acknowledgments

The authors thank the Directorate of the Natural Parks for supporting field work conducted in this study. María Dolores Infante-Izquierdo thanks Ministerio de Educación, Cultura y Deporte (Spain) for a predoctoral fellowship (FPU-2015).

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2022.104662>.

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