

Modeling germination responses of three stem-succulent halophytes of Mediterranean salt marshes to salinity and temperature

Zaineb Hayder

Arid Regions Institute (IRA) Medenine-Tunisia

Mansour Sekrafi

Arid Regions Institute (IRA) Medenine-Tunisia

Abderrazak Tlili

Arid Regions Institute (IRA) Medenine-Tunisia

Fayçal Boughalleb

Arid Regions Institute (IRA) Medenine-Tunisia

Esmail Bakhshandeh

Genetics and Agricultural Biotechnology Institute of Tabarestan & Sari Agricultural Sciences and Natural Resources University, Sari, Iran

Raoudha Abdellaoui (✉ raoudhamabdellaoui@yahoo.com)

Arid Regions Institute (IRA) Medenine-Tunisia <https://orcid.org/0000-0003-2767-9650>

Mohamed Tarhouni

Arid Regions Institute (IRA) Medenine-Tunisia

Research Article

Keywords: Cardinal temperatures, halophytes, halothermal time, median base NaCl concentration, population-based threshold models

Posted Date: April 26th, 2023

DOI: <https://doi.org/10.21203/rs.3.rs-2859687/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Abstract

Quantification of germination niches under salt stress, temperature, and their interaction using population-based threshold models is important to predict seedling emergence patterns. Seeds of *Sarcocornia fruticosa*, *Sarcocornia alpini*, and *Salicornia emerici* were treated with various temperatures at different NaCl concentrations. Results indicated that the median base NaCl concentration was roughly steady (0.68, 0.73, and 0.70M, respectively) at sub-optimal temperature, then decreased linearly at supra-optimal temperature until the ceiling temperature (T_c). The estimated base, optimum and ceiling temperatures, in water, were -0.5 , 15 and 29°C for *Sarcocornia fruticosa*, -2.5 , 11 and 24°C for *Sarcocornia alpini*, and 9.5 , 25 and 40°C for *Salicornia emerici*, respectively. At all species, the base temperature has not changed with the salinity while both optimum and ceiling temperatures decreased. Also, *Salicornia emerici* showed rapid and synchronized germination when salinity decreases during the rainy season coinciding with favorable temperatures compared with other species.

Introduction

Salinization, which is constantly increasing due to climate change, is the most serious threat to the Mediterranean basin in the world (Cuttelod et al. 2009). By 2050, rainfall will decrease between 4 and 30% and temperature (T) will rise by $2-4^\circ\text{C}$ (Panta et al. 2014). Concurrently, the Mediterranean basin will exhibit an increase in the sea level of approximately 35 cm by 2100 (Rosa et al. 2012). These environmental changes have increased the land cover marginalized lands that are usually typified by low yield and reduced economic incomes or by severe restrictions for farming use. Marginalized lands are generally frail and subject to high environmental risk. Currently, there is rising attention in worldwide using halophytes that can tolerate harmful conditions and high salinity levels which are toxic to conventional crops (Song and Wang 2015). Thus, successful germination is vital for the restoration and rehabilitation of marginalized lands.

Germination is the preliminary and decisive phase in plants' life cycle and contributes to population persistence, especially for those reproducing only by seeds (Keiffer and Ungar 1997). Seed population germination rate (GR) and germination percentage (GP) are fundamental measures used to study germination. They are affected by many abiotic factors such as temperature (T), salinity, water potential, and oxygen concentration, etc. (Grime and Campbell 1991; Ungar 1995). In salt marshes, salinity is the most important environmental factor conditioning the germination of halophytes. Indeed, halophytes are able to germinate at salinities that 99% of non-halophyte seeds do not support, indicating that halophytes are more tolerant to salt at the germination stage (Manousaki and Kalogerakis 2011). The GP of glycophytes declines severely at small amounts of NaCl, and totally inhibited above 100 mM NaCl (Yuan et al. 2019). Generally, most of the seeds of halophytic species germinate best under fresh water and preserve somewhat high GP under saline conditions, which gradually decreases with increase of NaCl concentrations (Gul et al. 2013).

Changes in T under salt conditions affect differently the germination of halophytes (Khan and Gul 2006). Cardinal temperatures are the range of T in which the seeds of a given species can germinate, including the base temperature (T_b), which is the very low T below which no germination takes place; the optimum temperature (T_o), which is the T at which germination is highest, and finally, the ceiling temperature (T_c) which is the maximum T beyond which no germination occurs (Rowse and Finch-Savage 2003; Taghvaei and Ghaedi 2010; Bradford and Bello 2022). The GR increases linearly with T ($< T_o$) and then decreases linearly at $T > T_o$ (Covell 1986; Hardegree et al. 2015; Bakhshandeh et al. 2017; Abdellaoui et al. 2019). The damaging effects of salinity may not affect T_o (Bakhshandeh et al. 2020; Bakhshandeh et al. 2021; Bakhshandeh et al. 2022; Alinia et al. 2022) and/or may decrease T_o with a decrease in GP observed in various species (Seal et al. 2018). A species may have different saline germination niches depending on the time of year; this is the typical result of the interaction between T and salinity (Gul et al. 2013). During the summer, the elevated T leads to a rapid evaporation of the water resulting in an increase in the salinity of the soils where the halophytes grow (Khan and Ungar 1996; Khan and Gul 1998). Seed germination of halophytes in semi-arid and arid regions usually takes place during a season with high precipitation when soil salinity concentrations are decreased and water potentials are increased (Khan 1999).

Halophytes are very different in terms of their salt tolerance range (Ventura and Sagi 2013) among which stem succulent halophytes are considered highly salt tolerant (Khan and Gul 2006). For example, *Salicornia europaea*, *Sarcocornia fruticosa*, *Salicornia bigelovii*, *Sarcocornia perennis*, and *Salicornia rubra* germinate above seawater salinities (800–1700 mM NaCl) (Khan and Gul 2006). Indeed, under high-salinity conditions, seeds of halophytes exhibit extremely dedicated adaptations such as seed dormancy and heteromorphism (Navarro and Guitian 2003; Gul et al. 2013; Guo et al. 2018).

Sarcocornia and *Salicornia* genera are important components of the halophytic pioneer vegetation of salt marshes. They are halophytic herbs with articulated succulent stems belonging to the *Chenopodiaceae* family (Davy et al. 2001). The genus *Sarcocornia* consists of perennial species with flowers roughly equal in size and arranged in a horizontal row whereas; *Salicornia sp* involves annual species with unequal size and triangularly arranged flowers (Kadereit et al. 2007; Zhu and Sanderson 2017). Annuals produce seeds once in their life and develop dormancy mechanisms that maintain seed viability. On the other hand, perennials have many reproductive events in their lifetime and use ramets to propagate clonally in addition to seeds (Gul et al. 2013). Nevertheless, Khan and Gul (2006) indicated that plant tolerance, during germination, to high salinity is rather independent of its life form. The interaction between T regime and the salinity levels has a strong impact on the GR of *Salicornia* and *Sarcocornia*. For both genera, the highest GP corresponds to the lowest concentrations of soil salts during winter and spring (Davy et al. 2001, 2006). The germination limits for some species of *Salicornia* and *Sarcocornia* can reach more than 2-fold of seawater concentration. For example, *Salicornia herbacea* seeds can germinate at 1700 mM and *Sarcocornia fruticosa* seeds at 1030 mM (Khan and Gul 2006; Ventura et al. 2011).

Seal et al. (2018) initially developed a halothermal time model (HaloTT) to predict the seed germination response of the halophyte '*Suaeda maritima*' to salt stress at sub-optimal temperatures. The model generates constants (thermal time, halo time or halothermal time) that point out how the *GR* changes with *T* or salinity (or a combination of both) over time, which are indicators of seed vigour. Since their introduction, thermal, halo and halothermal time models have successfully quantified the germination of wild species, crops, field emergence and dormancy loss (Seal et al. 2018; Bakhshandeh et al. 2020; Bakhshandeh et al. 2021; Bakhshandeh et al. 2022; Alinia et al. 2022). A benefit of these models is that they characterize the full range of germination niche requirements making them predominantly helpful in comparative studies among species and for predicting species responses to different climate change scenarios (Seal et al. 2018). This model was then modified by Bakhshandeh et al. (2020) to quantify seed germination response over both sub- and supra-optimal temperatures at various NaCl concentrations. This HaloTT model allow for quantifying the combined effect of *T* and salt stress on the dynamics of different crops seed germination (Bakhshandeh et al. 2021; Bakhshandeh et al. 2022).

Sarcocornia and *Salicornia* crops are characterized by great economic potential (Ventura and Sagi 2013). Both are used as food, feed, medicinal compounds, soil phytoremediation, carbon sequestration, as well as the convalescence of marginal saline soils and water (Rozema and Schat 2013; Panta et al. 2014). They are a natural source of sodium carbonate for glass manufacture (Chevalier 1922; Cardenas-Pérez et al. 2021) and also very adequate for bioethanol production due to their richness in suitable lignocellulosic materials (Cardenas-Pérez et al. 2021; Custódio et al. 2021). *Salicornia* genus is commonly used as a substitute bioenergy resource crop for NASA (Cardenas-Pérez et al. 2021). At the same time, it has been used in the production of soap because of its high ash content (Davy et al. 2001; Ortuno et al. 2020).

Generally, seed germination performance of plants is depending on high *GP* within a more rapid and uniform seed germination (Muscolo et al. 2014). Our hypothesis supposes that *Salicornia emerici* SG is assumed to show rapid and synchronized germination under salt and temperature stresses than *Sarcocornia* species.

Quantification of germination niche under salt stress, *T*, and their interaction is therefore important to understand the different species' seed germination patterns using population-based threshold models. To our knowledge, this is the first report dealing with seed germination modeling of *Sarcocornia* and *Salicornia* genera. Therefore, this study aimed (i) to investigate the response of both genera seed germination at different series of *T* and NaCl concentrations, individually, and simultaneously using the HaloTT model, (ii) to establish the base NaCl concentration and, (iii) to estimate the cardinal temperatures by the modeling approach.

Materials And Methods

Seed Collection

Seeds of *Sarcocornia fruticosa* and *Sarcocornia alpini* were collected from Zarzis- El Alandaya (33°25'49.4"N; 11°05'40.7"E) and *Salicornia emerici* seeds from Djerba- Sidi Jmour (33°51'59"N; 10°47'31"E) belonging to southern Tunisia in November and December 2021 for *Sarcocornia alpini* and *Sarcocornia fruticosa* and *Salicornia emerici*, respectively. Both sites are characterized by a mild lower arid climate with an average annual rainfall of 200–300 mm. Average monthly temperatures are around 10 to 12°C in winter, 18 at 25°C in spring, 30°C in summer and 20 to 22°C in autumn. The hottest months, for both stations, are July and August (28 to 32°C), while the coldest month is January with a temperature of around 10°C. The thermal amplitude is between 26 and 33°C (Atlas de la region économique du Sud-Est Tunisien).

Species were authenticated by Dr. Mohamed Tarhouni, Lecturer at the Arid Regions Institute (IRA) of Medenine, Tunisia. Besides, a molecular study was conducted and confirmed the presence of *S. fruticosa* (L.) A.J. Scott and two newly recorded species (*S. alpini* (Lag.) Rivas Mart. and *Sa. emerici* Duval-Jouve) in Tunisia (Hayder et al. 2022). The seeds are unprotected as they are located in a bract cavity so they fall when reaching maturity. It is required to be on time when collecting the parts that have already ripened the seeds and not to drop them during the cutting and bagging operations. At first, the seeds were manually detached from the inflorescence segments. Then the empty seeds and impurities were removed and mature seeds were stocked up in paper bags at 5°C until the start of the experiments.

Pretreatment And Germination Tests

Germination studies were conducted in January 2022 in a programmed incubator (Peltier-cooled incubator IPP30, Memmert). Foremost, seeds were disinfected with 5% sodium hypochlorite for 10 min and rinsed three times with distilled water to wash the remaining hypochlorite sodium (Leite et al. 2007). The 1000-seed weight was 0.88 ± 0.05 , 0.29 ± 0.02 , and 0.49 ± 0.07 g for *S. fruticosa*, *S. alpini*, and *Sa. emerici*, respectively. For the germination test, at each treatment, four sets of 25 seeds were used for each species and placed in 8-cm glass Petri dishes containing two layers of filter paper (Whatman No. 1) and conserved with adhesive tape (Parafilm™) to avoid water evaporation. Seeds were incubated in the dark at different constant T (2, 5, 10, 15, 20, 25, 30, and 35°C, depending on the species) under different concentrations of NaCl (0, 0.1, 0.2, 0.4, 0.6, and 0.8 Molar (M)). The salinity of the test solutions was checked using a multi-pH meter (Benchtop pH/Conductivity Meter LAQUA PC1500; HORIBA). To each Petri dish, 5 ml of distilled water (control treatment) or an aqueous solution of NaCl was added (Muñoz-Rodríguez et al. 2017). The solution was renewed every two days to avoid salt accumulation in the medium. Germination was recorded daily throughout the course of germination for 30 days and the experiment was stopped when no seeds germinated after three consecutive days. The germinated seeds, once the radicle protrusion is 2 mm, were counted and removed during the experiments.

Halotime And Halothermal Time Models

A repeated probit regression analysis (Bradford 1995) was used to describe and quantify the experimental data. Germination rate was also calculated as the inverse of the time to reach 50th percentile of germination in the seed population ($GR_{50} (h^{-1}) = 1 / t_{50}$).

The halotime model suggested by Bakhshandeh et al. (2020) was used to assess the germination time courses in different levels of salinity (0-0.8 M, NaCl) at each studied T . This model is expressed as:

$$\theta_{Halo} = (NaCl_{b(g)} - NaCl) t_g (1)$$

where θ_{Halo} is the halotime constant (M h); $NaCl$ is the actual NaCl concentration in the medium (M); $NaCl_{b(g)}$ is the base value of NaCl concentration inhibiting radicle emergence of percentage g (M) and t_g is the actual time to germination of percentage g (h).

The HaloTT model was also fitted across all T and NaCl concentrations based on the method that is fully described in Bakhshandeh et al. (2020).

At sub-optimal T range, the model can be written as:

$$\theta_{HaloTT} = (NaCl_{b(g)} - NaCl)(T - T_b) t_g (2) \text{ or}$$

$$\text{Probit } (g) = [NaCl + (\theta_{HaloTT} / (T - T_b) t_g) - NaCl_{b(g)}] / \sigma_{NaClb} (3)$$

and at supra-optimal T range:

$$\theta_{HaloTT} = [NaCl_{b(g)} - (NaCl + k_T(T - T_d))](T - T_b) t_g (4) \text{ or}$$

$$\text{Probit } (g) = [(NaCl + k_T(T - T_d)) + (\theta_{Halo} / (T - T_b) t_g) - NaCl_{b(g)}] / \sigma_{NaClb} (5)$$

where θ_{HaloTT} is the halothermal time constant (M °C h), σ_{NaClb} is the standard deviation of $NaCl_b$ within the seed population (M), k_T is the slope of the relationship between $NaCl_{b(g)}$ and $T \geq T_d$ (M °C⁻¹) and T_d is the T at which $NaCl_{b(g)}$ starts to change (°C) which can be equal and/or lower than T_o (Bakhshandeh and Gholamhossieni 2019).

In addition, the base value of NaCl concentration (M) was converted to water potential (ψ , MPa) according to the Van't Hoff equation (Van't Hoff 1887). The equation can be written as:

$$\psi = -RTCi / 1000 (6)$$

where R is the gas constant (0.0083 L/atm/mol/K), T is the absolute T in degrees in Kelvin, C is the solute concentration in mol L⁻¹, and i is the dissociation constant of the salt (NaCl = 1.8).

Statistical analysis

The data were analyzed using the statistical analysis system ver. 9.4 (SAS Institute 2015). A two-way ANOVA was realized to examine the effect of salinity, T , and their interaction on GP and maximum germination percentage (previously arcsine transformed). Excel and Sigma Plot ver. 11 softwares were used to draw the figures.

Results

Effect of salinity and temperature on GP and GR

Increasing salinity level in the medium had significantly ($P < 0.05$) decreased both GP and GR_{50} (Table 1). Moreover, the interaction between T and salinity ($T \times NaCl$) had also a significant effect ($P < 0.05$) on both germination parameters (Table 1). Generally, the increase in T degree enhanced GP and GR_{50} of all three studied species' but both germination parameters decreased as T exceeds a certain limit. Under control conditions (0 M NaCl), the highest GP was recorded at 15, 11, and 25°C for *S. fruticosa* (76.0%), *S. alpini* (89.7%), and *Sa. Emerici* (92.2%), respectively (Fig. 1a, b, and c). When seeds were subjected to salt stress, GP was highest under 0.1 M with 70.7, 85.5, and 88.6% at $T \approx T_o$ then decreased with increasing salinity reaching 28.2, 34.8, and 37.8% at 0.8 M for *S. fruticosa*, *S. alpini*, and *Sa. emerici*, respectively. However, they showed low GP at $T > T_o$ i.e., 11.1% at 25°C, 1.00% at 20°C, and 2.02% at 35°C for *S. fruticosa*, *S. alpini*, and *Sa. emerici*, respectively at 0.8 M (Fig. 1a, b, and c). Similarly, the GR_{50} showed the same patterns as GP (Fig. 1d, e, and f). Taking into account simultaneously both stresses, GP and GR_{50} increased for $T < 15, 11$, and 25°C then decreased when exceeding these temperatures for *S. fruticosa*, *S. alpini*, and *S. emerici*, respectively, under all studied salinity levels (Fig. 1d, e, and f).

Table 1

Analysis of means comparison for maximum germination percentage (GP_{max} , previously arcsine transformed) and median germination rate (GR_{50}) of *Sarcocornia fruticosa*, *Sarcocornia alpini*, and *Salicornia emerici* under the effect of both temperature (T) and NaCl concentrations.

Source of variation	<i>Sarcocornia fruticosa</i>			<i>Sarcocornia alpini</i>			<i>Salicornia emerici</i>		
	df	GP_{max}	GR_{50}	df	GP_{max}	GR_{50}	df	GP_{max}	GR_{50}
Temperature (T)	4	0.186**	0.0015**	4	0.808**	0.037**	5	0.834**	0.284**
Error1	15	0.012	0.0016	15	0.014	0.004	18	0.038	0.005
NaCl	5	0.470**	0.0188**	5	1.536**	0.114**	5	3.060**	0.436**
$T \times NaCl$	20	0.245**	0.0016**	20	0.033**	0.020**	25	0.054**	0.054**
Error2	75	0.006	0.0011	75	0.012	0.003	90	0.028	0.002
df: Degrees of freedom. The number of total data in salt stress is $n = 120$ ($T = 5$, NaCl (mM) = 6 and replication = 4).									
** significant at 0.001 probability level.									

Halotime Time Model

The halotime model fitted well with the germination data across all temperatures and NaCl concentrations (Table 2). Actually, R^2 ranged from 0.78 to 0.94 for *S. fruticosa*, from 0.86 to 0.93 for *S. alpini*, and from 0.86 to 0.97 for *Sa. emerici* at different salinities and temperatures (Table 2). For the three studied species, θ_{Halo} (M h) decreased non-linearly with increasing T , meaning that the values were dropped from 340.4 to 57.7 M h, from 238.8 to 40.6 M h, and from 539.8 to 15.3 M h for *S. fruticosa*, *S. alpini*, and *Sa. emerici*, respectively (Fig. 2a). Besides, *Sa. emerici* showed the highest θ_{Halo} (539.8 M h) compared to *S. fruticosa* (162.3 M h) and *S. alpini* (94.7 M h) at the same studied T (i.e., 10°C) (Table 2). Results also showed that the inverse of θ_{Halo} values ($1/\theta_{Halo}$) vs. T exhibited a linear regression and intercepted the x -axis at -0.5 , -2.5 , and 9°C corresponding to T_b of *S. fruticosa*, *S. alpini*, and *Sa. emerici*, respectively (Fig. 2b). The $NaCl_{b(50)}$ values, in the contrary, were steady (from 0.65 to 0.71 for *S. fruticosa*, from 0.73 to 0.75 for *S. alpini*, and from 0.69 to 0.71 for *Sa. emerici*) at $T \leq T_o$ then they were dropped off linearly ($k_T = 0.034$, $= 0.047$, and $= 0.041 \text{ M } ^\circ\text{C}^{-1}$) for $T > T_o$ reaching 0 M at T_c (i.e., 29, 24, and 40°C for *S. fruticosa*, *S. alpini*, and *Sa. emerici*, respectively) (Fig. 2c). The T_c calculated by extrapolated from the GR_{50} data at T above T_o (Fig. 2c).

Table 2

Parameter values which were estimated by applying the halotime (Eq. 1) model for the description of *Sarcocornia fruticosa*, *Sarcocornia alpini*, and *Salicornia emerici* seed germination with diverse seed lots under various temperature (T) and concentration of NaCl: 0, 0.1, 0.2, 0.4, 0.6, and 0.8 M. R^2 is the coefficient of determination.

Seed lots	T (°C)	θ_{Halo} (M h)	$NaCl_{b(50)}$ (M)	σ_{NaClb} (M)	R^2	GR_{50}	ψ (MPa)*
<i>Sarcocornia fruticosa</i>	5	340.4	0.71	0.78	0.78	0.0021	-2.96
	10	162.3	0.65	0.49	0.89	0.0039	-2.73
	15	109.2	0.44	0.58	0.92	0.0040	-1.89
	20	71.3	0.26	0.57	0.91	0.0036	-1.13
	25	57.7	0.15	0.60	0.94	0.0025	-0.64
	T (°C)	θ_{Halo} (M h)	$NaCl_{b(50)}$ (M)	σ_{NaClb} (M)	R^2	$GR_{(50)}$	ψ (MPa)
<i>Sarcocornia alpini</i>	2	238.8	0.73	0.52	0.91	0.0031	-3.00
	5	143.3	0.75	0.37	0.86	0.0052	-3.10
	10	94.7	0.74	0.32	0.89	0.0078	-3.11
	15	48.3	0.33	0.39	0.89	0.0068	-1.41
	20	40.6	0.22	0.34	0.93	0.0054	-0.96
	T (°C)	θ_{Halo} (M h)	$NaCl_{b(50)}$ (M)	σ_{NaClb} (M)	R^2	$GR_{(50)}$	ψ (MPa)
<i>Salicornia emerici</i>	10	539.8	0.69	0.56	0.86	0.0013	-2.93
	15	88.6	0.70	0.64	0.86	0.0079	-3.02
	20	36.1	0.71	0.40	0.97	0.0197	-3.12
	25	20.5	0.55	0.30	0.96	0.0267	-2.44
	30	17.1	0.42	0.29	0.93	0.0249	-1.92
	35	15.3	0.23	0.42	0.88	0.0151	-1.06
* Water potential (ψ) was calculated using the equation suggested by Van't Hoff (1887).							
T : Temperature; θ_{Halo} : Halotime constant; $NaCl_{b(50)}$: The median base or threshold value of NaCl concentration for the 50th percentile; σ_{NaClb} : Standard deviation of $NaCl_b$ within the seed population; $\psi_{b(50)}$: The base ψ of the 50th percentile; GR_{50} : median germination rate or germination rate of the 50th percentile.							

The $NaCl_{b(50)}$ values at each studied T were converted to ψ (MPa) using the equation suggested by Van't Hoff (1887). Results showed that the ψ values were increased from -2.96 to -0.64 MPa when T varied from 5 to 25°C for *S. fruticosa*. However, *S. alpini* revealed less negative ψ values with no significant difference (i.e., -3.00 , -3.10 , and -3.11 MPa at 2 , 5 , and 10°C , respectively), then decreased significantly at $T > 10^{\circ}\text{C}$ reaching less negative value (-0.96 MPa at 20°C). Moreover, *Sa. emerici* showed steady values of ψ at $T \leq T_o$ (i.e., -2.93 , -3.02 , and -3.12 MPa at 10 , 15 , and 20°C , respectively). When T was increased above T_o , ψ values increased significantly reaching its maximum (less negative, i.e., -1.06 MPa) at 35°C for this species. It is to be noticed that at the same T (i.e., 10°C), *S. alpini* had shown the less negative ψ value (-3.11 MPa) followed by *Sa. emerici* (-2.93 MPa) and *S. fruticosa* (-2.73 MPa) (Table 2).

Halothermal Time Model

Results revealed that the HaloTT model predicted well the germination time courses of the three species at all T and NaCl concentrations with high R^2 values ($R^2 = 0.80$, 0.81 , and 0.88 for *S. fruticosa*, *S. alpini*, and *Sa. emerici*, respectively) demonstrating a high correlation between predicted and observed germination data for each set of T (Fig. 3; Table 3). The estimated θ_{HaloTT} , $NaCl_{b(50)}$, and k_T values were $1813 \text{ M }^{\circ}\text{C h}$, 0.68 M and $0.034 \text{ M }^{\circ}\text{C}^{-1}$, respectively for *S. fruticosa*, $1067 \text{ M }^{\circ}\text{C h}$, 0.73 M , and $0.047 \text{ M }^{\circ}\text{C}^{-1}$ for *S. alpini* and $359 \text{ M }^{\circ}\text{C h}$, 0.70 M , and $0.041 \text{ M }^{\circ}\text{C}^{-1}$ for *Sa. emerici*, respectively (Table 3).

Table 3

Estimated values of the parameters by applying in the halothermal time model (Eqs. 2 and 4) for describing *Sarcocornia fruticosa*, *Sarcocornia alpini*, and *Salicornia emerici* seed germination at different temperatures (5, 10, 15, 20, and 25°C; 2, 5, 10, 15, and 20°C; 10, 15, 20, 25, 30, and 35°C, respectively) under various concentration of NaCl (0, 0.1, 0.2, 0.4, 0.6, and 0.8 M).

HaloTT parameters	<i>Sarcocornia fruticosa</i>	<i>Sarcocornia alpini</i>	<i>Salicornia emerici</i>
$NaCl_{b(50)}$ (M)	0.68	0.73	0.70
σ_{NaClb} (M)	0.62	0.48	0.46
θ_{HaloTT} (M °C h)	1813	1067	359
k_T (M °C ⁻¹)	0.034	0.047	0.041
T_d (°C)	9	9	23
Cardinal T_s at 0 M			
T_b (°C)	-0.5	-2.5	9.5
T_o (°C)	15	11	25
T_c (°C)	29	24	40
R^2	0.80	0.81	0.88
T_c is calculated by extrapolation from the germination rate data at T above T_o . R^2 is the coefficient of determination.			
$NaCl_{b(50)}$: The median base or threshold value of NaCl concentration for the 50th percentile; σ_{NaClb} : Standard deviation of $NaCl_b$ within the seed population ; θ_{HaloTT} : the halothermal time constant (M °C h or M °C d); k_T : The slope of the relationship between $NaCl_{b(50)}$ and T above T_o ; T_d (°C): The temperature at which $NaCl_{b(50)}$ trend begins to change ; T_b (°C): base temperature; T_o (°C): optimum temperature; T_c (°C): ceiling temperature.			

Cardinal Temperatures

The relationship between GR_{50} vs. T was linear at $T \leq T_o$ under all NaCl concentrations and intercepted the abscissa axis at a single point designated by T_b (Fig. 4). The T_b values were - 0.5, - 2.5, and 9°C for *S. fruticosa*, *S. alpini*, and *Sa. emerici*, respectively. However, at $T > T_o$, GR_{50} decreased curvilinearly until it became null at T_c which its value depends on the NaCl concentration (Fig. 4a, b, and c and Table 3). Indeed, the T_c was estimated by extrapolating from the GR_{50} data at T above T_o (Fig. 2c). The results showed that T_o values were 15, 11, and 25°C and T_c values were 29, 24, and 40°C for *S. fruticosa*, *S. alpini*, and *Sa. emerici*, respectively, when the HaloTT model was fitted to the experimental data (Table 3;

Fig. 3). Besides, this model demonstrated that T_d value (the T at which $NaCl_b(g)$ starts to change) is 9°C for both *Sarcocornia* species. However, it is 23°C for *Salicornia emerici* (Table 3).

At T_o , the GR_{50} decreased linearly with increasing NaCl concentration from 0.004, 0.008, and 0.026 h⁻¹ at 0 mM NaCl for *S. fruticosa*, *S. alpini*, and *Sa. emerici*, respectively to null values at concentrations of NaCl corresponding to $NaCl_{b(50)}$ values of 0.68, 0.73, and 0.70 M for these species, respectively (Fig. 5a). It is to be noticed that T_c decreased linearly when salinity is increased, and reaching the T_d value, where the $NaCl_b(g)$ starts to change (Fig. 5b). Besides, T_o dropped off linearly, then remained constant at 0.2 M for *S. alpini* and *Sa. emerici* and at 0.3 M for *S. fruticosa* (Fig. 5c).

Discussion

The results illustrated no significant difference of GP under 0-0.2 M at T_o for *S. alpini* and *Sa. emerici* and 0-0.3 M for *S. fruticosa*, reflecting the behavior of true halophytes (Gul et al. 2013; Freitas and Costa 2014). Besides, GR_{50} presented the same pattern as GP . Exceeding these salinity levels, both germination parameters (i.e., GP and GR_{50}) decreased significantly. However, *S. fruticosa* ($GP < 25\%$), *S. alpini* ($GP < 30\%$), and *Sa. emerici* ($GP < 29\%$) seeds have kept germinating at 0.8 M following the extremophytes behavior similarly to results on *S. ambigua* (Freitas and Costa 2014), *Sa. stricta*, *Sa. ramosissima* (Ungar 1995), *S. fruticosa* (Redondo-Gómez et al. 2004), and *Sa. persica* and *S. fruticosa* (Ventura and Sagi 2013). Moreover, the GP of *Sa. europaea* dimorphic seeds was high (90%) up to 342 mM NaCl for large seeds then drastically decreased to 20% at 513 mM NaCl and was totally inhibited at 855 mM (5% NaCl). Small seeds, however, showed low GP ($< 10\%$) at 342 mM (2% NaCl) (Orlovsky et al. 2016).

Under hypersalinity coinciding with a dry season, seed quiescence or dormancy is imposed for chenopodiaceae taxa (Singh et al. 2014; Muñoz-Rodríguez et al. 2017). In fact, by inhibiting germination at high salinities, halophytes counteract salinity constraints by enduring quiescent or dormant seeds at high salinity without affecting seed viability (Song et al. 2005). This also could be true for the seeds of the three studied species, as they could rest in the soil seed bank during high salinity, especially throughout the summer season coinciding with rare rainfall, high T and evaporation, and drought. The results presented above support the fact that *S. fruticosa*, *S. alpini*, and *Sa. emerici* behavior is dependent on the seasonal salinity profile of the Mediterranean salt marshes, where very high salinity predominates during the dry season (summer–early autumn) and where low salinity is prevalent in late winter and early spring (Muñoz-Rodríguez et al. 2017; Maaloul et al. 2021; Boughalleb et al. 2021). The seeds of *S. fruticosa*, *S. alpini*, and *Sa. emerici* subsequently find the most favorable saline conditions for germination in early spring. Actually, *S. fruticosa* and *S. alpini* are Mediterranean perennial halophytes with multiple and erect branches, which colonize middle-high and high-intertidal salt marshes, respectively dispersing their seeds during late autumn–early winter. However, *Sa. emerici* is a Mediterranean annual halophyte with few and erect branches that colonize low salt marches that are often flooded and its seed dissemination is in late autumn (Hayder et al. 2022). In their natural habitat, plants are not only affected by salt stress but also by T fluctuation. Indeed, both GP and GR increased

with increasing T until T_o then decreased when $T > T_o$. The T_o of the three studied species coincides with early spring T of their biotope confirming results on *S. fruticosa* (Valdés 1987; Steffen et al., 2015) and *S. alpini* (Valdés 1987; Castroviejo 1990). In addition to T , water is an essential constituent for seed germination and its accessibility is a key factor affecting germination timing and seed dormancy. In saline soils, plants are facing lower ψ due to the dissolved ions that decrease the osmotic potential of the soil solution. *S. fruticosa*, *S. alpini*, and *Sa. emerici* can germinate at low ψ , and a HaloTT model can exemplify their germination behavior in saline solutions. Our results showed that the θ_{Halo} decreased non-linearly with increasing T for the three studied species corroborating with results on chicory, cucumber, and green bean (Bakhshandeh et al. 2020, 2021, 2022), rapeseed (Bakhshandeh and Jamali 2021), and maize (Alinia et al., 2022). Besides, the θ_{HaloTT} calculated for the 50th percentile of germination of *Sa. emerici* (359 M °C h) was lower than that of *S. fruticosa* (1813 M °C h) and *S. alpini* (1067 M °C h) indicating that *Sa. emerici* necessitates fewer time to accomplish 50th percentile of germination under the same salt stress conditions compared to the two other species. However, the θ_{HaloTT} of these stem succulent halophyte species are higher than glycophytes such as chicory (74.9 M °C h) (Bakhshandeh et al. 2020), cucumber (108.1 mM °C h) (Bakhshandeh et al. 2021), green bean (165.9 M °C h) (Bakhshandeh et al. 2022), and maize (186.6 mM °C h for large seeds) (Alinia et al. 2022). Similarly, Bradford (1990) remarked that halophytes are predisposed to have high θ_{HTT} and $\sigma_{\psi b}$ values that resulted in a greater extent of germination times at reduced ψ . By applying the halotime model, the $NaCl_{b(50)}$ values of the three species were relatively constant at $T \leq T_o$, then decreased when T exceeded T_o similar to other results (Nisar et al. 2019; Steiner et al. 2019; Alinia et al. 2022). On the contrary, Seal et al. (2018) showed that the $NaCl_{b(50)}$ varied at the sub-optimal T ranges. At sub-optimal T , $NaCl_{b(50)}$ values are very high (very low ψ (MPa)); consequently the seed germination is more rapid and uniform, whereas at supra-optimal T the $NaCl_{b(50)}$ values are low, and so the seed germination is postponed and more dispersed, even at 0 mM. Accordingly, GR_{50} increased linearly at $T \leq T_o$ at all NaCl concentrations and then decreased curvilinearly at $T > T_o$. The GR_{50} became null at two different T corresponding to T_b , which is a single point and below which the seed germination is inhibited, and T_o which depends on the NaCl concentration and beyond which the seed germination is also inhibited. These results are contradictory to Seal et al. (2018) study where they showed that T_b of *Suaeda maritima* depended on NaCl concentration and became negative at ≥ 200 mM. Both *Sarcocornia* species presented very low T_b (−0.5 and −2.5°C for *S. fruticosa* and *S. alpini*, respectively). However, *Sa. emerici* showed a high T_b (9.5°C). Gummerson (1986), using the hydrotime model, found a single T_b value in sugar beet (*Beta vulgaris* subsp. *vulgaris*) under different concentrations of NaCl. Most of the studies carried out on halophytes haven't tested low temperatures (< 5°C), i.e., Alonso et al. (2017) studied the seed germination of *S. neei* under salt stress at 20°C, Calone et al. (2020) tested the seed germination of *Sa. europaea* under different NaCl concentrations at 24°C, and Muñoz-Rodríguez et al. (2017) studied seed germination of *S. alpini* and *S. fruticosa* at 24/20°C day/night under five different concentrations of NaCl.

Our results showed that T_o values of *S. fruticosa* (15°C) and *S. alpine* (11°C) are lower than *Sa. emerici* T_o (25°C). Khan et al. (2000) and Van Regteren et al. (2020) showed that seed germination of different

Salicornia species was inhibited at low T . However, Muñoz-Rodríguez et al. (2017) found that GP of *S. alpini* was < 42% at 24/20°C day/night. In addition, the T_c was 29, 24, and 40°C for *S. fruticosa*, *S. alpini*, and *Sa. emerici*, respectively. Furthermore, the T_d values were 9 and 23°C for both *Sarcocornia* species and *Sa. emerici*, respectively.

From the present study, it can be concluded that there are no differences between the $NaCl_{b(50)}$ of perennial species (*S. fruticosa* and *S. alpini*) and the annual species *Sa. emerici* under saline conditions. However, they showed differences in their θ_{HaloTT} and their cardinal temperatures. Also, the obtained results contribute to reinforce the information on the susceptibility presented by *Salicornia* and *Sarcocornia* spp. at high salinity levels (0.8 M) during their germination. However, salinity did not completely inhibit their germination. These results support the fact that *Sa. emerici*, besides its tolerance to salt stress, hypoxia due to flooding, and its annual growth cycle, show rapid and synchronized germination when salinity decreases during the rainy season coinciding with favorable temperature. This phenomenon helps *Sa. emerici* develop seedlings rapidly as much as necessary to protect them during the dry season. All these features suggest that *Sa. emerici* could persist and spread under global warming and climatic change since it is characterized by low θ_{HaloTT} and high T_b and T_o .

Accordingly, *Salicornia* cultivation could be considered a promising strategy to rehabilitation and restoration of marginalized, degraded, and salinized lands, which are inadequate for traditional agricultural purposes, with an economic income as food, feed, and medicinal uses.

Abbreviations

HaloTT

Halothermal time model

T

Temperature

T_b

Base temperature

T_o

Optimum temperature

T_c

Ceiling temperature

T_d

The T at which $NaCl_{b(g)}$ starts to change (°C) which can be equal and/or lower than T_o

$NaCl_{b(g)}$

Median base NaCl concentration

θ_{Halo}

Halotime constant

σ_{NaClb}

Standard deviation distribution of $NaCl_b$

GR

Germination rate

GP

Germination percentage

SG

Seed germination

t_g

Time to a particular germination percent g

θ_{HaloTT}

Halothermal time constant

k_T

Line slope of the relation between $NaCl_{b(g)}$ and $T \geq T_d$

Declarations

Acknowledgment

This study was supported by the ERANETMED2-72-303 PACTORES project financed by the Ministry of Higher Education and Scientific Research of Tunisia.

Dr. Esmaeil Bakhshandeh from the Genetics and Agricultural Biotechnology Institute of Tabarestan (GABIT), and Sari Agricultural Sciences and Natural Resources University (SANRU), Iran was added in this study based on the memorandum of understanding between IRA-Medenine and GABIT, signed in January 2020.

CRedit authorship contribution statement

Zaineb Hayder: Collect of seed material, conducting the experiments, and writing the original draft.

Mansour Sekrefi: Collect of seed material, conducting the experiments

Abderrazak Tlili: Collect of seed material, conducting the experiments

Fayçal Boughalleb: Conceptualization, writing – review & editing.

Esmaeil Bakhshandeh: Implementing the modeling, data analysis, and review & editing.

Raoudha Abdellaoui: Conceptualization, Writing – original draft, review & editing.

Mohamed Tarhouni: Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no competing interests.

References

1. Abdellaoui, R., F. Boughalleb, D. Zayoud, M. Neffati, and E. Bakhshandeh. 2019. Quantification of *Retama raetam* seed germination response to temperature and water potential using hydrothermal time concept. *Environ. Exp. Bot.* 157: 211–216. <https://doi.org/10.1016/j.envexpbot.2018.10.014>
2. Alinia, M., A.H. Jalali, S.A. Kazemeini, and E. Bakhshandeh. 2022. Modeling seed germination response of maize with different shapes and sizes using halotime and halothermal time concept. *Acta Physiol. Plant.* 44 (12): 1–13. <https://doi.org/10.1007/s11738-022-03462-y>
3. Alonso, C., M. Medrano, R. Pérez, P. Bazaga, and C.M. Herrera. 2017. Tissue-specific response to experimental demethylation at seed germination in the non-model herb *Erodium cicutarium*. *Epigenomes.* 1 (3): 16. <https://doi.org/10.3390/epigenomes1030016>
4. Atlas de la région économique du Sud-est tunisien. 2010. Schéma Directeur d'Aménagement de la Région Economique du Nord-Ouest, p48.
5. Bakhshandeh, E., R. Abdellaoui, and F. Boughalleb. 2021. Modeling the effects of salt stress and temperature on seed germination of cucumber using halothermal time concept. *Theor. Exp. Plant Physiol.* 33 (1): 79–93. <https://doi.org/10.1007/s40626-021-00196-z>
6. Bakhshandeh, E., R. Abdellaoui, F. Boughalleb, and M. Jamali. 2022. Quantification of green bean germination response to simultaneous salt and temperature stress: a modeling approach. *Acta Physiol. Plant.* 44 (12): 1–10. <https://doi.org/10.1007/s11738-022-03461-z>
7. Bakhshandeh, E., K.J. Bradford, H. Pirdashti, F. Vahabinia, and R. Abdellaoui. 2020. A new halothermal time model describes seed germination responses to salinity across both sub-and supra-optimal temperatures. *Acta Physiol. Plant.* 42 (8): 1–15. <https://doi.org/10.1007/s11738-020-03126-9>
8. Bakhshandeh, E., and M. Gholamhossieni. 2019. Modelling the effects of water stress and temperature on seed germination of radish and cantaloupe. *J. Plant Growth Regul.* 38 (4): 1402–1411. <https://doi.org/10.1007/s00344-019-09942-9>
9. Bakhshandeh, E., and M. Jamali. 2021. Halothermal and hydrothermal time models describe germination responses of canola seeds to ageing. *Plant Biol.* 23 (4): 621–629. <https://doi.org/10.1111/plb.13251>
10. Bakhshandeh, E., M. Jamali, E. Afshoon, and M. Gholamhossieni. 2017. Using hydrothermal time concept to describe sesame (*Sesamum indicum* L.) seed germination response to temperature and water potential. *Acta Physiol Plant.* 39 (11): 1–9. <https://doi.org/10.1007/s11738-017-2549-8>
11. Boughalleb, F., S. Maaloul, M. Mahmoudi, M. Mabrouk, E. Bakhshandeh, and R. Abdellaoui. 2021. *Limoniastrum guyonianum* behavior under seasonal conditions fluctuations of Sabkha Aïn Maïder (Tunisia). *Plant Physiology and Biochemistry.* 168: 305–320. <https://doi.org/10.1016/j.plaphy.2021.10.014>

12. Bradford, K.J. 1990. A water relations analysis of seed germination rates. *Plant Physiol.* 94 (2): 840–849. <https://doi.org/10.1104/pp.94.2.840>
13. Bradford, K.J. 1995. Water relations in seed germination. In: Kigel, J., Galili, G. (Eds.), *Seed Development and Germination*. Marcel Dekker, New York, pp. 351–396.
14. Bradford, K.J., and P. Bello, 2022. Applying population-based threshold models to quantify and improve seed quality attributes. In: Buitink, J., Leprince, O. (Eds.), *Advances in seed science and technology for more sustainable crop production*. Burleigh Dodds Science Publishing, Cambridge, UK.
15. Calone, R., R. Sanoubar, E. Noli, and L. Barbanti. 2020. Assessing *Salicornia europaea* tolerance to salinity at seed germination stage. *Agriculture*. 10 (2) : 29. <https://doi.org/10.3390/agriculture10020029>
16. Cardenas-Pérez, S., A. Piernik, J. J. Chanona-Pérez, M.N. Grigore, and M. J. Perea-Flores. 2021. An overview of the emerging trends of the *Salicornia* L. genus as a sustainable crop. *Environ. Exp. Bot.* 191: 104606. <https://doi.org/10.1016/j.envexpbot.2021.104606>
17. Castroviejo, S. 1990. *Sarcocornia*. In: Castroviejo, S., Laínz, M., López González, G., Montserrat, P., Muñoz Garmendia, F., Paiva, J., Villar, L. (Eds.), *Flora Iberica: Plantas Vasculares de la Península Ibérica e Islas Baleares*. Real Jardín Botánico, CSIC, Madrid, pp. 526–531.
18. Chevalier, A. 1922. Les Salicornes et leur emploi dans l'alimentation: étude historique, botanique, économique. *Journal d'agriculture traditionnelle et de botanique appliquée*. 2 (16) : 697–785.
19. Covell, S., R.H. Ellis, E.H. Roberts, and R.J. Summerfield. 1986. The influence of temperature on seed germination rate in grain legumes. I. A comparison of chickpea, lentil, soyabean, and cowpea at constant temperatures. *J. Exp. Bot.* 37 (5): 705–715. <https://doi.org/10.1093/jxb/37.5.705>
20. Custódio, L., M.J. Rodrigues, C.G. Pereira, V. Castañeda-Loaiza, E. Fernandes, D. Standing, A. Neori, M. Shpigel, and M. Sagi. 2021. A review on *sarcocornia* species: Ethnopharmacology, nutritional properties, phytochemistry, biological activities and propagation. *Foods*. 10 (11): 2778. <https://doi.org/10.3390/foods10112778>
21. Cuttelod, A., N. García, D. Abdul Malak, H. Temple, and V. Katariya. 2009. The Mediterranean: a biodiversity hotspot under threat. In: Vié, J.C., Hilton-Taylor, C., Stuart, S.N. (Eds.), *The 2008 Review of The IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland, pp. 89–101.
22. Davy, A.J., G.F. Bishop, and C.S.B. Costa. 2001. *Salicornia* L. (*Salicornia pusilla* J. Woods, *S. ramosissima* J. Woods, *S. europaea* L., *S. Obscura* P. W. Ball & Tutin, *S. nitens* P. W. Ball & Tutin, *S. fragilis* P. W. Ball & Tutin, and *S. dolichostachya* Moss). *J. Ecol.* 89 (4): 681–707.
23. Davy, A.J., G.F. Bishop, H. Mossman, S. Redondo-Gomez, J.M. Castillo, E.M. Castellanos, T. Luque, and M.E. Figueroa. 2006. Biological flora of the British Isles: *Sarcocornia perennis* (Miller) A.J. Scott. *J. Ecol.* 94: 1035–1048. <https://doi.org/10.1111/j.1365-2745.2006.01156.x>
24. Freitas, R.F., and C.S. Costa. 2014. Germination responses to salt stress of two intertidal populations of the perennial glasswort *Sarcocornia ambigua*. *Aquat. Bot.* 117: 12–17. <https://doi.org/10.1016/j.aquabot.2014.04.002>

25. Grime, J.P., and B.D. Campbell. 1991. Growth rate, habitat productivity, and plant strategy as predictors of stress response. In: Mooney, H.A., Winner, W.E., Pell, E.J., Chu, E. (Eds.), *Response of Plants to Multiple Stresses*. Academic Press, London, pp. 143–159.
26. Gul, B., R. Ansari, T.J. Flowers, and M.A. Khan. 2013. Germination strategies of halophyte seeds under salinity. *Environ. Exp. Bot.* 92 : 4–18. <https://doi.org/10.1016/j.envexpbot.2012.11.006>
27. Gummerson, R.J. 1986. The effect of constant temperatures and osmotic potentials on the germination of sugar beet. *J. Exp. Bot.* 37 (6): 729–741. <https://doi.org/10.1093/jxb/37.6.729>
28. Guo, J., Y. Li, G. Han, J. Song, and B. Wang. 2018. NaCl markedly improved the reproductive capacity of the euhalophyte *Suaeda salsa*. *Funct. Plant Biol.* 45 (3): 350–361. <https://doi.org/10.1071/FP17181>
29. Hardegree, S.P., C.T. Walters, A.R. Boehm, P.J. Olsoy, P.E. Clark, and F.B. Pierson. 2015. Hydrothermal Germination Models: Comparison of Two Data Fitting Approaches with Probit Optimization. *Crop Sci.* 55 (5) : 2276–2290. <https://doi.org/10.2135/cropsci2014.10.0703>
30. Hayder, Z., R.B. Gaied, A. Tlili, I. Sbissi, M. Tarhouni. 2022. Phylogenetic and morphological studies of *Sarcocornia* (L.) AJ Scott and *Salicornia* L. (*Chenopodiaceae*) and insights into plant diversity with first record of two species new for Tunisia. *Genet. Resour. Crop Evol.* 1–13. <https://doi.org/10.1007/s10722-022-01454-y>
31. Kadereit, G., P. Ball, S. Beer, L. Mucina, D. Sokoloff, P. Teege, A.E. Yaprak, and H. Freitag. 2007. A taxonomic nightmare comes true: phylogeny and biogeography of glassworts (*Salicornia* L., *Chenopodiaceae*). *Taxon.* 56 (4): 1143–1170. <https://doi.org/10.2307/25065909>
32. Keiffer, C.H., and I.A. Ungar. 1997. The effect of extended exposure to hypersaline conditions on the germination of five inland halophyte species. *Am. J. Bot.* 84 (1): 104–111. <https://doi.org/10.2307/2445887>
33. Khan, M.A., and I.A. Ungar. 1996. Influence of salinity and temperature on the germination of *Haloxylon recurvum*. *Ann Bot* 78: 547–551. <https://doi.org/10.1006/anbo.1996.0159>
34. Khan, M.A. 1999. Comparative influence of salinity and temperature on the germination of subtropical halophytes. In: Lieth, H., Moschenko, M., Lohman, M., Koyro, H.W., Hamdy, A. (Eds.), *Halophyte Uses in different climates I: Ecological and Ecophysiological Studies*. Backhuys Publishers, Leiden, Netherlands, pp. 77–88.
35. Khan, M.A., B. Gul. 1998. High salt tolerance in germinating dimorphic seeds of *Arthrocnemum indicum*. *Int. J. Plant Sci.* 159 (5): 826–832. <https://doi.org/10.1086/297603>
36. Khan, M.A., and B. Gul. 2006. Halophyte seed germination. In: Khan, M.A., Weber, D.J. (Eds.), *Ecophysiology of High Salinity Tolerant Plants*. Springer Academic Publishers: Dordrecht, The Netherlands, pp. 11–31.
37. Khan, M.A., B. Gul, and D.J. Weber. 2000. Germination responses of *Salicornia rubra* to temperature and salinity. *J. Arid Environ.* 45 (3): 207–214. <https://doi.org/10.1006/jare.2000.0640>
38. Leite, M.S., F.J. Andrade Barros, S.H. Khoury, O.H. Bonilla, and C.S. Bonifácio Costa. 2007. Cultivo de Plântulas de *Salicornia gaudichaudiana* Mog. para uso em Bioremediação junto a Viveiros de

- Criação de Camarão. *Revista Brasileira de Biociências, Porto Alegre*. 5 (1) : 297–299.
39. Maaloul, S., R. Abdellaoui, M. Mahmoudi, T. Bouhamda, E. Bakhshandeh, and F. Boughalleb, 2021. Seasonal environmental changes affect differently the physiological and biochemical responses of two *Limonium* species in Sabkha biotope. *Physiol. Plant.* 172 (4): 2112–2128.
<https://doi.org/10.1111/ppl.13446>
40. Manousaki, E., and N. Kalogerakis. 2011. Halophytes present new opportunities in phytoremediation of heavy metals and saline soils. *Ind. Eng. Chem. Res.* 50 (2): 656–660.
<https://doi.org/10.1021/ie100270x>
41. Muñoz-Rodríguez, A.F., I. Sanjosé, B. Márquez-García, M.D. Infante-Izquierdo, A. Polo-Ávila, F.J.J. Nieva, and J.M. Castillo. 2017. Germination syndromes in response to salinity of Chenopodiaceae halophytes along the intertidal gradient. *Aquat. Bot.* 139: 48–56.
<https://doi.org/10.1016/j.aquabot.2017.02.003>
42. Navarro, L., and J. Guitián. 2003. Seed germination and seedling survival of two threatened endemic species of the northwest Iberian Peninsula. *Biol. Conserv.* 109 (3): 313–320.
[https://doi.org/10.1016/S0006-3207\(02\)00151-9](https://doi.org/10.1016/S0006-3207(02)00151-9)
43. Nisar, F., B. Gul, M.A. Khan, and A. Hameed. 2019. Germination and recovery responses of heteromorphic seeds of two co-occurring *Arthrocnemum* species to salinity, temperature, and light. *S. Afr. J. Bot.* 121: 143–151. <https://doi.org/10.1016/j.sajb.2018.10.035>
44. Orlovsky, N., U. Japakova, H. Zhang, and S. Volis. 2016. Effect of salinity on seed germination, growth, and ion content in dimorphic seeds of *Salicornia europaea* L. (*Chenopodiaceae*). *Plant Divers.* 38 (4): 183–189. <https://doi.org/10.1016/j.pld.2016.06.005>
45. Ortuno, J.A., A. Verde, J. Fajardo, D. Rivera, C. Obon, and F. Alcaraz. 2020. Halophytes in Arts and Crafts: Ethnobotany of Glassmaking. In: Grigore, M.N. (Eds), Handbook of Halophytes. Springer, Cham, pp. 1–32.
46. Panta, S., T. Flowers, P. Lane, R. Doyle, G. Haros, and S. Shabala. 2014. Halophyte agriculture: Success stories. *Environ. Exp. Bot.* 107: 71–83. <https://doi.org/10.1016/j.envexpbot.2014.05.006>
47. Panuccio, M. R., S. E. Jacobsen, S. S. Akhtar, and A. Muscolo. 2014. Effect of saline water on seed germination and early seedling growth of the halophyte quinoa. *AoB plants.* 6.
<https://doi.org/10.1093/aobpla/plu047>
48. Redondo-Gómez, S. 2004. Aspectos ecológicos del género *Sarcocornia* en el suroeste de la Península Ibérica : papel en la sucesión, diversidad genética y ecofisiología de sus poblaciones. Doctoral Thesis. University of Sevilla, Sevilla, pp. 43–56.
49. Rosa, R., A. Marques, and M.L. Nunes. 2012. Impact of climate change in Mediterranean aquaculture. *Rev Aquac.* 4 (3): 163–177. <https://doi.org/10.1111/j.1753-5131.2012.01071.x>
50. Rowse, H.R., and W.E. Finch-Savage. 2003. Hydrothermal threshold models can describe the germination response of carrot (*Daucus carota*) and onion (*Allium cepa*) seed populations across both sub-and supra-optimal temperatures. *New Phytol.* 158 (1): 101–108.
<https://doi.org/10.1046/j.1469-8137.2003.00707.x>

51. Rozema, J., and H. Schat. 2013. Salt tolerance of halophytes, research questions reviewed in the perspective of saline agriculture. *Environ. Exp. Bot.* 92: 83–95.
<https://doi.org/10.1016/j.envexpbot.2012.08.004>
52. Seal, C.E., L.J. Barwell, T.J. Flowers, E.M. Wade, and H.W. Pritchard. 2018. Seed germination niche of the halophyte *Suaeda maritima* to combined salinity and temperature is characterised by a halothermal time model. *Environ. Exp. Bot.* 155:177–184.
<https://doi.org/10.1016/j.envexpbot.2018.06.035>
53. Singh, D., A.K. Buhmann, T.J. Flowers, C.E. Seal, and J. Papenbrock. 2014. *Salicornia* as a crop plant in temperate regions: selection of genetically characterized ecotypes and optimization of their cultivation conditions. *AoB plants*, 6. <https://doi.org/10.1093/aobpla/plu071>
54. Song, J.I.E., G.U. Feng, C. Tian, and F. Zhang. 2005. Strategies for adaptation of *Suaeda physophora*, *Haloxylon ammodendron* and *Haloxylon persicum* to a saline environment during seed–germination stage. *Ann. Bot.* 96 (3): 399–405. <https://doi.org/10.1093/aob/mci196>
55. Song, J., and B., Wang. 2015. Using euhalophytes to understand salt tolerance and to develop saline agriculture: *Suaeda salsa* as a promising model. *Ann. Bot.* 115 (3): 541–553.
<https://doi.org/10.1093/aob/mcu194>
56. Steiner, F., A.M. Zuffo, A. Busch, T.D.O. Sousa, and T. Zoz. 2019. Does seed size affect the germination rate and seedling growth of peanut under salinity and water stress. *Pesqui. Agropecu. Trop.* 49.
57. Taghvaei, M., and M. Ghaedi. 2010. The impact of cardinal temperature variation on the germination of *Haloxylon aphyllum* L. seeds. *J Ecol Environ.* 33(3) : 187–193.
<https://doi.org/10.5141/JEFB.2010.33.3.187>
58. Ungar, I.A. 1995. Seed germination and seed-bank ecology of halophytes. In: Kigel, J., Galili, G., (Eds.), *Seed development and germination*. Marcel Dekker Inc, New York, pp. 599–627.
59. Valdés, B. 1987. *Salicornia*. In: Valdés, B., S. Talavera, and E. Fernández-Galiano, (Eds), *Flora vascular de Andalucía occidental*, vol I. Ketres, Barcelona, pp. 184–185.
60. Van Regteren, M., E.H. Meesters, M.J. Baptist, A.V. De Groot, T.J. Bouma, and K. Elschot. 2020. Multiple environmental variables affect germination and mortality of an annual salt marsh pioneer: *Salicornia procumbens*. *Estuaries Coasts*. 43 (6): 1489–1501. <https://doi.org/10.1007/s12237-020-00735-y>
61. Van't Hoff, J.H. 1887. Die Rolle des osmotischen Druckes in der Analogie zwischen Lösungen und Gasen. *Zeitschrift für physikalische Chemie*. 1 (1): 481–508. <https://doi.org/10.1515/zpch-1887-0151>
62. Ventura, Y., and M. Sagi. 2013. Halophyte crop cultivation: the case for *Salicornia* and *Sarcocornia*. *Environ. Exp. Bot.* 92: 144–153. <https://doi.org/10.1016/j.envexpbot.2012.07.010>
63. Ventura, Y., W.A. Wuddineh, M. Myrzabayeva, Z. Alikulov, I. Khozin-Goldberg, M. Shpigel, T.M. Samocha, and M. Sagi. 2011. Effect of seawater concentration on the productivity and nutritional

- value of annual *Salicornia* and perennial *Sarcocornia* halophytes as leafy vegetable crops. *Sci. Hortic.* 128 (3): 189–196. <https://doi.org/10.1016/j.scienta.2011.02.001>
64. Yuan, F., J. Guo, S. Shabala, and B. Wang. 2019. Reproductive physiology of halophytes: current standing. *Front. Plant Sci.* 9: 1954. <https://doi.org/10.3389/fpls.2018.01954>
65. Zhu, G.L., and S.C. Sanderson. 2017. Genera and a new evolutionary system of World *Chenopodiaceae*. Science Press, Beijing, 1-150.

Figures

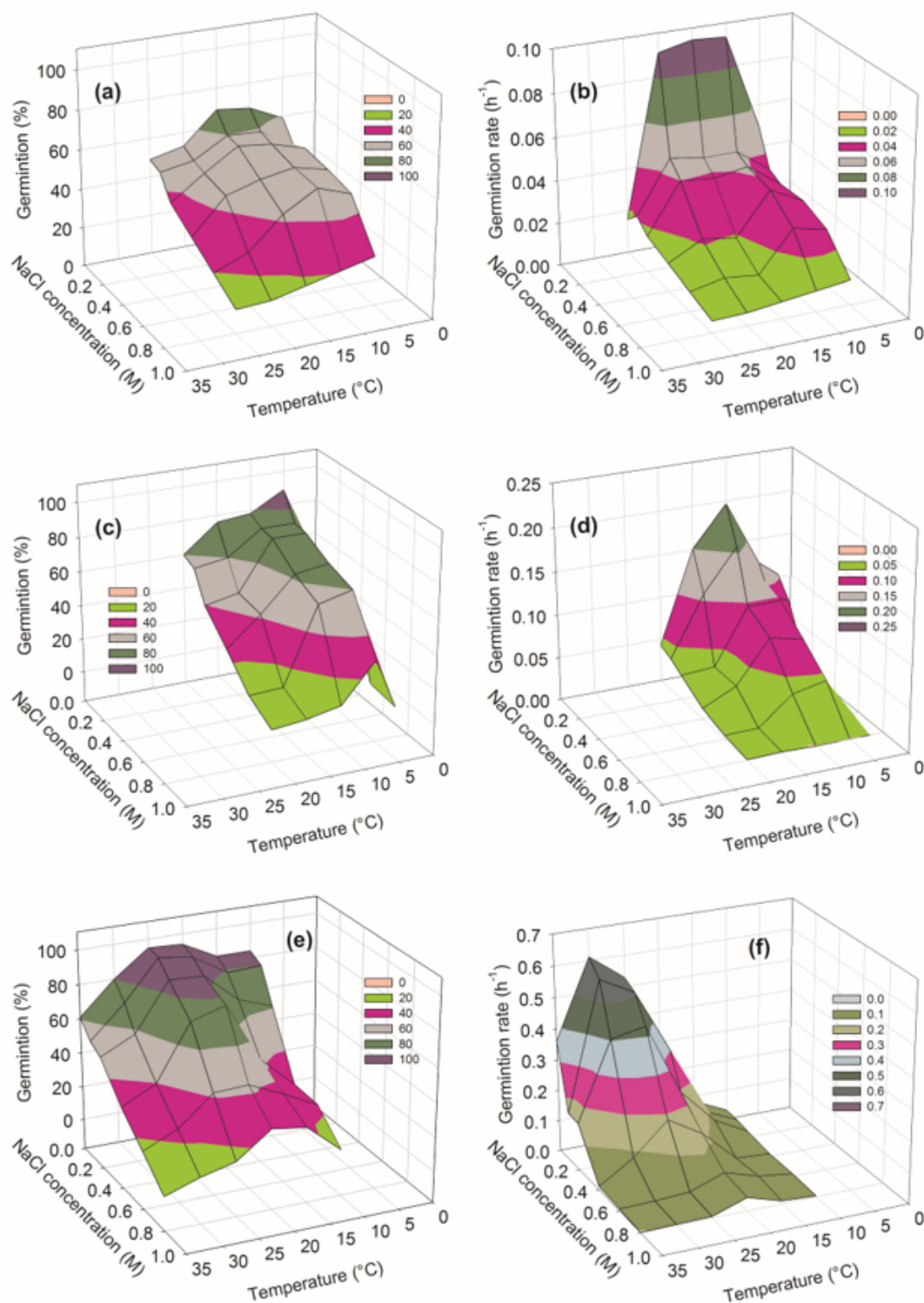


Figure 1

Effect of various temperatures on GP (a, c, and e) and GR_{50} (b, d, and f) under different concentrations of NaCl for *Sarcocornia fruticosa*, *Sarcocornia alpini*, and *Salicornia emerici*, respectively.

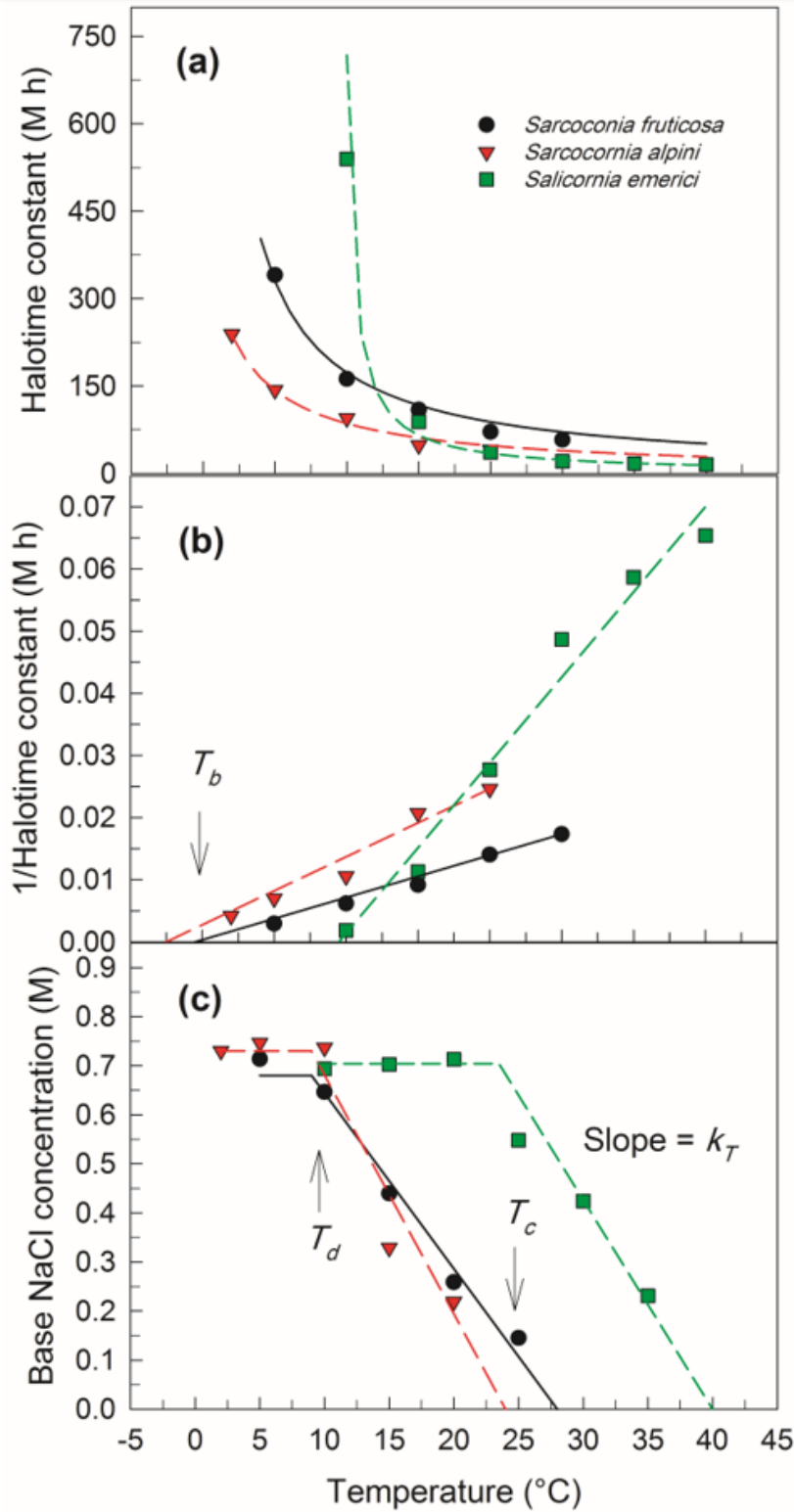


Figure 2

(a) Halotime constant (θ_{Halo}) and (c) base NaCl concentration ($NaCl_{b(50)}$) according to temperature (T) for *Sarcocornia fruticosa*, *Sarcocornia alpini*, and *Salicornia emerici* seed lots. In (b), the inverse of θ_{Halo} vs. T , which will be linear below T_o (and extrapolated to T_b (−0.5, −2.5, and 9 °C, respectively) at the intercept

on the x -axis. In (c), the predicted lines are for the 50th percentile intercepts $NaCl_{b(50)} = 0$ M at T_c (29, 24, and 40 °C for *Sarcocornia fruticosa*, *Sarcocornia alpini*, and *Salicornia emerici*, respectively).

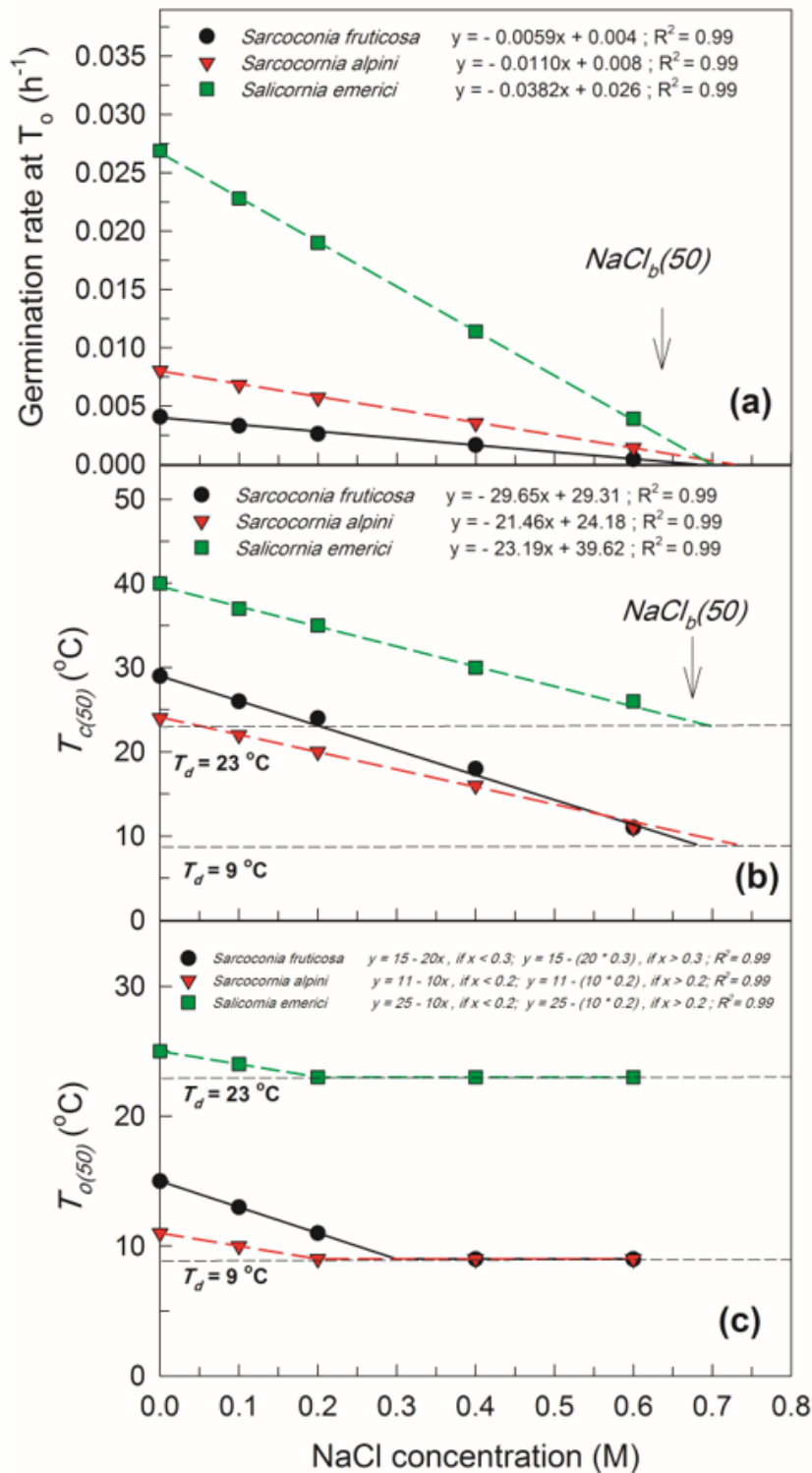


Figure 3

Linear regression of probit (g) as plotted vs. base NaCl concentrations ($NaCl_{b(g)}$, M) and adjusted base NaCl concentrations ($-NaCl_{b(g)} + k_T(T - T_o)$) for each of the seed lots of *Sarcocornia fruticosa*,

Sarcocornia alpini, and *Salicornia emerici*. Symbols represent the probit germination fraction observed values at each T vs. the calculated base values for diverse germination fractions (g).

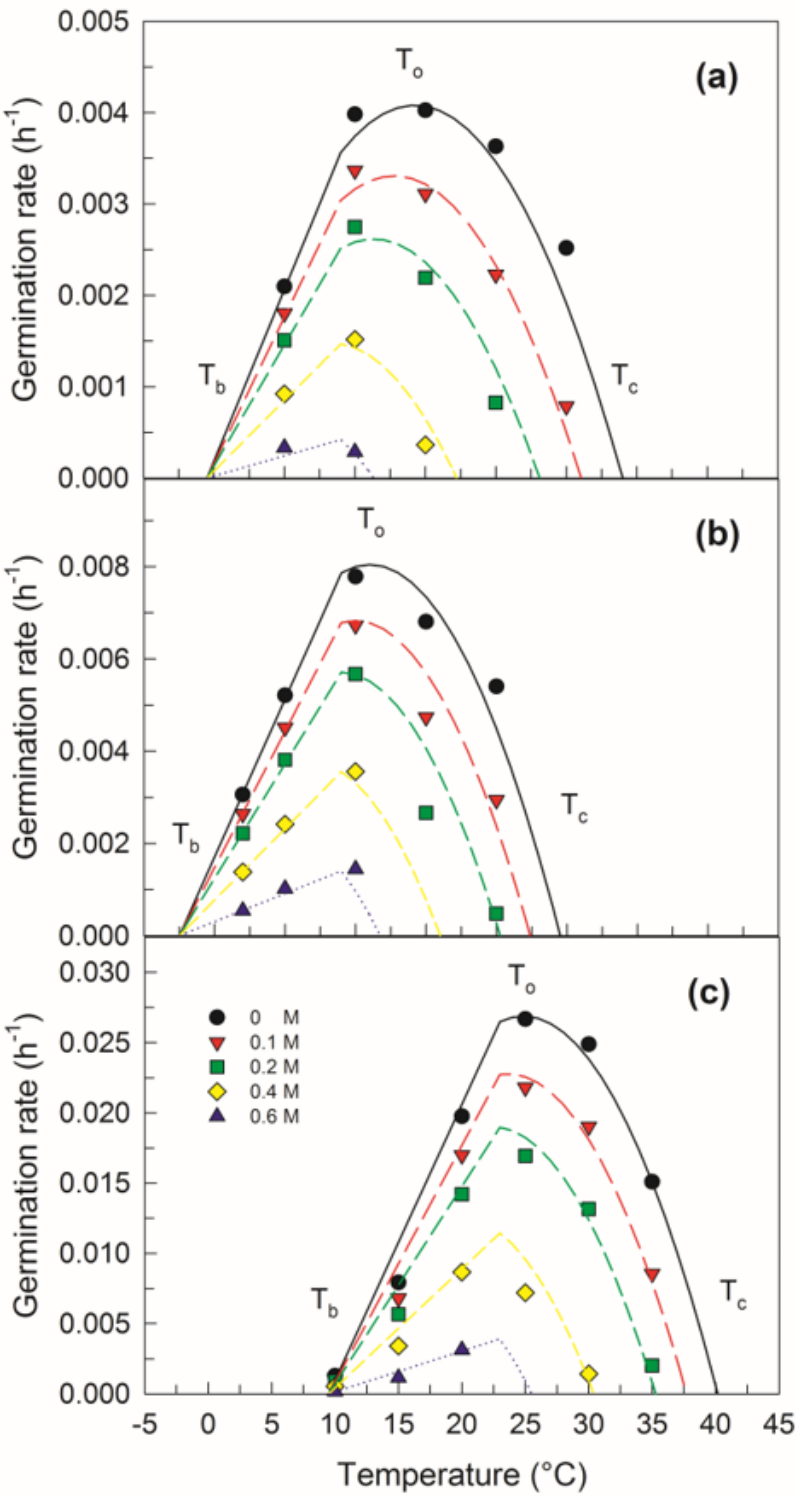


Figure 4

Effect of temperature (T) on the median germination rates ($= 1/t_{50}$) of (a) *Sarcocornia fruticosa*, (b) *Sarcocornia alpini*, and (c) *Salicornia emerici* seed lots at the different NaCl concentrations (M).The

symbols represent the actual data and the lines drawn through these points are based on the parameters of the halothermal time model (Table 3).

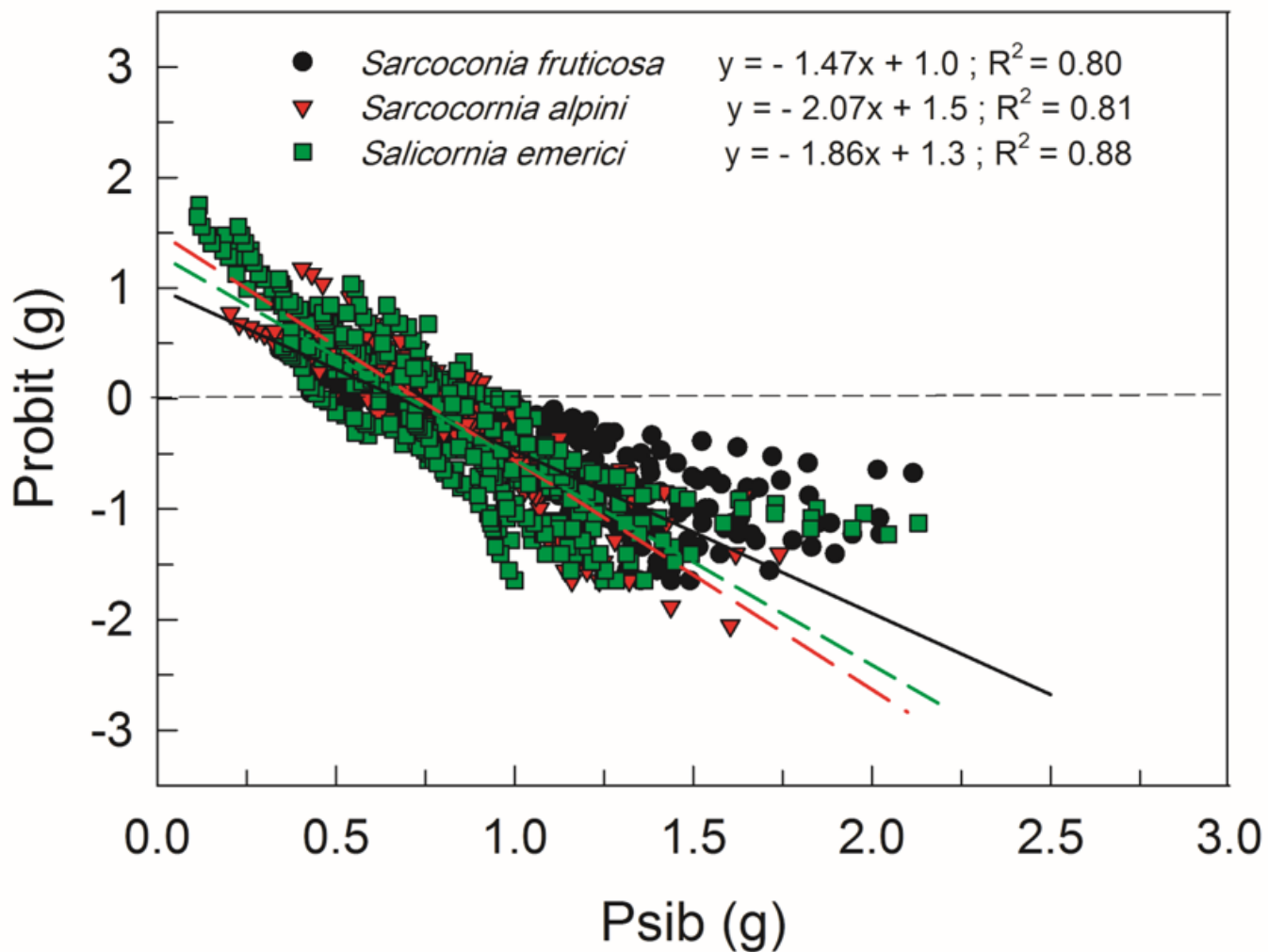


Figure 5

Effect of the different NaCl concentrations (M) on the median germination rate ($= 1/t_{50}$) at T_o , the $T_{c(50)}$, and the $T_{o(50)}$ of *Sarcoconia fruticosa*, *Sarcoconia alpini*, and *Salicornia emerici* seed lots.