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SALT AND DROUGHT EFFECT ON GERMINATION AND INITIAL GROWTH OF *Lavandula stoechas*: A POTENTIAL CANDIDATE FOR REHABILITATION OF THE MEDITERRANEAN DISTURBED COASTAL LANDS

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Abstract

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Information relating to germination and seedling emergence of a plant aids in determining the species spatiotemporal distribution and also facilitates in designing appropriate plant management strategies within an ecosystem. *Lavandula stoechas* L. (Lamiaceae), a naturally occurring shrub, is particularly used in pharmaceutical and cosmetic industries. This species, indeed, has the potential for rehabilitation of degraded costal lands. However, various aspects of its seed biology have not yet been recognised. Here, we aimed to assess the effects of different soluble salts (NaCl, $CaCl_2$, $MgCl_2$ and Na_2SO_4) and drought (as simulated by polyethylene glycol, $[PEG]_{6000}$) on seed germination patterns and early seedling growth responses. Seeds treated with five iso-concentration (0–100 mM) salinities and five PEG_{6000} (0 to −1 MPa) levels were incubated in a controlled germinator set at 20°C. The preliminary results revealed that seeds of *L. stoechas* lacked primary/innate dormancy and they germinated abundantly (89.2% germination) and fast (7.4% day^{-1}) in the absence of stress. Regardless of the kind of salt applied, the germination percentage (GP) and germination rate index (GRI) fell significantly with increasing salinity, and germination ceased completely at 100 mM Na_2SO_4. In fact, the salinity tolerance index (STI) showed that, among all salts tested, Na_2SO_4 appeared to have more inhibitory action on germination. In addition, *L. stoechas* was found to be tolerant to moderate salty stress (<50 mM) in early growth phase. The salt solution parameters (i.e. concentration, electrical conductivity [EC] and salt content) were best correlated with seed/seedling metrics. pH was not a good predictor for salt effects at the germination/seedling stages. Overall, this species seems to be sensitive to drought at the germination and initial growth phases. The germination recovery potential of *L. stoechas* in both stresses stipulates that this species can be regarded as a promising candidate in the rehabilitation of Mediterranean disturbed coastal habitats.

Key words: *Lavandula stoechas*, salt stress, water stress, germination patterns, seedling growth.

Introduction

The Mediterranean ecosystem is currently undergoing indubitably advanced degradation, as compared to other regions around the world, already exacerbated by substrate salinisation, prolonged drought, land clearing and plant overexploitation (Cherifi et al., 2017; Sardans et al., 2020). These threats are causing multiple negative impacts on the Mediterranean coastal habitat vegetation in the form of low emergence of new seedlings, limitation of plant population distribution, shift in phenology and reproduction timing (Belgacem et al., 2008). Critically, rehabilitation of these habitats is often barely feasible due to soil salinity, sporadic rainfall patterns and rough topography (Martínez-Valderrama et al., 2018). Under such circumstances, various attempts in management practices have been implemented, including ecosystem resilience and afforestation programmes with which native plants are utilised, and some of these attempts, fortunately, have shown promising results particularly under desirable climatic conditions (Nedjimi, 2012).

Seed germination and early seedling growth, being the most fragile and vulnerable phases in plant life cycle, are intimately connected and closely effected by various overlapping environmental factors such as temperature, water availability, soil salinity and light, thereby seedling establishment requirements are the bottleneck that should be framed, whether for the crop production or land restoration (Zhang et al., 2018; Paraskevopoulou et al., 2020). For example, soil salinity could disturb directly plant plasticity via the harmful effects of excessive ion accumulation (i.e. ion toxicity) or indirectly through osmosis by obstructing plant imbibition by water (Tuteja, 2007), and thus, both circumstances lead to an oxidative stress and severe impairment in germination and plant growth (De Souza et al., 2016).

High salinization rate is the most pernicious stress factor facing soils, which leads to restriction in plant distribution and productivity (Farooq et al., 2017). Affecting 20% of irrigated lands and 7% of the earth's land surface, this widespread threat is often owing to either excessive evaporation induced by aridity, intensive use of brackish groundwater, seawater intrusion or soil-unsustainable practices (Machado, Serralheiro, 2017; Alfarrah, Walraevens, 2018). To investigate the effect of salt on germination and seedling growth, various studies have conventionally used sodium chloride (NaCl), since it is the most preponderant salt contained in soils (El-Keblawy, Al-Rawai, 2005; Mehdadi et al., 2017). Moreover, in addition to Na^+ and Cl^-, there are many other cations (e.g. Mg^{2+}, Ca^{2+}, K^+) and anions (e.g. SO_4^{2-}, HCO_3^-, CO_3^{2-}) held in salty soils (Qadir et al., 2000). These inorganic ions can either act in soil as osmoticum and restrict plant emergence (Sosa et al., 2005) or cause toxic effect and inflect embryo mortality (Llanes et al., 2005). Sosa et al. (2005) suggested that salt ion effects would have less influence on seed germination in *Prosopis strombulifera* than the soil water content. Comparable constatations were also drawn on the seed germination of *Chenopodium glaucum* (Duan et al., 2004), *Suaeda vermiculata* (El-Keblawy et al., 2018), *Haloxylon stocksii* (Rasheed et al., 2019) and *Prosopis pallida* (Aljasm et al., 2021). Zehra et al. (2013) reported the germination inhibition in *Phragmites karka* by using different salts of sodium, magnesium and potassium. They postulated that if such seeds did not recover, the mortality may be due to specific ion injury.

Mediterranean soils are not only affected by NaCl, but also by other saline agents (e.g. $MgCl_2$, $CaCl_2$ and Na_2SO_4). In many cases, these are present at higher doses than NaCl (Alexakis et al., 2015; Nedjimi et al., 2020); each of them affects seed germination and plant emergence in distinct ways (Li et al., 2010).Testing the influence of multiple salt agents on seed germination and seedling growth not only sheds light into plant tolerance under these salts, but also helps in extrapolating the results from laboratory to natural conditions with increased reliability (Zhang et al., 2018). A large number of studies have mainly focused on the impact of soluble salts on germination, distribution, exploitation and physiological resistance mechanisms in halophytes (i.e. salt-tolerant plants) (Zhang et al., 2015; Zhao et al., 2014). However, there are much less investigations highlighting the influence of these salts upon seed germination and plant growth of glycophytes (i.e. salt-sensitive plants) (Nedjimi, Zemmiri, 2019).

In high-salty habitats, the plants can suffer a break in cells' ion homeostasis, disturbance in ionic balance, inhibition in enzyme activity and severe restraint in the distribution of K^+ and Ca^{2+} in cells (Niu et al., 1995). In such an environment, plants can tolerate the influence of stress only if they can adjust their osmotic pressure and restore their ionic balance (Li et al., 2011). In barley (*Hordeum vulgare* L.), maintenance of high germination under salt stress necessitated (1) synthesis of organic solutes that conferred to seeds an osmotic adjustment and facilitated seed water imbibition and (2) compartmentalisation of Na^+ in the vacuole, thereby countering the toxic effects of Na^+ on the cell (Zhang et al., 2010). Khan and Gulzar (2003) postulated that in coastal lands, generally suffering rising salinity levels, the increase in relative humidity substantially dilutes the salt concentration in soil. They further suggested that, to enhance the prospects of successful recovery of coastal land, assessing plant tolerance against salt stress during germination is critical prior to planning such projects.

In nature, drought is the most common and lethal stress for plants, particularly in critical growth stages, and it may result in complete cessation of plant development (Hossain et al., 2016). Besides, several approaches in the climate change scenarios forecast an outstanding increase in water shortage associated with more frequent, prolonged and intense droughts in many regions around the world (Zhang et al., 1999). In the Mediterranean region, aridity has deleterious repercussions on plant physiology. Indeed, water deficit leads to a decrease in soil water potential that prevents and delays plant emergence (Krichen et al., 2014; Dadach, Mehdadi, 2018). Owing to these concerns, considerable efforts were undertaken in the hope of deciphering mechanisms underlying plant responses to water stress, with the objective to breed resistant crops. Wild plants, meanwhile, deploy a number of adaptive mechanisms to cope with aridity. Postponing germination till the arrival of adequate conditions, including sufficient rainfall, is one such mechanism (Aljasmi et al., 2021). Till date, little is known about seed germination performance and plant growth response against drought, particularly in the North African natural flora (Dadach, Mehdadi, 2021). Understanding the level of moisture stimulating germination and species-specific threshold tolerance to water stress is the cornerstone towards achieving sustainable plant reintroduction and land restoration projects in degraded habitats (De Carvalho et al., 2020; Aljasmi et al., 2021).

Lavandula stoechas (Lamiaceae) is a well-known multipurpose plant that is often used throughout the Mediterranean region in traditional medicine, perfumes and other personal care products or sold as an ornamental plant for gardening (Ernst, 2017). Lavender is distributed over North Africa, the Mediterranean basin, Europe and western India. This species is found naturally growing in the coastal shrub lands, coastal garrigues and sea cliffs, often exposed to sea spray (Paraskevopoulou et al., 2020). It is commercially cultivated worldwide in a number of countries mainly in Europe and Asia (Shawl, Kumar, 2000; Lawrence, 2008). In controlled conditions, optimum temperature for germination of *L. stoechas* seeds is 20 °C (Catav et al., 2012). Previously, many assays were done for the domestication of lavender in India during the British period. Later, in 2000, the Institute of Himalayan Bioresource successfully introduced this shrub in Himachal Pradesh, India (Singh et al., 2007).

Several phytopharmacological reports have emphasised that *L. stoechas* has the potential to treat nephrotic syndromes and rheumatic diseases, acts as an antispasmodic agent, and reduces the level of hyperglycemia, pain and inflammatory problems (Benabdelkader et al., 2011; Ez zoubi et al., 2016). Many essential oils extracted from *L. stoechas* leaves have shown effective antibacterial and antiviral activities. For example, camphor and 1,8-cineole have an antibacterial effect, mainly against *Escherichia coli*, *Listeria monocytogenes* and *Staphylococcus aureus* (Sarac, Ugur, 2009). Recently, El Ouali et al. (2016) inferred that *Lavandula stoechas* essential oils have a positive effect against *Anopheles labranchiae*, a malaria transmission vector, at a dose of 500 mg ml^{-1}. These essential oils are often obtained either by infusion or from the decoction of leaves or the whole aerial part (Ez zoubi et al., 2020).

Taking the above into account and considering the lack of data on the effect of salinity and water stress on *Lavandula stoechas* seed germination and growth, and in the context to carry out restoration of the Algerian disturbed coastal habitats, characterised by high salt influence and unpredictable precipitation, this work was conducted in an attempt to highlight the effects of different salt agents (mostly encountered in these lands) and drought on seed germination patterns and early growth parameters in this valuable species. The results would also provide more insight about the effectiveness of *L. stoechas* regeneration through seeds under the most common abiotic stresses affecting the Mediterranean ecosystem.

Material and methods

Study species and seed harvesting site

Butterfly lavender (*L. stoechas*), also named toupee lavender or wild lavender (Boukhatem et al., 2020), is a perennial, evergreen, low-growing shrub (chamaephyte) that usually grows to 0.3–1 m in height, with erect, quadrangular and floriferous stems that become woody and rough on ageing. The flowers are pink to purple, having pedicel and tubular calyx and arranged in whorls tied in dense cylindrical clusters up to 5 cm long. Each flower is subtended by a bract 4–8 mm long. Leaves are opposite, sessile, 1–4 cm long, greyish and tomentose (covered with dense small hairs) with a strong aromatic odour (Fig. 1). *L. stoechas* starts flowering in late winter and it reaches the full bloom from mid-June to mid-July (Quézel, Santa, 1963; Ez zoubi et al., 2020). Fruit is an achene that is woody, brown and dehiscent containing four blackish-brown subglobose seeds (Lim, 2014). This species grows in rocky, calcareous areas and prefers acidic soils, but it can thrive in clay soils (pH > 8.5).

Ripe inflorescences, containing *L. stoechas* mature seeds, were collected in August 2020 from a wild-growing population in the vicinity of Bejaia city, Northeast Algeria (36°44´N, 05°01´E). The seed-harvesting site has a typical Mediterranean climate, where precipitation is less than 800 mm per annum, with extreme heterogeneity in time, most of the rains occurring in winter, and an average temperature of about 19.5 °C. The soil is non-saline, with an electrical conductivity (EC) of 0.55 mS cm^{-1}, and slightly alkaline (pH = 7.8). Seeds were randomly collected from almost a whole population (>60 plants) in order to avoid genetic homogeneity. The associated plants with *L. stoechas* are garrigue characteristic species such as *Scabiosa columbaria*, *Galactites tomentosa*, *Echium creticum*, *Myrtus communis*, *Genista tinctoria* and *Cistus monspeliensis*. Once at laboratory, the mature seeds were peeled by hand from achenes-pericarp and kept at ambient temperature till the experiment was conducted.

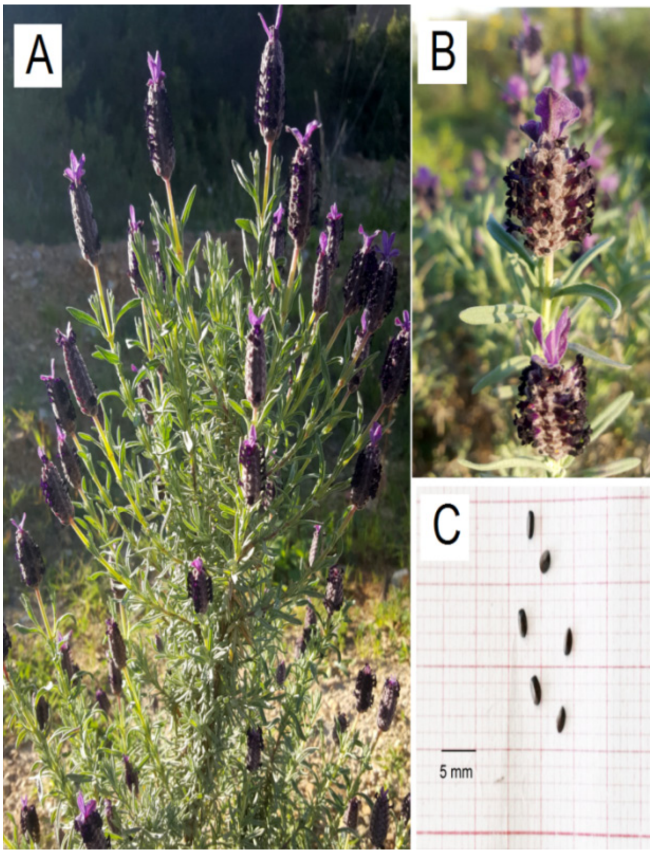

Fig. 1. Butterfly lavender (*Lavandula stoechas*) aerial part (A), flower cluster (B), seeds (C).

Seed germination experiment

Before being used for tests, healthy and intact seeds were surface sterilised by hypochlorite solution (10% NaOCl) for 5 min and washed abundantly with distilled water. In order to assess the impact of various salt agents (NaCl, $CaCl_2$, $MgCl_2$ and Na_2SO_4) and drought upon the germination pattern and initial seedling growth in *Lavandula stoechas*, seeds were germinated at five salt (0, 25, 50, 75 and 100 mM) iso-concentrations and five polyethylene glycol $(PEG)_{6000}$ (0, −0.25, −0.5, −0.75 and −1 MPa) levels. The EC and pH of all salt solutions as well as the salt content of each solution are given in Table 1. EC and pH were measured by WTW Multi 9310 instrument at 20 ± 1 °C (the same germination T°). PEG solutions were obtained by dissolving different concentrations of PEG_{6000} in deionised H_2O according to the required water potential to be induced, as described by Michel and Kaufmann (1973). Seeds were laid on double-layer filter paper sheet containing within 90 mm Petri dishes and supplied with 7 ml of the test solutions. For each treatment, 100 seeds were split evenly into four replicates (25 seeds each). As a precaution to minimise evaporation, the dishes were wrapped hermetically with parafilm. The dishes were randomised in the dark at a constant optimum temperature of 20 ± 1 °C in a thermostatically controlled germinator (Catav et al., 2012).

Data calculation

The final germination percentage (GP), as noted by radicle appearance, was counted every 48 h until no germination was observed for four following days. The experiment lasted 22 days. Seeds with significant signs of rottenness were removed.

Using the modified Timson velocity index, the germination rate index (GRI) was expressed by the formula: GRI = $\Sigma G/t$, where G is the final germination (%) and t is the germination period (days) (Khan, Zia, 2007). The higher the value, the faster the germination.

In order to compare seed tolerance against various tested soluble salts, germination tolerance index (GTI %) was used. GTI was estimated according to the formula given by Ali et al. (2017):

Table 1. Salt concentration (C, mM), salt content (S, g 100g^{-1} or %), electrical conductivity (EC, mS cm^{-1}), and pH of different soluble salt agents.

Salt agent	C	S	EC	pH
Control	0	0	0.01	7.2
NaCl	25	0.15	3.03	7.9
	50	0.29	6.09	8.13
	75	0.44	7.69	7.80
	100	0.58	13.01	7.70
$CaCl_2$	25	0.28	6.96	7.63
	50	0.56	10.71	7.61
	75	0.83	15.73	7.58
	100	1.11	18.17	7.51
$MgCl_2$	25	0.24	2.67	7.88
	50	0.48	5.18	7.68
	75	0.71	6.32	7.72
	100	0.95	8.52	7.86
Na_2SO_4	25	0.36	5.04	8.37
	50	0.71	9.20	8.65
	75	1.06	12.55	8.39
	100	1.42	18.23	8.48

Table 2. Results of two–way analysis of variance (F values; p < 0.05) testing the effects of salts (S), concentrations (C), and their interaction (S × C) on seed germination characteristics and seedlings responses of *Lavandula stoechas*.

Independent variables	Salts (S)	Concentrations (c)	S × C
GP (%)	25.79	222.69	7.89
GRI (% day^{-1})	16.10	145.90	4.21
GTI (%)	42.20	362.31	12.92
RG(%)	9.70	1.34^{ns}	2.17^{ns}
SL (cm)	55.05	289.81	9.71
RL (cm)	64.77	80.01	8.94
FW (mg)	31.43	140.07	6.49
DW (mg)	27.12	13.21	8.49

Notes: GP – germination percentage; RGI – germination rate index; GTI – %, germination tolerance index; RG – germination recovery; SL – shoot length; RL –radicle length; FW,– fresh weight; DW – dry weight; ^{ns} – not significant difference.

Table 3. Germination tolerance index (%) of *Lavandula stoechas* seeds treated with different soluble salts. *Different letters indicate a significant difference between means (p < 0.05).*

Salt levels (mM)	NaCl	$CaCl_2$	$MgCl_2$	Na_2SO_4
0	100a	100a	100a	100a
25	75.2b	66.5b	64b	74.6b
50	67.7b	49.8c	59.6b	25.4c
75	37.8c	41.6c	54.2b	6.2d
100	19.2c	29.6c	32.6c	0d
Mean	**50.0**	**46.9**	**52.5**	**26.5**
F value	37.81	97.89	89.10	1087.3

GTI (%) = (GP in salt stress/GP in control) × 100. The lower the value, the less the tolerance.

Any seeds that failed to germinate in the different soluble salt treatments or PEG_{6000} solutions were transferred to distilled water to test their ability to recover germination. This recovery experiment was conducted at the same optimum conditions mentioned above. The recovery GP (RG) was calculated using the following formula (Zhang et al., 2015): RG = a/(c – b) × 100, where 'a' is the seed portion that germinated after being transferred to distilled water, 'b' is the total number of seeds that already germinated in a given stress condition and 'c' is the total number of seeds.

Growth parameters were also evaluated at the end of the germination incubation period (22 days) on seedlings submitted to 0 to 0.75 mM salt concentration and 0 to -0.5 MPa water potentials of PEG_{6000}. For this purpose, five seedlings were sampled randomly from each Petri dish to measure shoot and radicle length. Fresh and dry weights were determined by using a high-precision analytical balance (0.1 mg). Dry weight was measured after placing the seedlings at 60 °C for 48 h.

Statistical analysis

To ensure homogeneity of variance between means, data were tabulated and transformed (arcsine) before statistical analysis. Tukey's test was applied to perform comparison between treatments ($p < 0.05$). A two-way analysis of variance (ANOVA) was carried out to test the effects of soluble salts, concentration and their interaction on the germination patterns (GP, GRI, GTI and recovery) and growth parameters (shoot and radicle length, fresh and dry weights). On the other hand, Pearson correlation between early seed/seedling metrics and salt parameters was calculated, too. A one-way ANOVA was applied to examine the effect of PEG_{6000} on both germination features and seedling emergence parameters. Statistical analyses were performed by using the IBM SPSS statistics software package version 22.0.

Results

Effects of soluble salts on germination parameters

Two-way ANOVA (Table 2) indicated significant differences ($p < 0.05$) among salt agent, concentrations and their interactions, except the concentrations and salt type × concentration upon RG ($p = 0.483$ and 0.174, respectively).

The maximum germination of 89.2% was observed in the absence of salt (control). Beyond this and regardless of the kind of salt, germination dropped steadily on increasing the stress and reached the minima at 100 mM, at which germination was severely depressed and seeds failed entirely to germinate in Na_2SO_4. At the mildest iso-concentration (25 mM), however, seeds stressed by Na_2SO_4 exhibited higher GP (Fig. 2).

In the seeds that did not receive any treatments, the germination rate, assessed using Timson index, showed the highest amount (7.4% day^{-1}), whereas salinity stress increase decreased GRI, except in seeds treated with $MgCl_2$, the higher value of GRI was recorded at 75 mM (4.5% day^{-1}). On the other hand, even though at the iso-concentration of 25 mM, the highest GRI

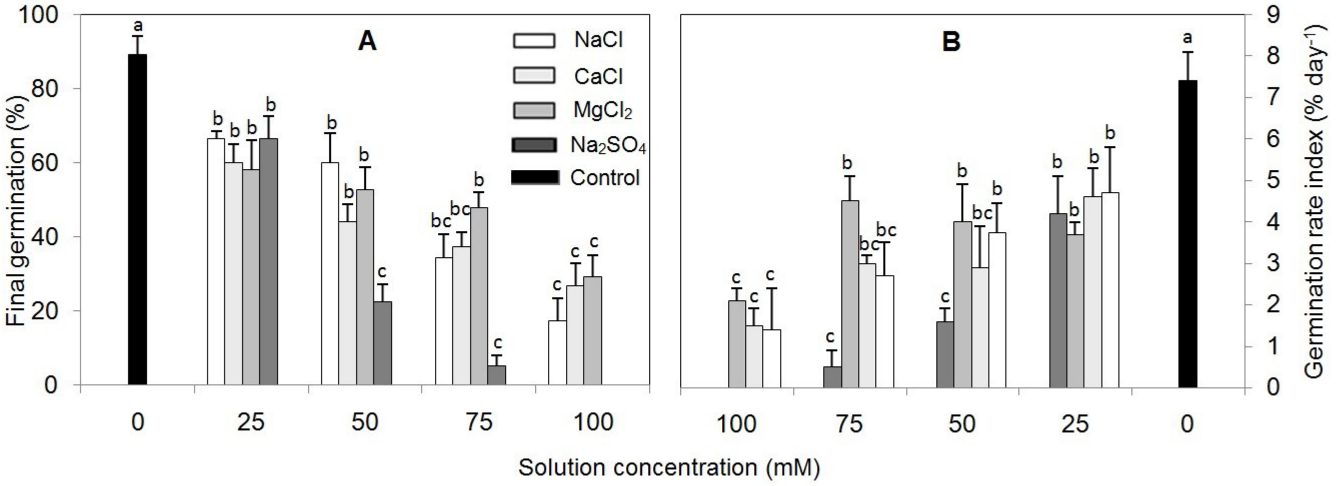

Fig. 2. Final germination percentage (**A**) and germination rate index (**B**) of *Lavandula stoechas* seeds at different concentrations of soluble salts. Bars represent mean ± S.E (n=4). *Different letters indicate a significant difference between means (p < 0.05).*

value was noticed in the seeds treated with NaCl, no significant differences were recorded among the four salts; while at 50 and 75 mM, seeds of *L. stoechas* showed a significant decrease in GRI when stressed by Na_2SO_4 (Fig. 2). Overall, the inhibitory effect of salts on GRI was most pronounced at 100 mM.

A little portion of seeds among those that failed to germinate in different $MgCl_2$ concentrations were capable of recovering germination when transferred to distilled water (>31.5%) as compared to other salts. However, the concentration of 25 mM NaCl had affected less the seeds' ability to recover (despite statistically insignificant effects being recorded among NaCl concentrations) (Fig. 3). Surprisingly, the RGs of seeds stressed by 75 and 100 mM $CaCl_2$ were higher than those of 25 and 50 mM $CaCl_2$ (60 and 58.7% vs. 49.2 and 30.6%, respectively).

The GTI of *L. stoechas* seeds declined with increasing salinity, and the lowest GTI was recorded at 100 mM Na_2SO_4. Moreover, at this same concentration, GTI was decreased more by NaCl, $CaCl_2$ and, $MgCl_2$ (19.2, 29.6 and 32.6%, respectively) compared to other concentrations. At moderate salt concentrations (25 and 50 mM), *L. stoechas* seeds tolerated better NaCl, whereas at 75 and 100 mM, the seeds' salt tolerance was higher in $MgCl_2$. Overall, the GTI revealed that *L. stoechas* has a better tolerance with $MgCl_2$ than with NaCl, $CaCl_2$ and Na_2SO_4 (Table 3).

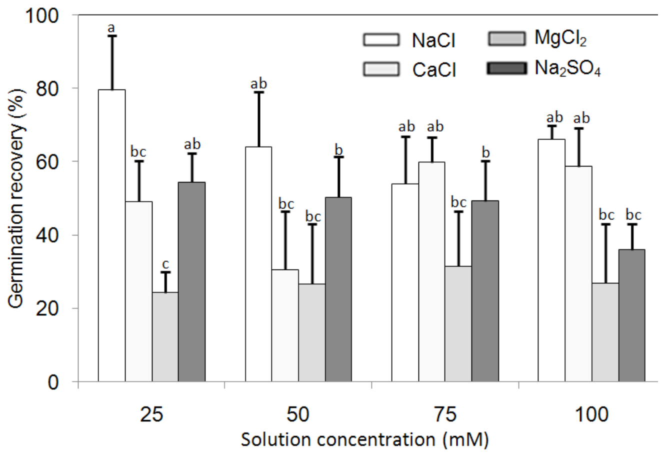

Fig. 3. Recovery germination percentage of *Lavandula stoechas* seeds stressed with different soluble salts. Bars represent mean ± S.E (n =4). *Different letters indicate a significant difference between means (p < 0.05).*

Effect of soluble salts on early plant growth

All salts tested adversely influenced shoot and radicle length. Seedlings sprouting in control reached the maximum shoot length (up to 3.9 cm tall). Regarding root length, a higher value was recorded at 25 mM $MgCl_2$ (1.8 cm long), while Na_2SO_4 had more inhibitory effects on shoot and radicle length than other salts. Even 50 mM Na_2SO_4 decreased steeply shoot and radicle length by 94.9% and 87.5%, respectively, compared to distilled water (Fig. 4). In spite of the decrease in length, neither of these two parameters, indeed, was significantly affected by $CaCl_2$ (no statistically significant differences were obtained among means).

Salinity had a significant impact on seedlings' fresh weight, and the non-stressed seedlings, in fact, attained a maximum average of up to 7.25 mg. The fresh weight decreased by increasing salinity (Fig. 5), albeit no significant differences ($p < 0.05$) were obtained among NaCl, $CaCl_2$ and $MgCl_2$ at all tested concentrations. The increase in dry weight, however, was promoted by these three salts at all concentrations, many of which exceeded that of control (0.28 mg); it ranged from 0.38 mg (25 mM $MgCl_2$) to 0.30 mg (75 mM $CaCl_2$), except at 75 mM $MgCl_2$ (0.26 mg) (Fig. 5). Na_2SO_4 declined dramatically fresh and dry weights at both concentrations (25 and 50 mM).

Correlation among seed/seedling metrics and salts

Germination metrics (i.e. GP, GRI, GTI and RG) and almost all early seedling response parameters (i.e. shoot length, radicle length and fresh weight) were best correlated mainly with EC, salt content and concentration of all tested soluble salts. Notably, the correlation coefficients were equal in NaCl treatment among

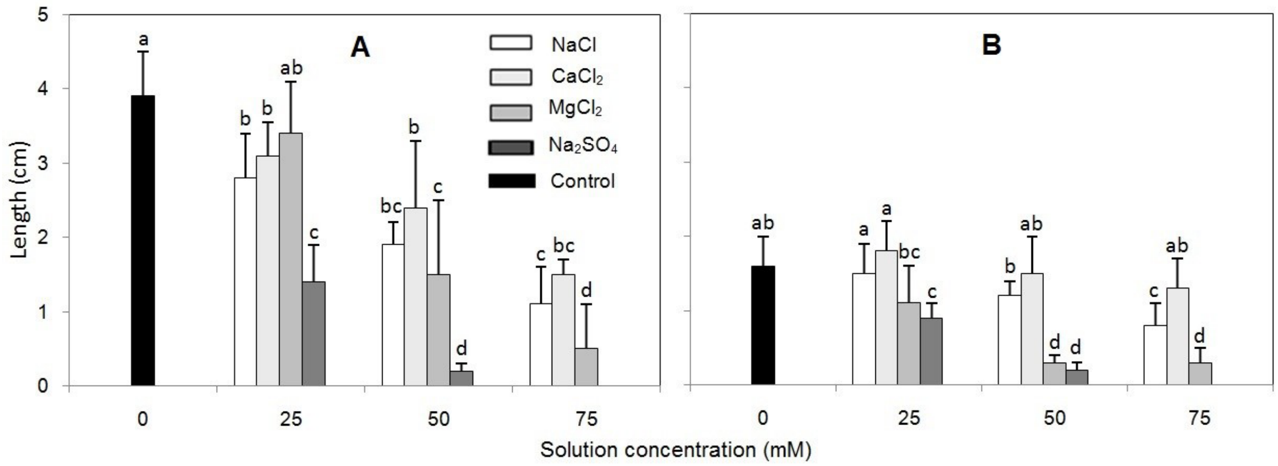

Fig. 4. Shoot (**A**) and radicle length (**B**) of *Lavandula stoechas* seedlings (22 days) at different concentrations of salt agents. Bars represent mean ± S.E (n = 20). *Different letters indicate a significant difference between means (p < 0.05).*

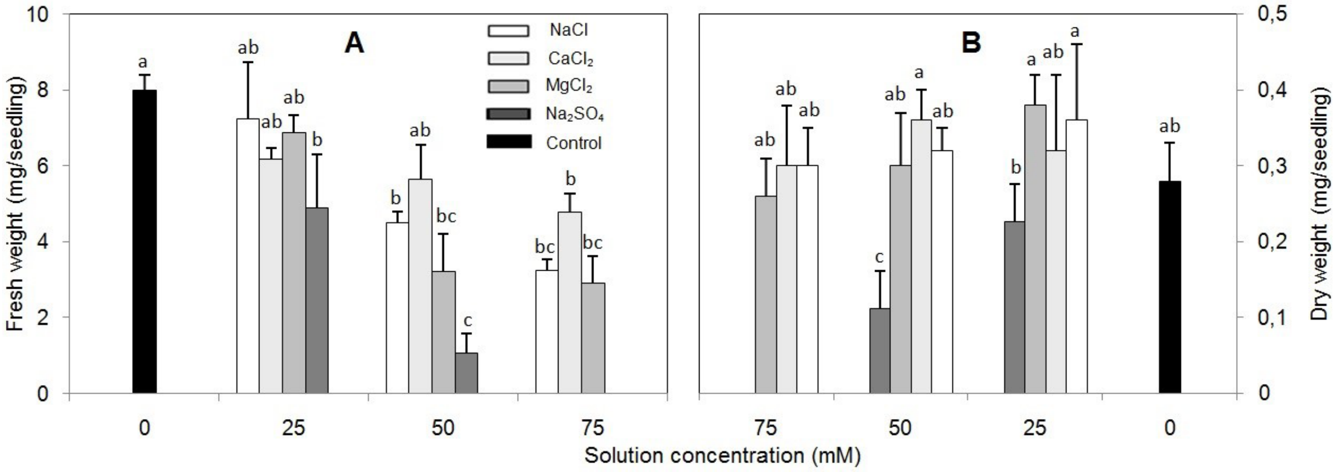

Fig. 5. Fresh (**A**) and dry weight (**B**) of *Lavandula stoechas* seedlings grown under different soluble salt agents. Bars represent mean ± S.E (n = 20). *Different letters indicate a significant difference between means (p < 0.05).*

C, S, EC and shoot length ($r = -0.957$) and among S, C and fresh weight ($r = -0.928$). Dry weight, meanwhile, was best correlated with pH in NaCl, $CaCl_2$ and $MgCl_2$. The pH was strongly correlated ($r = -0.900$; $p < 0.01$) as well with GR in $MgCl_2$ (Table 4).

Response to water stress induced by using PEG6000

Water stress application depressed germination of *L. stoechas* seeds (Table 5). Control showed the maximum GP, whereas the GP decreased significantly when water stress increased from −0.25 MPa upwards, with total inhibition in seed germinability observed at −1 MPa. As the water potential fell, GRI dropped too (0 MPa, 7.4% day^{-1} vs. −0.75 MPa, 0.8% day^{-1}). Despite the negative effect of moisture stress upon RG, insignificant statistical difference was noticed among the levels. The water stress prevented shoot growth, water imbibition as well as dry mass production, as reflected by their lower values as the water potential decreases (from 0 to −0.5 MPa). Interestingly, low water potential had almost no effect on *L. stoechas* radicle length, as the values ranged between 1.5 and 1.6 cm (see Table 5).

Discussion

Few studies have been conducted to examine the effects of diverse soluble salts and water stress on seed emergence and seedling growth in medicinal plants. In this study, we evaluated salt and drought tolerance of *L. stoechas* under the presence of four soluble salts and different levels of PEG_{6000} and their effects on seed germination and early seedling growth.

Seeds of *L. stoechas* displayed a wide viability range, 89.2% germination at non-stress condition, with a characteristic non-deep dormancy; however, as supposed, salinity induced resulted in a corresponding decrease in seed germination. Such results in germination reduction have been reported by using either NaCl only, as in *Retama raetam* (Mehdadi et al., 2017) and *P. pallida* (Aljasmi et al., 2021), or various single soluble salts, as in *Artemisia herba-alba* (Nedjimi, Zemmiri, 2019) and *Marrubium vulgare* (Nedjimi et al., 2020).

In our study, Na_2SO_4 was more aggressive than other soluble salts on *Lavandula stoechas* seed germination and seedling growth. The results of previous studies on the effects of different salts in germination are contradictory and species specific. For example, NaCl was more inhibitory than Na_2SO_4 on the germination of the glycophyte *Pinus halepensis* (Nedjimi, 2017) and the halophytes *Juncus acutus* and *Arthrocnemum macrostachyum* (Vicente et al., 2009), but the toxicity of Na_2SO_4 was more pronounced than NaCl on the germination of *Prosopis strombulifera* (Sosa et al., 2005), *Ceratoides latens* (Zhang et al., 2015), *Medicago sativa*, *Elymus dahuricus* (Zhang et al., 2018) and *M. vulgare* (Nedjimi et al., 2020). Glycophytes are usually less tolerant to salt stress than halophytes and both use different mechanisms in tackling salt ions (Qudir et al., 2008). However, the contradictory germination response is not necessarily linked to whether a species is salt tolerant or salt sensitive (Zhang et al., 2018).

The salt tolerance of *Lavandula stoechas* seeds is ordered as follows: $MgCl_2$ > NaCl > $CaCl_2$ > Na_2SO_4. This indicates that evaluating multiple kinds of salts, rather than just NaCl, should be considered when testing a plant's salt tolerance. Panuccio et al. (2014) reported that *Chenopodium quinoa* seed germination tolerance was in the order: $MgCl_2$ > CaCl2 > NaCl. Nedjimi and Zemmiri (2019) reported the order of toxicity on seed germination of *Artemisia herba-alba* as $MgCl_2$ > Na_2SO4 > NaCl > $CaCl_2$. The latter trend was the same in the halophyte *Suaeda salsa* (Duan et al., 2007) and the xerophyte *Zygophyllum simplex* (Al-Khateeb et al., 2010). Interestingly, seeds of *Phragmites karka* demonstrated enhanced tolerance to and germinated significantly more with $MgCl_2$ at a low temperature; at moderate and high temperatures, however, it became more sensitive to $MgCl_2$ than other salts that were applied (Zehra et al., 2013).

There is a perception that the variation in response of seeds to different soluble salts is due to the difference in osmotic stress caused by these salts at the same concentrations, albeit specific ion injury effects cannot be discarded. Moreover, salts may act specifically in saline soils, with effects ranging from beneficial to noxious for germination depending on doses (Tobe et al., 2004). The relatively high germination in *Lavandula stoechas* at lower salt concentration indicates that seeds might benefit from salts. Several studies demonstrated that seeds could stamp out the negative osmotic effects of the exogenous application of salts

Table 4. Pearson correlation coefficients between seed germination/early seedling metrics and salt parameters.

Salt agent		C	S	EC	pH
NaCl	GP	-0.963**	__-0.964**__	-0.944**	-0.361
	GR	-0.905**	__-0.926**__	-0.912**	-0.552*
	GTI	-0.958**	__-0.959**__	-0.940**	-0.352
	RG	-0.318	**-0.319**	-0.232	0.064
	SL	__-0.957**__	__-0.957**__	__-0.957**__	-0.689**
	RL	__-0.851**__	-0.810**	-0.765**	-0.293
	FW	__-0.928**__	__-0.928**__	-0.927**	-0.588*
	DW	0.115	0.119	0.153	**0.423**
$CaCl_2$	GP	-0.936**	-0.937**	__-0.961**__	-0.771**
	GR	-0.905**	-0.907**	__-0.928**__	-0.718**
	GTI	-0.948**	-0.949**	__-0.973**__	-0.714**
	RG	0.427	0.423	**0.459**	-0.446
	SL	-0.935**	__-0.945**__	-0.936**	-0.649**
	RL	**-0.385**	-0.383	-0.340	-0.016
	FW	-0.899**	-0.900**	-0.922**	-0.809**
	DW	0.259	0.263	0.272	**0.378**
$MgCl_2$	GP	-0.899**	-0.901**	__-0.919**__	-0.883**
	GR	-0.772**	-0.774**	-0.812**	__-0.900**__
	GTI	-0.924**	-0.926**	__-0.946**__	-0.860
	RG	0.113	0.112	0.103	**-0.119**
	SL	__-0.936**__	__-0.936**__	-0.919**	-0.416
	RL	-0.901**	-0.904**	__-0.932**__	-0.576**
	FW	-0.925**	-0.927**	-0.944**	-0.482
	DW	-0.207	-0.204	-0.145	**0.389**
Na_2SO_4	GP	__-0.957**__	-0.956**	-0.945**	-0.763**
	GR	-0.817**	-0.816**	__-0.936**__	-0.848**
	GTI	__-0.963**__	-0.962**	-0.951**	-0.786**
	RG	-0.603*	-0.605*	__-0.628*__	-0.098
	SL	-0.919**	-0.922**	__-0.948**__	-0.938**
	RL	-0.942**	-0.943**	__-0.953**__	-0.827**
	FW	-0.960**	-0.961**	__-0.971**__	-0.834**
	DW	__-0.937**__	-0.936**	-0.921**	-0.631*

Notes: GP – germination percentage; GRI – germination rate index; GTI – germination tolerance index; RG – germination recovery; SL – shoot length; RL – radicle length; FW – fresh weight; DW – dry weight. In bold are the highest values of correlation coefficients for each seed/seedling metric, which means the best correlated parameter: * – Correlation is significant at the 0.05 level; ** – Correlation is significant at the 0.01 level.

Table 5. Seeds germination/early seedling parameters of *Lavandula stoechas*, incubated at 20 °C, in response to water stress (mean ± SE, n = 4) as induced by PEG_{6000}. *Different letters indicate a significant difference between means (p < 0.05).*

Water potential (MPa)	GP (%)	GRI (% day^{-1})	RG (%)	SL (cm)	RL (cm)	FW (mg/seedling)	DW (mg/seedling)
0	89.2 ± 5^{a}	7.4 ± 0.7^{a}	/	4.1 ± 0.4^{a}	1.5 ± 0.2^{a}	8.2 ± 1.2^{a}	0.28 ± 0.06^{a}
- 0.25	41.2 ± 2.2^{b}	3.6 ± 0.4^{b}	63.4 ± 8^{a}	3.2 ± 0.2^{b}	1.6 ± 0.4^{a}	3.5 ± 0.5^{b}	0.20 ± 0.05^{ab}
- 0.5	26.6 ± 6^{c}	2.0 ± 0.8^{c}	49.2 ± 4^{a}	1.8 ± 0.4^{c}	1.5 ± 0.5^{a}	1.6 ± 0.4^{c}	0.14 ± 0.06^{b}
- 0.75	8 ± 2^{d}	0.8 ± 0.2^{c}	45.2 ± 10^{a}	/	/	/	/
- 1.0	0.0^{d}	/	42.2 ± 6^{a}	/	/	/	/
F value	161.54	82.13	2.47	41.93	0.19	151.0	5.40

Notes: GP – germination percentage; GRI – germination rate index; RG – germination recovery; SL – shoot length; RL – radicle length; FW – fresh weight; DW – dry weight.

through accumulation of ions to maintain lower water potential, and thus increase water absorption (Yagmur, Kaydan, 2008; Li et al., 2011). This trait is considered as a passive metabolic process that does not require energy/respiration. Under salinity, the slowdown in germination speed, expressed here by GRI, could be owing to the duration necessary for seeds to trigger mechanisms allowing them to adjust their osmotic pressure (Medjebeur et al., 2018).

All plant species might deploy either salt-tolerance or salt-avoidance strategies to withstand soil salinity increment. Salt tolerance characteristics are reflected by maintenance of highest GPs and germination rates under high salinities, while a high RG after the alleviation of salinity reflects a salt-avoidance strategy (Zhang et al., 2015). Unlike the final GP, a poor RG was exhibited when seeds were stressed with $MgCl_2$regadless of the applied concentration,and transferred to distilled water (<30%). Similar results were reported in *Phragmites karka*, in which seeds failed to recover germination in $MgCl_2$ when incubated at the temperature regime of 25/35 °C and transferred to proper condition (Zehra et al., 2013). In the remaining soluble salts, *Lavandula stoechas* seeds showed a relatively high RG. Our results are in close agreement with those of Zhang et al. (2015) who reported that *Suaeda microphylla*, *Chenopodium rubrum* and *Kalidium foliatum* resumed high recovery germination after the seeds were transferred from NaCl and Na_2SO_4 to deionised water. The recovery response seems to indicate that the germination inhibition of *Lavandula stoechas* in different salts is probably due to both osmotic stress and specific ion toxicity. In this case, Zehra et al. (2013) suggested that the osmotic and specific ion effects may combine and make it difficult to distinguish the proportional contribution of two stresses. Ungar (1996) stated that, in salty habitat, instead of commencing germination promptly after being released from the maternal plant, dormancy of seeds for an extended period may be a selective advantage, since it enables seeds to emerge and establish a plant as soon as excessive concentrations of salts are leached by rains.

Concomitant to osmotic adjustment governed by salt ion absorption, salt-adaptive plants are also capable to synthesise compatible organic solutes, such as proline, glycine betaine, free sugar and polyalcohol, in the cytoplasm to prevent water loss (Yang et al., 2007); thus, this trait is an active metabolic process. Despite being a glycophyte, *L. stoechas* has a tendency to uptake water, as reflected by maintaining high shoot and root growth performance as well as high fresh weight value at moderate salt concentration (25 mM), whereas these parameters dropped as salinity increased. This suggests that, at milder salt solution, the mechanisms preventing ions from acting as toxic substances are active, mainly the osmotic adjustment process, and the accumulated osmolytes are involved in protection against free radicals (De Souza et al., 2016). Further, salt-sensitive plants, such *Medicago sativa* and *Elymus dahuricus*, had shown a dramatic decrease in the radicle length, but not in shoot length, when they were subjected to low NaCl and Na_2SO_4 levels (Zhang et al., 2018). However, *Physalis angulata*, an ethnomedicinal glycophyte, kept a high seedling fresh weight at 8 mS cm^{-1} NaCl (>75 mM) (De Souza et al., 2016). Different soluble salts, except Na_2SO_4, had a positive effect on dry weight compared to the control. This could be attributed to the beneficial roles of Mg^{2+} and Ca^{2+}. The former is involved in translocation of assimilates and enhanced nutrient utilisation (Senbayram et al., 2015). The latter helps in preserving the membrane stability, reduction of membrane leakage, forming cell walls and regulation of ion selectivity (White, Broadley, 2003).

Numerous studies have simulated salinity by using different concentration levels (C, mM) (Sosa et al., 2005; Zehra et al., 2013). This approach may be used because halophyte is defined as a plant that has the ability to complete its life cycle under salinity levels of ≥200 mM NaCl (Flowers, Colmer, 2008). Salt content (S, g 100 g^{-1}) and EC (mS dm^{-1}), however, have been used relatively less frequently than salt concentration to assess the effects of salts on germination and seedling growth (Ungar, 1996; Bina, Bostani, 2017). These two salt parameters were preferred by some researchers for use in studying glycophyte germination behaviour or crop yield under controlled conditions or in field (Qudir et al., 2008; Kanawapee et al., 2012, De Souza et al., 2016). The three salt parameters (i.e. C, S and EC) are strongly correlated with almost all germination/early seedling metrics. These parameters are considered appropriate for the evaluation of salinity tolerance in *Lavandula stoechas* seed germination and early seedling growth. It is also clear that pH was weakly significantly correlated to germination and seedling growth, even though many researchers have emphasised the effect of pH on the growth of plants exposed to salts (Basto et al., 2013; Huang et al., 2017). Ali et al. (2017) studied the effect of buffer solutions on seed germination of *Salsola foetida*, a North African halophyte. They concluded that pH is not a limiting factor on the final seed GP and germination rate of this species. In addition, pH was not a limiting factor on germination either in *Sorghum bicolor* (Zhao et al., 2014) or in *Leymus chinensis* (Ma et al., 2015). Zhang et al. (2018) hypothesised that, even in sodic conditions, the pH is not a relevant indicator for the negative effects in salty soils on the early phases of plant establishment. The strong correlation between pH and the germination rate in $MgCl_2$ ($r = -0.900$, $p < 0.01$) appears to be unique and deserves further investigation.

Higher tolerance to lower water potential during seed germination has been considered as an adaptive strategy for plants inhabiting unpredictable ecosystems (Fyfield, Gregory, 1989; Zeng et al., 2010). Both seed germination and the germination rate of *Lavandula stoechas* decreased significantly with increasing water stress, and germination stopped completely at −1 MPa. This figure is considered as the germination threshold tolerance value of this species. Consistent results have already been obtained in many studies on other Lamiaceae species, as Abbad et al. (2011) and Dadach and Mehdadi (2018) reported that the seeds of *Thymus broussonetii*, *T. maroccanus* and *Ballota hirsuta* were harshly affected by the drop in water potential and, per contra, they exhibited high seed germinability in the absence of stress. Similarly, *Sideritis incana* and *Stachys ocymastrum*, two medicinal plants, showed lower GP and GRI at −0.5 MPa, and germination was absolutely inhibited at −1 MPa (Dadach, Mehdadi, 2021). Other plants flourishing in the Mediterranean climate, such as *Stipa tenacissima* and *Thymus fontanesii*, showed higher tolerance threshold reaching up to −1.6 MPa (Krichen et al., 2014; Dadach, Mehdadi, 2021). Ali et al. (2017) anticipated that, in the drought-sensitive seeds, process of water percolation remains incomplete. The decrease in water potential increases the osmotic potential, creating deficiency in seed hydration and causing changes in enzymatic activities, a general reduction in hydrolysis and utilisation of major natural food reserves of seeds, notably carbohydrates, lipids and proteins, which subsequently prevent seed germination (Steiner, Zufo, 2019).

Seedling growth was also affected by the rise in water stress, whereas the root length was relatively constant at all PEG-tested solutions, indicating that *Lavandula stoechas* entertains root growth as a coping strategy to overcome drought, and this can ensure that root system, during the earliest phases after germination, reaches deeper groundwater. In fact, Faisal et al. (2019) emphasised that the effects of drought depend not only upon the degree and length of water scarcity, but also upon the plant growth phase. Seeds that failed to germinate under water stress and had germinated after being transferred to distilled water are the portion of seeds that form transient soil seed banks germinating naturally in the period of years receiving sufficient amount of rainfall. We assume rainfalls are the predominant environmental cue in triggering seed germination of butterfly lavender. Adequate precipitation adjusts temperatures, mitigates soil salinity and raises water potential (Khan, Gulzar, 2003).

Conclusion

The present study was conducted to evaluate the impact of different soluble salts and water stress on germination and early growth of *L. stoechas*, a potential species for rehabilitation of degraded coastal lands. Our results demonstrate that despite the negative effect of salinity on germination and seedling growth, *L. stoechas* seeds were capable to emerge at moderate salt concentrations (<75 mM) in all applied salt agents. Susceptibility to salt stress indicates that this species is able to thrive in a wide range of habitats where particular ion composition may act favourably for its subsistence. *L. stoechas* is a promising plant for use in the restoration of the Mediterranean coastal lands, which are under serious threat of soil salinisation. Regarding the confirmed dreadful effects of water stress on germinability and seedling response, we recommend introducing this species in habitats with sufficient annual precipitation amounts to mitigating the impacts of prolonged drought spell and improving seedling fitness. Still, results of germination experiments with a single salt would not always be applicable to field conditions. Complementary studies on germination and seedling growth of this species must focus more on the effects of different combinations of salts (two mixed or more) on seeds/seedlings responses.

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