Acta Universitatis Sapientiae
Agriculture and Environment, **16** (2024) 48–63

DOI: 10.47745/ausae-2024-0005

Salinity tolerance in *Atriplex halimus* L.: Differential effects of soluble salts on seed germination and recovery

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Manuscript received October 21, 2024; revised Nov. 15, 2024; accepted Nov. 20, 2024

Abstract. The soils of arid rangelands contain a variety of salts that have differential effects on seed germination. In these regions, *Atriplex halimus* (L.) (Amaranthaceae) is one of the most commonly used medicinal and fodder plants. Little is known about its germination under saline stress operated by various soluble salts. The present work was designed to determine the effect of four soluble salts (NaCl, Na_2SO_4, $CaCl_2$, and $CaCO_3$) on the germination of *A. halimus* seeds. We tested the effect of salinity on final germination percentage (FGP%) and germination tolerance index (GTI%) using five concentrations (0, 200, 300, 400, and 600 mM) of each salt (NaCl, Na_2SO_4, $CaCl_2$, and $CaCO_3$). In addition, experiments were also conducted to assess the effects of salinity on germination recovery (GRP%) from high saline conditions (600 mM). Salinity level and salt composition significantly influenced germination characteristics. *A. halimus* seeds were non-dormant, exhibited approximately 90% germination in distilled water. Both FGP and GTI gradually decreased with increasing salinity. This study showed that the seeds of *A. halimus* can germinate under 400 mM in all tested salts. The salts causing germination inhibition exhibited specificity, with an increasing trend observed in the following sequence: Na_2SO_4 > NaCl > $CaCl_2$ > $CaCO_3$. When ungerminated seeds are transferred from 600 mM to distilled water, their germination ability is recovered according to the type of salt used. *A. halimus* is a highly salt-tolerant species that can tolerate a variety of salts and can be, therefore, a promising species for improving ecological balance in saline soils.

Keywords: arid rangelands, *Atriplex halimus*, germination, tolerance, soluble salts, recovery

1. Introduction

Among the approximately 2,400 halophyte species, information on seed germination is limited to only a few hundred species, mainly concentrated in subtropical halophytes [1]. Plant species that are able to thrive in saline regions have developed a variety of adaptation strategies to cope with the challenging environmental conditions, including preserving seed viability, facultative dormancy, and prompt seed germination when hypersaline conditions are alleviated [2]. One of the most significant characteristics of halophytes is their ability to germinate despite exposure to high salinity. However, a considerable degree of heterogeneity can be discerned between halophytes in terms of their ability to recover from high salinity [3].

For the successful restoration of species, direct sowing is one of the most important steps in seed germination, and it requires an exhaustive understanding of how to create the ideal conditions for seed germination in order to maximize the success of the restoration process [4]. Many halophyte seeds can germinate when appropriate conditions for germination are met, including hypersaline conditions and other physicochemical factors [5]. The native environment of halophyte seeds is defined by the existence of saline stress, primarily caused by the prevalence of sodium chloride (NaCl), the predominant salt. The soils in the saline regions of Algeria, specifically, have been observed to accumulate high concentrations of chlorides and sulphates, with NaCl being the most prevalent salt in these soil compositions. The predominant cationic components in these soils consist of Na^+, Ca^{2+}, K^+, and Mg^{2+}, with SO_4^{2-} being identified as the secondary major anionic element after Cl- [6, 7]. The salinity present in the environment negatively affects most glycophytes. However, halophyte seeds often exhibit complete recovery after the removal of saline stress, suggesting the presence of an osmotic response [8].

Atriplex halimus L. (Amaranthaceae), commonly known as Mediterranean saltbush in English and *Gtaf* in Arabic (Algeria), is a perennial shrub that thrives in saline conditions. It grows in semi-arid and arid environments across Eurasia, spanning from the Atlantic coasts through the countries of the Mediterranean basin and into the Middle East [9]. *A. halimus*'s capacity to thrive in challenging environmental conditions has led to its traditional utilization as a source of grazing fodder for livestock in these regions [10]. It grows in regions characterized by low annual rainfall and high potential evapotranspiration, typically at limited altitudes, below approximately 1,200 m above sea level [11]. The primary mode of propagation for *A. halimus* is through seeds. *A. halimus* generally forms part of the halophilic communities on saline soils. Le Houérou [11] also classified *A. halimus* as a "euhalophyte", capable of tolerating soil salinity levels equivalent to saturated paste EC values ranging from 25 to 30 dS.m-1. *A. halimus* belongs to a group of species demonstrating moderate cold tolerance, enduring temperatures between -10 and -12 °C.

Since the 1960s, *A. halimus* has been intentionally grown in the Mediterranean arid zone to serve as standing feed for browsing, as well as to provide silage for various animals, including small ruminants like sheep and goats, as well as larger livestock such as cattle and camels [12, 13]. The cultivation of *A. halimus* fosters the recycling of nutrients, contributes to phytoremediation, reduces ground-level wind speed, and plays a role in decreasing runoff and erosion [14]. Indigenous herbal practitioners in Arabic regions used the leaves of *A. halimus* to treat heart diseases and rheumatism. They prepare an extract by boiling the leaves, which is then added to bath water for therapeutic purposes [15]. The antidiabetic effect has been further developed in a product called "Glucolevel", which combines leaf extracts of *A. halimus*, Juglans regia L., *Olea europaea* L., and *Urtica dioica* L. [16]. Extracts derived from the aerial parts of *A. halimus* exhibited antibacterial activity against a range of $Gram^+$ and Gram pathogenic bacteria [17]. Endophytic fungi isolated from *A. halimus* demonstrated antimicrobial effects against specific species [18].

In most experiments assessing the impact of salt stress on seed germinability characteristics of *A. halimus*, sodium chloride (NaCl) is used alone to assess the impact of salt stress [19, 20, 21, 22]. Few studies explore the effects of other prevalent soluble salts. The present study describes the effect of different salts on seed germination and recovery of *A. halimus* after exposure to high salinity level. We attempt to establish the effects of the most abundant soluble salts in Algerian arid rangelands *viz*. NaCl, Na_2SO_4, $CaCl_2$, and $CaCO_3$ on the germination of this important plant species. The findings of this research will significantly contribute to enhancing our comprehension of the germination requisites of this species, thereby aiding in the restoration of degraded rangelands and the establishment of new territories. These efforts are crucial to provide valuable food for humans and animals, offering both medicinal and nutritional benefits.

2. Materials and Methods

Seed harvesting

Mature seeds of *A. halimus* were collected randomly in 2022 from the arid rangeland of T'Kout, located in Batna, southeastern Algeria. At least 10 plants were sampled for seed collection in this area (Latitude 35°09' N; Longitude 6°20' E; 1049 m a.s.l.). The seeds were manually separated from the fruits (pericarp). Typically, these seeds exhibit a brown to dark brown colour, and their shape ranges from reniform to sub-orbicular, with an entire or toothed appearance. The weight of 100 seeds of *A. halimus* is 2.89 g. Following collection, the seeds were stored in opaque paper bags at room temperature, maintaining a humidity level between 30 and 50%, until they were used three months later [23].

Experimental design and application of salt stress

We conducted germination tests using a 90-mm Petri dish containing a disk of Whatman No. 1 filter paper moistened with distilled water for a control as well as various saline solutions containing various concentrations (200, 300, 400, and 600 mM) of the following soluble salts: NaCl, Na_2SO_4, $CaCl_2$, and $CaCO_3$. For each test (salt/concentration), four replicate Petri dishes, each with 100 seeds, were wrapped in aluminium foil (continuous dark) and incubated at 25 °C [6, 7]. The emergence of radicles was considered as the criterion for germination. The Petri dishes remained sealed for 15 days after the experiment had concluded. Maintaining appropriate humidity levels throughout the experiment was crucial for seed viability. The germination test was conducted using a complete randomized design.

Germination traits

Based on the results of the quantitative evaluation of seed germination behaviour, the following formulas have been used to calculate both the final germination percentage (FGP) [24] and the germination tolerance index (GTI) [25]:

$$FGP\ (\%) = \frac{Number\ of\ germinated\ seeds}{Total\ number\ of\ seeds} \times 100$$

$$GTI\ (\%) = \frac{FGP\ under\ stress\ condition}{FGP\ under\ non-stress\ condition} \times 100$$

After 15 days of every salt exposure, seeds that failed to germinate at 600 mM under different types of salt were washed with distilled water and then placed in new Petri dishes with new filter paper moistened with distilled water and were then monitored for another 15 days under the same conditions for their germination recovery aptitude. The germination recovery percentage (GRP) was calculated for each treatment as follows:

$$GRP\ (\%) = \frac{(A - B)}{(C - B)} \times 100,$$

where A is the number of seeds germinated over the entire experiment, B is the number of seeds germinated in saline solution, and C is the total number of seeds used for processing [25].

Statistical analysis

Statistical analysis was carried out using two-way analysis of variance (ANOVA) to test the effects of salt type, concentration, and their interaction on germination characteristics. Multiple comparisons of means were carried out using Tukey's test ($P < 0.05$). Mean values were presented in terms of mean ± standard error (mean ± SE). Pearson's correlation coefficient was also considered to establish the relationships between the values of salt concentrations and germination parameters ($P < 0.05$). All statistical analyses were performed using SAS software Version 9.0 (Statistical Analysis System) (2002).

3. Results and discussion

Effects of salinity on final germination

Salinity and drought are two of the most significant abiotic challenges impeding seed germination and the establishment of plants in Mediterranean regions [26]. The use of resilient plant species could be considered a possible strategy for cultivating saline soils, which are unsuitable for most traditional agricultural crops due to their elevated salinity levels [27].

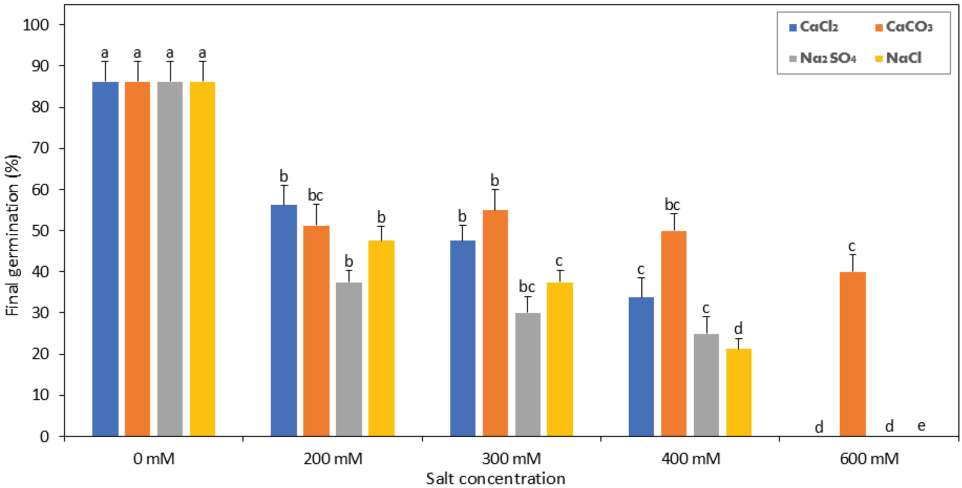
Table 1. Results of two-way analysis of variance (F values) testing the effects of salts (S), concentrations (C), and their interaction (S × C) on the germination characteristics of *Atriplex halimus* seeds

Independent variables	**Salts (S)**	**Concentration (C)**	**(S × C)**
FGP	75.57*	549.78*	14.32*
GTI	82.30*	599.80*	15.68*

Notes: FGP – Final Germination Percentage; GTI – Germination Tolerance Index; * $P < 0.0001$.

The results from the two-way ANOVA analysis revealed significant adverse effects on the germination percentages of *A. halimus* seeds attributed to both salt type ($F = 75.57$, $P < 0.0001$) and salt concentration ($F = 549.78$, $P < 0.0001$), as well as their interactions ($F = 14.32$, $P < 0.0001$) (*Table 1*).

In the presence of all types of salts at 600 mM, germination is completely inhibited. However, only seeds treated with $CaCO_3$ germinated, by recording 40% FGP (*Figure 1*). According to *Figure 1*, *A. halimus* seeds germinate better under relatively moderate salinity conditions of 200–300 mM. A significant reduction in germination percentages was observed beyond these levels, regardless of the type of salt.



Notes: Bars represent mean ± SE (n = 4). Different letters indicate significant difference between treatments (Tukey test, P < 0.05).

Figure 1. Final germination percentages (FGP) of *Atriplex halimus* seeds treated with different soluble salts

A notable decrease in Final Germination Percentage (FGP) was evident for all four salts compared to the control (*Figure 1*). The relationship between FGP and soluble salt concentrations displayed strong statistical regressions, exhibiting coefficients of determination (R^2) ranging from 0.73 to 0.96 (*Figure 2*).

It is important to emphasize that in comparison to the other types of salt solutions tested, the germination capacity of *A. halimus* seeds was more adversely affected by solutions of NaCl and Na_2SO_4. According to *Figure 2*, the FGP had highly significant and negative linear relationships with concentrations in all salt types, indicating that salt treatments negatively affected *A. halimus* seed germination. According to our results, *A. halimus* seed germination was best obtained in distilled water (control) and in all concentrations of $CaCO_3$ when a salt solution was applied; however, with an increasing degree of other salt solutions, there was a gradual decrease in germination potential depending on the salt type as well as the concentration of salts. At 400 mM, sodium chloride and sodium sulphate were more detrimental than calcium chloride (*figures 1–2*).

Based on our previous research on the glycophyte *Phaseolus vulgaris*, we found that under various salts, germination would decrease in the order of NaCl > KCl > $CaCO_3$ > Na_2SO_4 > $CaCl_2$ [6]. The study conducted by Bernstein [28] highlighted a significant correlation between plant response and soil osmotic potential, particularly in the presence of elevated concentrations of Ca^{2+} and Na^+ in saline soils. Conversely, non-saline sodic soils characterized by high Na^+ levels and minimal Ca^{2+} and Mg^{2+} concentrations can lead to distinct nutritional deficiencies not typically observed in saline soils. The short-term adaptations to changes in osmotic pressure due to salination are regulated by the concentrations of K^+ and organic acids within the plant cells. As osmotic adjustment progresses over the subsequent days, additional cations and anions might start replacing the organic salts of potassium, influencing the overall process of osmotic adjustment [29]. Several forage species classified as halophytes and belonging to families such as Poaceae, Fabaceae, and Amaranthaceae have been observed to undergo similar effects when exposed to various soluble salts [30].

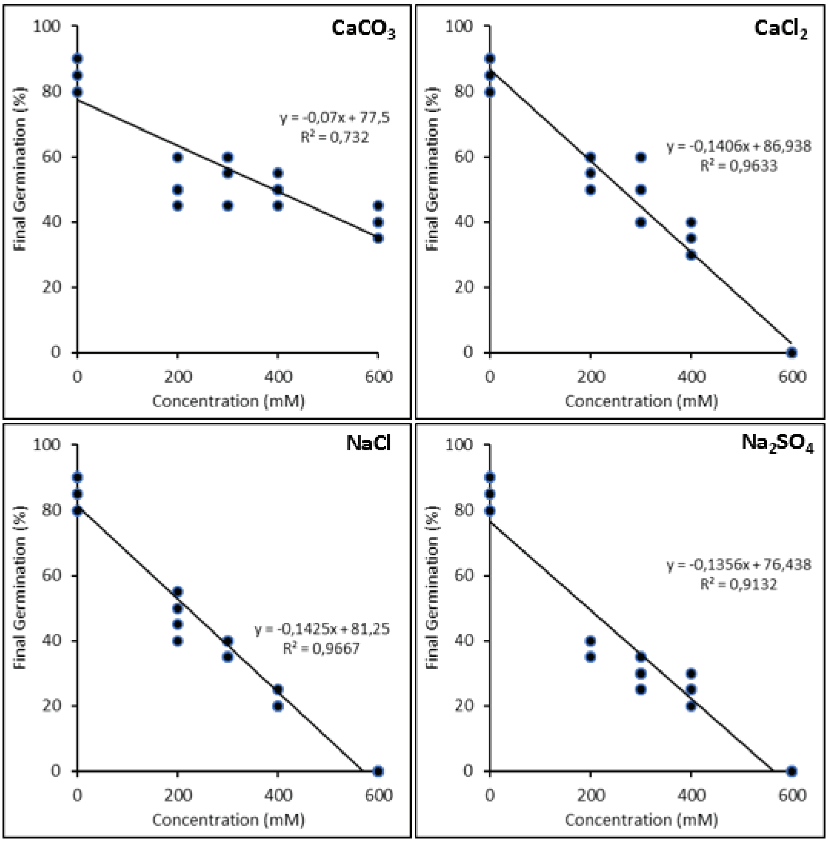


Figure 2. Regression plots of final germination percentages of *Atriplex halimus* seeds with different soluble salts

Debez et al. [31] showed that the seed germination of a coastal population of *A. halimus* exhibited greater salt tolerance compared to a population from a non-saline site. Complete inhibition of germination occurred at 700 mM NaCl for the coastal population and at 350 mM NaCl for the non-saline site, signifying very high tolerance levels in both cases. According to [32], the application of NaCl and Na_2SO_4 at a concentration of 200 mM to the seeds of the halophyte *Portulca oleracea* led to a significant reduction in germination rates. This reduction in germination could potentially be attributed to prolonged germination times, likely caused by the challenge in seed hydration due to the high osmotic potential induced by these salts. Indeed, the extended duration for seeds to establish mechanisms facilitating internal osmotic pressure adjustment could account for the prolonged germination process. This delay might occur as the seed initiates adaptations to cope with the altered osmotic conditions induced by salt stress, contributing to the prolonged germination period [33].

McGaughey et al. [34] demonstrated that alterations in salinity levels could affect seed aquaporin function, consequently influencing seed germination. In saline environments, the prompt germination of Mediterranean halophyte fodder species plays a crucial role in facilitating successful plant establishment. Consequently, these plants exhibit rapid propagation and the development of deep root systems, enabling them to absorb moisture from deeper soil layers during periods of drought. This adaptive ability assists in their resilience during dry seasons by accessing moisture from deeper areas in the soil [35].

Effects of salinity on germination tolerance index

Salinity in soils is influenced by a wide range of ions such as Cl^-, SO_4^{2-}, HCO_3^-, Na^+, Ca^{2+}, Mg^{2+}, and, more rarely, NO_3^- or K^+. It is common in nature to find salts of these ions at highly variable concentrations and proportions. Although these ions may be indigenous to an area, most often they are brought into it through irrigation water or water flowing from adjacent areas [36]. In arid regions, the natural drainage systems frequently exhibit inadequate functionality, leading to the accumulation of salts within inland basins instead of their discharge to the sea [1].

Table 2. The Germination Tolerance Index (%) of *Atriplex halimus* seeds treated with different soluble salts

Concentrations	**$CaCO_3$**	**$CaCl_2$**	**NaCl**	**Na_2SO_4**
0 mM	100^a	100^a	100^a	100^a
200 mM	59.5^b	65.1^b	55.2^b	43.5^b
300 mM	63.8^b	55.7^b	43.5^c	34.9^c
400 mM	57.9^b	39.4^c	24.6^d	29.1^c
600 mM	46.4^c	0.00^d	0.00^e	0.00^d

Note: Different letters indicate significant difference between treatments (Tukey test, $P < 0.05$).

Results of a two-way ANOVA indicated a significant effect of salts (S) ($F = 82.3$, $P < 0.0001$) and concentrations (C) ($F = 599.8$, $P < 0.0001$) and their interaction (S × C) ($F=15.68$, $P < 0.0001$) on the GTI (*Table 1*). The inhibitory effect of salt stress on the Germination Tolerance Index (GTI) was more pronounced for NaCl and Na_2SO_4 at a concentration of 400 mM (*Table 2*).

In sodic soils, the primary cations predominantly present are sodium alongside carbonate, and bicarbonate serves as the most prevalent complementary anion. Therefore, soils characterized by excessive levels of soluble salts are categorized as saline soils, those exhibiting high levels of exchangeable sodium are termed sodic soils, and soils that possess elevated concentrations of both salts and exchangeable sodium are identified as saline-sodic soils [37]. The salts causing germination inhibition exhibited specificity, with a decreasing trend observed in the following sequence: $CaCO_3 < CaCl_2 < NaCl < Na_2SO_4$ (*Table 2*). Nedjimi and Zemmiri [38] found that $MgCl_2$ and Na_2SO_4 were generally the most toxic salts regarding *Artemisia herba-alba* seed germination, followed by NaCl and $CaCl_2$.

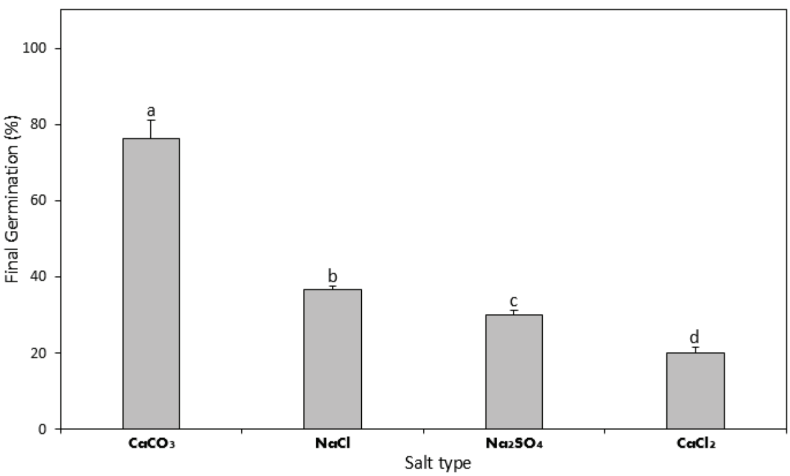
According to [39], saline soils primarily contain NaCl and Na_2SO_4 as the major solutes. Sodium chloride exhibits high solubility at 264 g L^{-1}, posing a significant threat to plant growth. Even soils with just 0.1% NaCl are considered highly unsuitable for supporting plant growth. Saline soils can contain concentrations of 2–5% NaCl, necessitating modifications through leaching to decrease its concentration and create a more favourable environment for plant growth. While sodium chloride is rarely directly observed in soils, it forms calcium sulphate and carbonate, precipitating due to reactions with sodium sulphate and carbonate, unless water salinity is exceptionally high (ranging from 500 to 400 mg) within the soil. Calcium chloride ($CaCl_2$), though toxic to plants, exhibits lower toxicity compared to sodium chloride. Sodium sulphate is a prominent component found in saline soils, saline groundwater, and saline lakes. Its solubility increases with higher temperatures.

The less toxic salts regarding the germination of *A. halimus* seeds were calcium chloride ($CaCl_2$) and calcium carbonate ($CaCO_3$) (*Table 2*). This could be attributed to the beneficial impact of calcium on maintaining membrane integrity, regulating ion selectivity, and reducing ion leakage from the membrane [40]. [41] demonstrated that the application of organic amendments would likely elevate the quantity of calcium (Ca^{2+}) derived from calcium carbonate ($CaCO_3$). This increase is attributed to the formation of organic acids during the application of organic amendments. During saline conditions, the starch hydrolysis and mobilization of reserves from the endosperm to the embryo were inhibited primarily by excessive levels of soluble salts in the endosperm. It is possible to observe a correlation between germination tolerance and species ecology [42].

Nevertheless, despite the detrimental impacts of soluble salts, this study demonstrates that the seeds of *A. halimus* have the capability to germinate even under high concentrations of 400 mM for all tested salts (*Table 2*). This level of salinity exceeds the salinity tolerance level of the majority of cultivated vegetable species, as well as of several halophytes [43, 44]. According to [45] and the recent results of [46], seeds from various steppe plant species exhibit the capacity to maintain their viability for extended durations even when subjected to severe conditions, particularly salinity and drought. They retain this ability to propagate when ecological conditions become favourable again. Seeds from plants common to arid climates typically mature during the autumn, and their germination begins shortly after the initial precipitation of the spring season. These seeds are commonly situated in the upper layers of the soil and germinate when elevated salt concentrations are leached from the soil by rainwater.

Effects of salinity on seed germination recovery

Results of a one-way ANOVA indicated a significant effect of salts ($P < 0.0001$) on the GRP. The test of germination recovery in the presence of salt consists of transferring seeds that have not germinated on a medium containing salt to a medium devoid of salt in order to detect the nature of the effect of salt if it is toxic or osmotic for the same period of time as the germination test. When seeds that have not germinated at high concentration (600 mM) are transferred to distilled water, the process of germinating the seeds is enhanced to 76.3%, 36.7%, 30%, and 20%, using $CaCO_3$, NaCl, Na_2SO_4, and $CaCl_2$ respectively (*Figure 3*). Based on these results, it is possible to classify *A. halimus* as a highly salt-tolerant species. Seeds of *A. halimus* did not recover completely and showed average recovery response (< 30% FGP) when subjected to high salinity of NaCl, Na_2SO_4, and $CaCl_2$.



Notes: Bars represent mean ± SE (n = 4). Different letters indicate significant difference between treatments (Tukey test, $P < 0.05$).

Figure 3. Germination recovery of ungerminated salt-treated seeds of *Atriplex halimus* at 600 mM

Exposure to high temperatures combined with salinity can lead to a decline in seed viability, consequently resulting in poor recovery response [47]. Certainly, the capability to recover following salt exposure varies among different species. Seeds from various species possess the ability to sustain their viability even under hyper-saline conditions and subsequently initiate germination once the salinity stress reduces. This phenomenon is notably observed in halophytes [48, 49].

Indeed, while there are differences in salt sensitivity among various species during germination, most halophytes maintain seed viability even when exposed to high salt concentrations during their dormancy period [48]. In this study, after ungerminated seeds were transferred to distilled water, *A. halimus* seeds exhibited rapid recovery under conditions involving $CaCO_3$, $CaCl_2$, Na_2SO_4, and NaCl. A proteomic analysis uncovered that in the presence of salt, the extensive conversion of reserve proteins into 20 amino acids, which could be further transformed into other amino acids, as well as the conversion of fatty acids into carbohydrates, was decelerated. However, under favourable recovery conditions, this conversion process was promptly reinitiated [50].

The distribution and prevalence of halophytes in saline environments are influenced by the variances in germination responses. Halophyte seeds maintain their viability even after prolonged exposure to salt stress, remaining dormant until favourable conditions for germination arise. However, excessive salinity levels can entirely prevent seed germination, surpassing the tolerance limits of the species [51]. [52] showed that *Salicornia europaea* and *Suaeda calceoformis* seeds recovered significantly faster than controls from two-year saline pre-treatments. This observation confirms the osmotic influence of salt on the germination process of halophytes. Such behaviour represents a typical life cycle strategy adopted by halophytes residing in desert regions to enhance their chances of survival. This strategy allows populations to sustain stability and uphold ecological balance over time [47].

4. Conclusions

The current study aimed to explore the impact of soluble salts on the germination process of *A. halimus*, a plant renowned for its forage, nutritional, and medicinal properties, particularly in the arid and semi-arid rangelands of Algeria. Our findings revealed that *A. halimus* seeds exhibited germination capability even under high concentrations (≤ 400 mM) of soluble salts despite the overall negative influence of salinity. Notably, salts like NaCl and Na_2SO4 displayed a more pronounced inhibitory effect on *A. halimus* seed germination compared to $CaCO_3$ and $CaCl_2$. This varying behaviour observed in *A. halimus* seeds in response to different salt types is attributed to the generation of distinct osmotic potentials by the same concentration of salt, with the osmotic effect playing a more significant role in influencing germination in this scenario. *A. halimus* emerges as a highly promising crop for enhancing land productivity in arid and semi-arid regions. The purpose of this practice is not just to address the needs of the food industry but also to contribute to sustainable land management practices in challenging environmental conditions.

Acknowledgements

The authors are grateful to the Ministry of Higher Education and Scientific Research, Algeria. The research was conducted as part of the PRFU research project D00L02UN050220220001 (University of Batna 2, Algeria), entitled *Ecophysiological analysis and plant production for the rehabilitation of degraded ecosystems in the Aurès region (Algeria)*.

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