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Germination Strategy of *Chenopodium acuminatum* Willd. under Fluctuating Salinity Habitats

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Abstract: Germination events of plants often occur after rainfall in saline environments where the soil salinity is diluted, viz recovery germination. Previous germination studies have rarely considered the duration of exposure to salt stress, and none of them have investigated recovery germination under low-salt concentration, other than in distilled water. The main objective of this study was to investigate the effects of salinity, exposure duration and low-salt recovery solutions on seed germination of the weed *Chenopodium acuminatum* to get a clear insight about the germination strategy exhibited by this species in a saline habitat. Seeds were initially exposed to 0–400 mM NaCl for 10, 20 and 30 d. The subsequent recovery experiment was conducted differently. For those initially treated with 100 and 200 mM NaCl, the recovery solution was distilled water, while for those initially treated with 300 and 400 mM NaCl, the recovery solution was distilled water, at 50 and 100 mM NaCl. Results showed that the recovery germination percentage and rate significantly decreased when the exposure duration extended. Seeds could subsequently recover to germinate at high percentages at recovery salt solution concentrations for a short duration, but the recovery percentages and rates in high salinity, combined with high exposure duration and relatively high recovery salt concentrations, were remarkably lower. More than 30% of the ungerminated seeds were viable after the recovery experiment. We suggest that *Ch. acuminatum* exhibits a 'cautious' strategy of germination to avoid injury from long-term salt stress and ensure survival for the subsequent continuation of its population under unfavorable saline conditions.

Keywords: prolonged exposure duration; recovery germination; salt stress; seed secondary dormancy

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1. Introduction

Soil salinization influences numerous ecosystems worldwide, especially in arid and semiarid climatic zones [1], which was mainly driven by sea level rises, climate change, and/or anthropogenic factors [2]. A significant increasing tendency of salinization has caused a great challenge for agricultural production and also the natural vegetation [3–5]. Thus, the remediation of salty soils and the cultivation of salt-tolerant plants and crops can be regarded as some of the viable strategies that could help solve this problem. Given that a plant can survive and complete the whole life cycle in salty environments, the prerequisite for such habitats is seed germination and seedling establishment [6]. Thus, seed the germination tolerance of various plants to salt has received much attention [7–10].

Seed germination response to salt stress includes a reduction in germination percentage and a delay in germination, which is caused by the osmotic and ion effects of salt [11,12].

Hyper-saline conditions may also lead to the death of seeds [13]. Therefore, the tolerance of seeds at the germination stage reflects in two aspects: the ability to germinate under salt stress, and the ability to recover germination after exposure to salt stress and then the relief of salinity [14]. Seed recovery germination ability is an adaptive strategy in salty environments to ensure successful establishment. For example, some halophytes have the inherited ability to maintain a fairly long seed dormancy period when they are exposed to hyper-saline conditions, and subsequently can germinate when the unfavorable salt stress is alleviated [11,15,16].

Previous studies investigating germination and recovery responses to salt have usually exposed seeds to different salinity levels over a specific duration (e.g., duration vary from 7 d to 30 d) before the experiment was terminated [11,12,15,16]. However, germination responses of halophytes depend on the duration and concentration of salt to which they are exposed. Prolonged exposure to saline solutions can stimulate germination of certain species [17]. For example, after 30 d exposure to 3–10% NaCl solutions, the seeds of *Suaeda calceoliformis* (Hook.) Moq., *Hordeum jubatum* L., *Salicornia europaea* L. and *Spergularia marina* (L.) Besser could rapidly recover germination and reach or exceed the germination percentages of those treated with distilled water. Different salt exposure duration to salt stress for seeds are common in the field of salinized environments. However, the effects of saline exposure duration on the recovery germination is not clear.

Under natural conditions of salt regions, the salinity of the soil surface could be substantially reduced after rainfall events, which is a prerequisite for successful germination of most species in such habitats [16]. However, the rainfall alone cannot ensure a complete leach of the saline soil. Most rainfall events may just dilute salty soil to an appropriate salinity level that facilitates seed germination. Thus, the testing of recovery germination responses to low salinity level is a valuable angle to further understand strategies of seed germination and seedling establishment in saline environments. The recovery germination experiments in previous studies have always transferred ungerminated seeds to distilled water [11,16,18]. Studies on recovery germination responses of seeds to low salinity are lacking. Furthermore, little is known about the interactive effects of exposure duration and recovery solution concentration on recovery germination.

To unravel these research gaps, we investigated the common weed species *Chenopodium acuminatum* Willd., belonging to the family Amaranthaceae. It is an annual inland halophyte, widely distributed in grazing grasslands and croplands in the temperate biome [19], and also plays an important role in the restoration succession in degraded grasslands [20,21]. The native range of this species include the southeast of European, Japan and Philippines, and was introduced into Bulgaria and Czechoslovakia [22]. It causes serious problems in agricultural production and forage quality owing to the abundant soil seed bank in saline habitats [23].

In order to understand the germination and recovery germination responsive strategy comprehensively and help control the problematic weed of *Ch. acuminatum*, we tested the following: (1) the effects of salinity and exposure duration on the initial germination and recovery germination in distilled water, (2) the influences of salinity, exposure duration and recovery solution concentrations on recovery germination of *Ch. acuminatum.* We hypothesized that prolonged exposure duration to high salinity inhibited initial germination and recovery germination. We also predicted that low-salinity solution as a recovery medium might decrease recovery germination.

2. Materials and Methods

2.1. Seed Collection and Study Region

Seeds of *Ch. acuminatum* Willd. were collected from more than 50 individuals of natural populations at maturity in the Songnen Plain of Northeast China (44°45′ N, 123°45′ E; 160 m a.s.l) [24,25]. The region has a semi-arid, continental climate. The mean annual temperature is around 5 °C, varying from −16 °C in January to 25 °C in July. The average annual precipitation is 350–450 mm and occurs mostly between June and August [26].

The pericarps of seeds were removed by hand. Seeds were stored in a paper bag at room temperature (15–22 °C, 40% relative humidity) for seven months before the germination experiment. The viability of the randomly selected seed sample was tested before the germination experiment and ungerminated seeds were tested after the recovery experiment using tetrazolium test [27].

2.2. Effects of Salinity and Exposure Duration on Initial Germination

Five salinity treatments including 0, 100, 200, 300, 400 mM NaCl solutions and three duration (10, 20 and 30 d) were used for the initial germination experiment. There were 4 replicates (4 petri dishes) for 0 mM (distilled water), 12 replicates (4 petri dishes × 3 duration) for 100 and 200 mM NaCl treatments and 36 replicates (12 petri dishes × 3 duration) for 300 and 400 mM NaCl treatments used for recovery treatments with subsequent salt concentrations (distilled water, 50 and 100 mM NaCl), resulting in 100 petri dishes (Figure 1). The initial germination experiment and the recovery experiment in distilled water were factorial designs with two factors (salinity × exposure duration). The recovery experiment was initially exposed to 300 and 400 mM and recovered in distilled water, 50 and 100 mM salt solutions was a factorial design with three factors (salinity × exposure duration × recovery solution concentration). Thirty seeds were surface sterilized by $NaClO_3$ and then placed on double layer filter paper in each of the 9 cm diameter petri dishes with 7 mL of the test solution. The petri dishes were sealed with parafilm and incubated at 20 °C under completely dark conditions (60% relative humidity) in incubators (HPG-400, Haerbin, China). Germinated seeds were counted under green light. Seeds were considered to be germinated when the radicle has emerged approximately 1 mm. Germination was examined every 2 d and germinated seeds were removed from petri dishes at each counting.

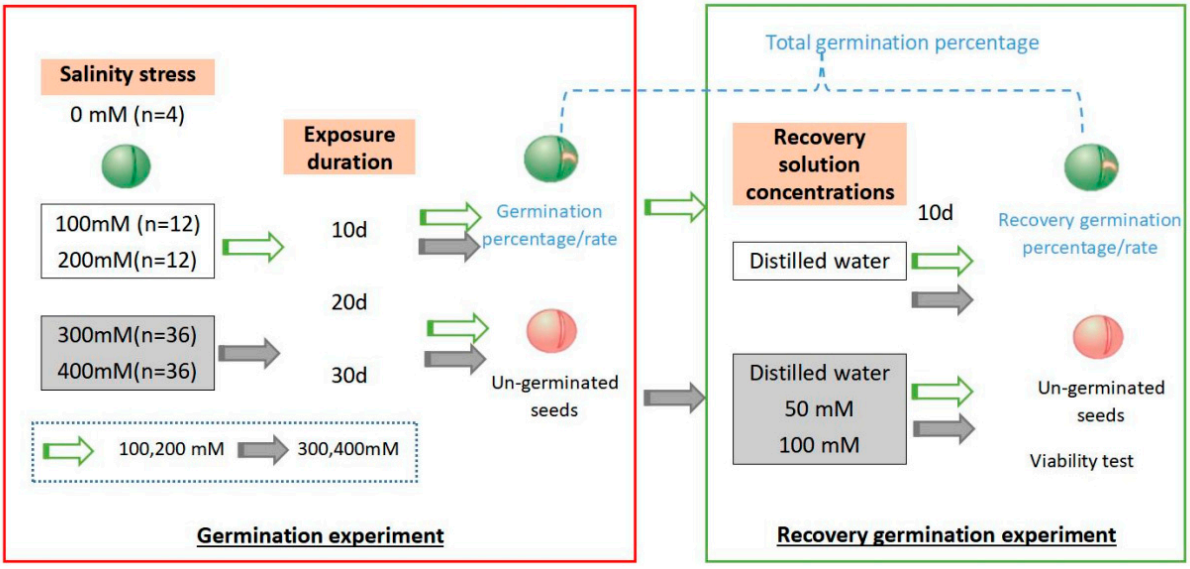

Figure 1. Flow chart and terminology of germination and recovery germination experiments.

At the end of each exposure duration, the initial germination percentage was calculated by the equation: $B/(C - NV) \times 100\%$, where B is the number of seeds germinated in salt solutions and C is the total number of seeds (30 seeds), and NV is the non-viable ungerminated seeds. Germination rate was calculated using the modified Timson index: $\sum G/t \times 100\%$; in this study G is the accumulate germination percentage at each day and t is the total germination period [28]. According to this equation, the highest value obtained was 100 (i.e., 1000/10), and a higher value indicates a more rapid germination. Germination percentage and germination rate here were referred to as initial germination percentage and initial germination rate, to distinguish them from the following recovery germination percentage and recovery germination rate.

2.3. Recovery Test

Ungerminated seeds in each of the above treatments were thoroughly washed by distilled water to get rid of any remnant solutes on seed surfaces after 10 20, and 30 d duration. Those ungerminated seeds of 100 and 200 mM NaCl treatments were transferred to distilled water for recovery. The ungerminated seeds from 300 and 400 mM NaCl treatments were transferred to distilled water of 50 and 100 mM NaCl solutions for recovery, respectively. Each recovery treatment had four replicates. The duration of the recovery test was 10 d.

Through the tetrazolium test of the ungerminated seeds after the recovery experiment, only viable seeds were used to calculate recovery germination and total germination percentages. The recovery germination percentage was calculated by the equation $A/(C - B - NV) \times 100\%$, where A is the number of seeds germinated in recovery solutions, B is the number of seeds germinated in salt solutions in previous germination experiment, C is the total number of seeds tested (30 seeds), and NV are the non-viable ungerminated seeds present in recovery experiment [29]. Total germination percentage was calculated as $(A + B)/(C - NV) \times 100\%$. The recovery germination rate was also calculated using the modified Timson index.

2.4. Statistical Analysis

The germination percentage was arcsine square root transformed before analysis to ensure homogeneity of variance [30]. Two-way ANOVA was performed to test the effects of salinity (0–400 mM) and exposure duration and their interaction on initial seed germination, recovery germination in distilled water and total germination percentages. Three-way ANOVA was performed to test the effects of salinity (300 and 400 mM), exposure duration and recovery solution concentration and their interactions on recovery germination and total germination percentage. LSD tests were used for multiple comparisons to determine significant differences between treatments at $p < 0.05$ level. Regression analysis was used to describe the relationships between total germination percentage and salinity combined exposure duration. All data were analyzed using SPSS (Version 19.0 for Windows).

3. Results

3.1. Effects of Salinity and Exposure Duration on Initial Germination

Ninety-five percent of the *Ch. acuminatum* seeds were viable in the tetrazolium test before the experiment and most seeds were germinated within 8 d in all treatments. The low salinity of 100 and 200 mM NaCl had no effects on the initial germination percentage. The maximum germination percentage and rate were obtained at 100 mM after 20 d exposure, which was significantly higher than that in distilled water (Figure 2). There was only 1%, 6%, and 7% seeds germinated at 300 mM in 10, 20, 30 d exposure duration, respectively. None of the seeds germinated at 400 mM NaCl treatment. Exposure duration in salt stress had no effect on the initial germination percentage, but significantly affected germination rate ($p < 0.05$; Table 1). The initial germination rate significantly decreased at 30 d exposure for 100 and 200 mM NaCl treatments, compared with 10 d and 20 d exposure duration (Figure 2).

3.2. Effects of Salinity and Exposure Duration on Recovery of Germination in Distilled Water

Salinity has significant effects on recovery germination percentage and recovery germination rate of *Ch. acuminatum* seeds in distilled water ($p < 0.05$, Table 1). The increased salinity 'pre-treatment' level increased the recovery percentage and recovery germination rate, with higher values in hyper-salinity (300 and 400 mM) than in low salinity treatments (100 and 200 mM). However, the recovery germination percentage and rate decreased when the exposure duration extended, especially in the case of 400 mM NaCl treatment (Figure 3a,b). The total germination was promoted in salt treatments at shorter exposure duration (10 d), compared with that in distilled water (Figure 3c). By contrast, longer exposure duration (30 d) decreased the total germination percentage for 400 mM NaCl treatment.

Table 1. Two-way ANOVA showed the effects of salinity (0–400 mM), exposure duration (10, 20 and 30 d) and their interactions on initial germination, recovery germination and total germination percentage in distilled water of *Ch. acuminatum*. F values were given, and asterisks indicate significant effects at $p < 0.05$.

Source		Initial Germination Percentage	Initial Germination Rate	Recovery Percentage	Recovery Germination Rate	Total Germination Percentage
	df	F	F	F	F	F
Salinity (S)	4	4.208 *	1.637	9.589 *	44.858 *	10.303 *
Exposure duration (ED)	2	2.138	20.816 *	1.100	35.151 *	1.588
S × ED	8	0.986	5.252 *	2.624	60.065 *	1.745

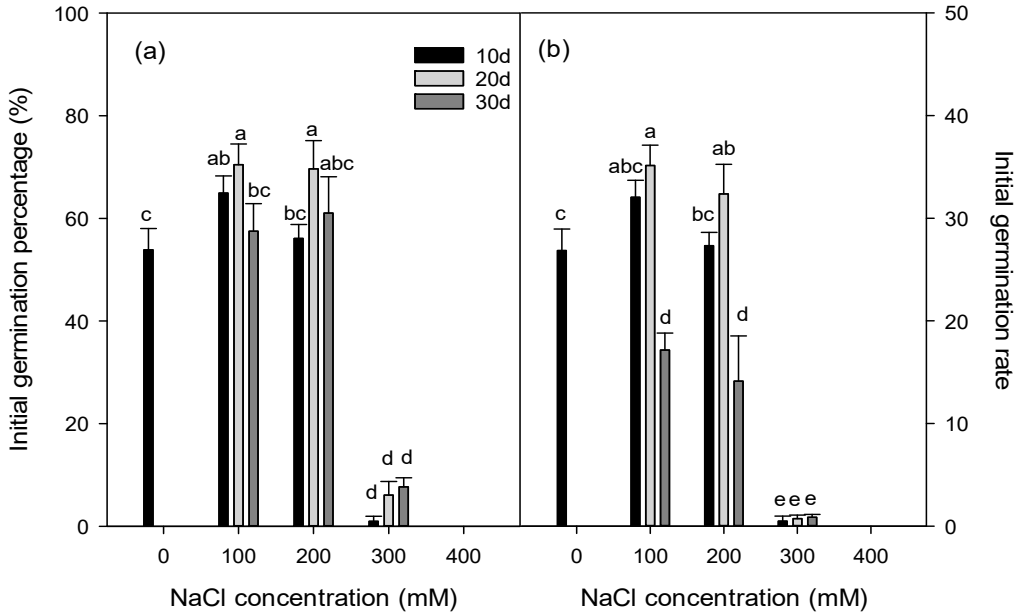

Figure 2. Initial germination percentage (**a**) and germination rate (**b**) of *Ch. acuminatum* when exposed to different salinity and exposure duration. Different letters between treatments indicate significant differences at $p < 0.05$.

3.3. Effects of Salinity, Exposure Duration and Recovery Solution Concentrations on Recovery of Germination

Salinity (300 and 400 mM), exposure duration (10, 20 and 30 d), and recovery concentration (0, 50, and 100 mM) significantly influenced recovery germination percentages and rates ($p < 0.05$; Table 2). Few seeds (<10%) could germinate at 300 mM and 400 mM NaCl levels in the initial germination experiment (Figure 2a). But seeds recovered to germinate at a high percentage in distilled water and 50 and 100 mM NaCl recovery solutions with 10 d exposure duration (Figure 4a,b). However, recovery in salt solutions (50 and 100 mM NaCl) greatly decreased recovery germination percentage and germination rate for 20 d and 30 d exposure duration treatments, compared with recovery in distilled water (Figure 4a,d). The recovery germination percentage of 300 mM was 65.3%, 57.1% and 64.9%, respectively, for 10, 20, and 30 d exposure duration in distilled water. Recovery germination percentage of 300 mM was 68.9%, 35.0%, and 31.2%, respectively, for 10, 20, and 30 d exposure duration in 100 mM recovery solution (Figure 4a).

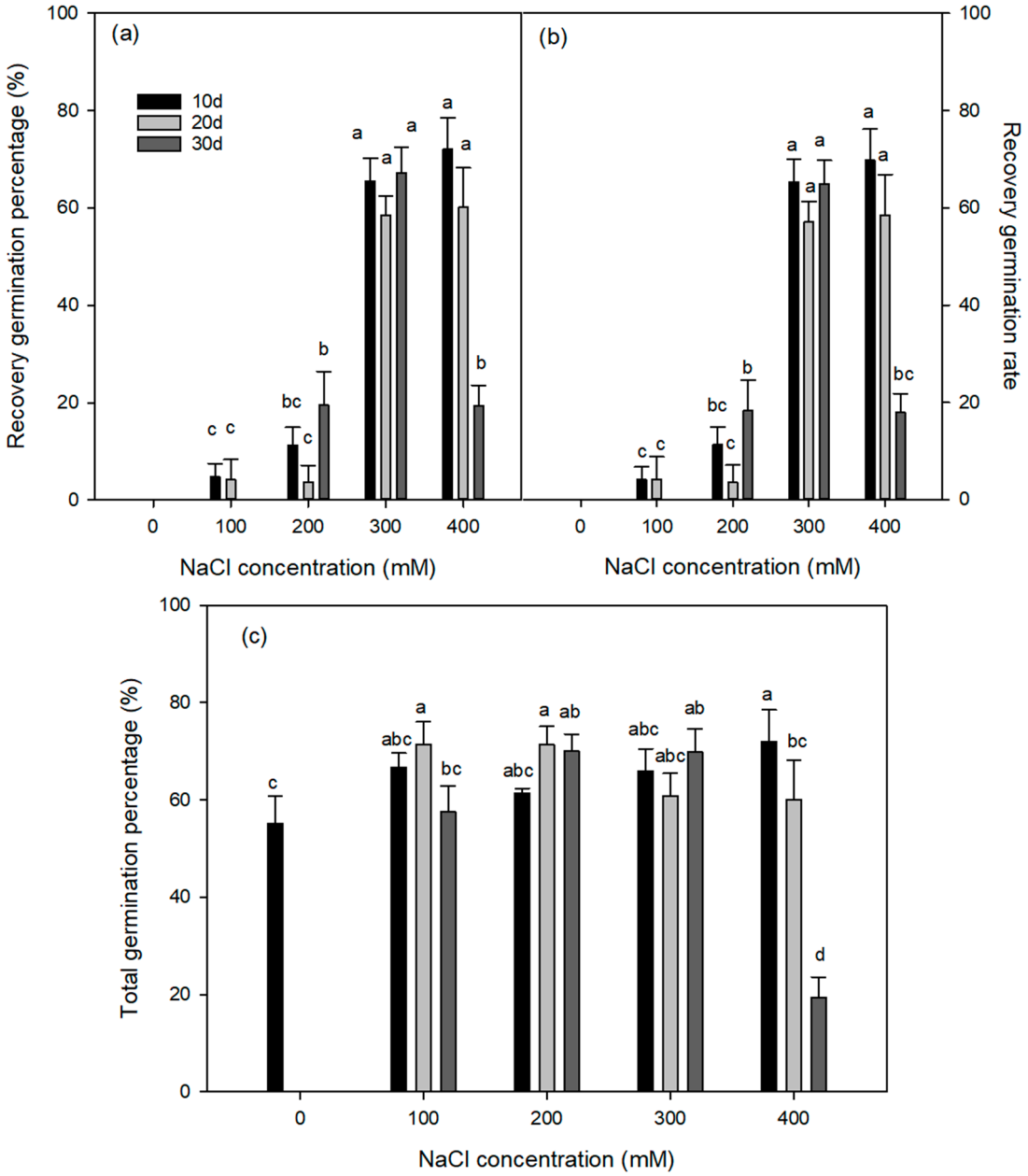

Figure 3. Effects of salinity and exposure duration on recovery germination percentage (**a**), recovery germination rate (**b**) and total germination percentage (**c**) of *Ch. acuminatum* seeds initially subjected to five salinity treatments and then recovered in distilled water (see Section 2.3 Recovery Test). Different letters between treatments indicate significant differences at $p < 0.05$.

The total germination percentages at 300 mM and 400 mM salinity levels in all recovery solution concentrations were not significantly different with that of the control (germination in distilled water in the germination experiment) for 10 d exposure duration (Figure 4e,f). High exposure duration also had greater effects on the total germination percentage than that of low exposure duration. The adverse influence of exposure duration and recovery solution concentration was greater for 400 mM than 300 mM salinity level (Figure 4). However, more than 30% of the ungerminated seeds after the recovery experiments were viable. The viable seed percentages of 300 and 400 mM initial salt treatments for 20 d and 30 d exposure duration recovering in 50 and 100 mM solutions were much higher than the other treatments (Figure 5).

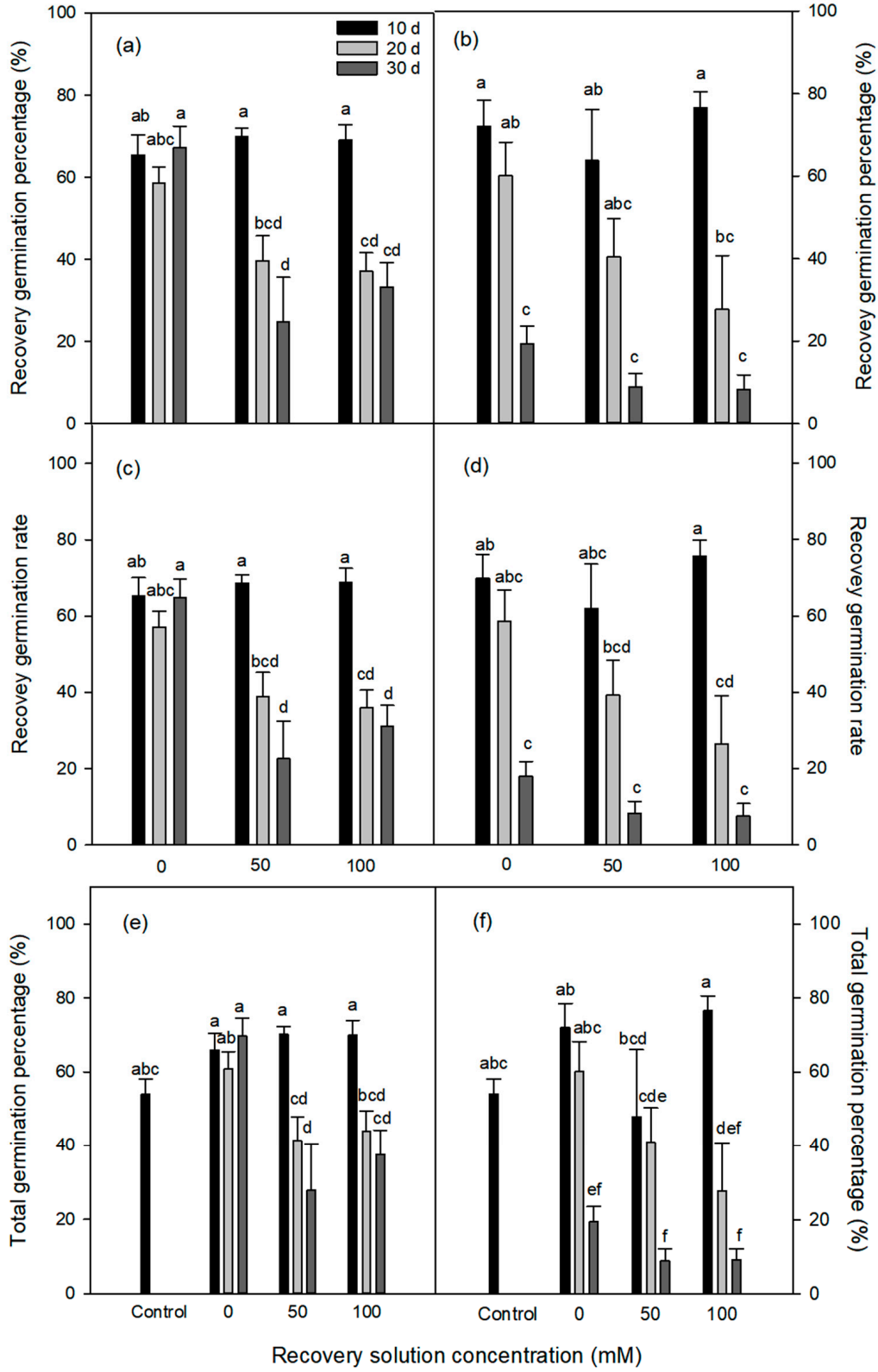

Figure 4. Effects of salinity (300 mM, (**a**,**c**,**e**); 400 mM, (**b**,**d**,**f**)), exposure duration and recovery solution concentration on recovery of germination and total germination percentage of *Ch. acuminatum* seeds. Different letters between treatments indicate significant differences at $p < 0.05$.

Table 2. Three-way ANOVA showing the effects of salinity (300 and 400 mM), exposure duration (10, 20 and 30 d), recovery concentration (0, 50, and 100 mM) and their interactions on seed recovery germination percentage, recovery rate and total germination percentage of *Ch. acuminatum* seeds, F values were given, and asterisks indicate significant effects at $p < 0.05$.

Source		Recovery Germination Percentage	Recovery Germination Rate	Total Germination Percentage
	df	F	F	F
Salinity (S)	1	9.519 *	10.116 *	14.069 *
Exposure duration (ED)	2	59.583 *	64.875 *	35.931 *
Recovery concentration (RC)	2	10.661 *	10.846 *	9.042 *
S × ED	2	9.907 *	9.159 *	6.466 *
S × RC	2	0.316	0.43	0.033
ED × RC	4	3.659 *	3.929 *	2.241
S × ED × RC	4	1.826	1.945	2.489

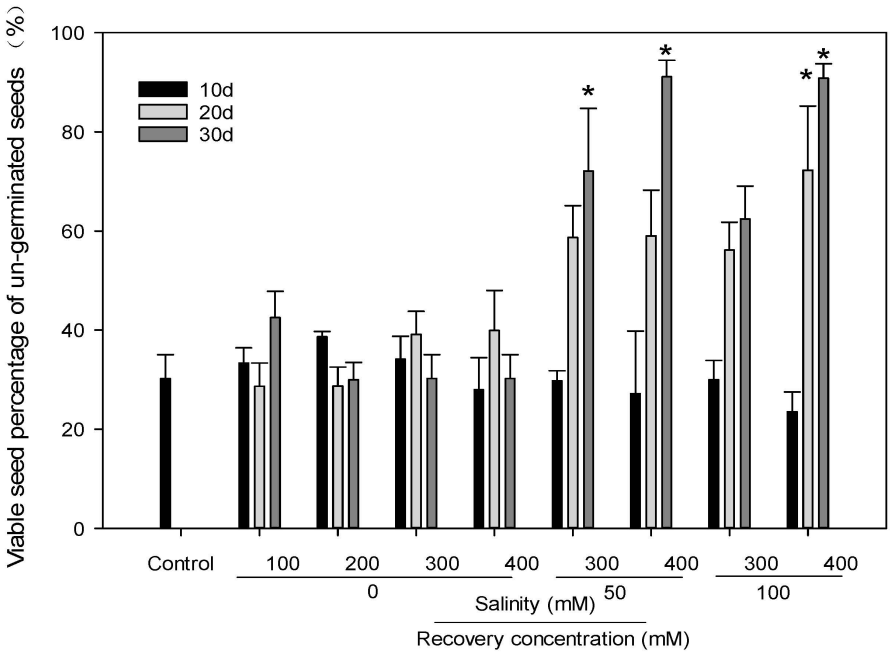

Figure 5. Viable seed percentage of non-germinated seeds in different salinity exposure duration and exposure salt solutions after recovery experiment. The asterisks for different treatments indicate a significant difference when compared to control at $p < 0.05$.

The relationships between total germination percentage and the combination of salinity multiplying exposure duration were parabolic. Total germination can be promoted under low salinity conditions, but the highest values occurred at different salinity and exposure duration for recovery in distilled water and 50 or 100 mM salt solutions. The total germination percentage might decrease 20% approximately in 50 and 100 mM recovery solutions compared with those seeds recovering in distilled water at medium and high salinity combined exposure duration. For example, the total germination percentage of recovery in distilled water was 65% under a stress of 6000 mM · d (subjected to 200 mM NaCl stress for 30 days or 300 mM NaCl stress for 20 days), while the total germination percentage of recovery in 50 mM and 100 mM was 41% and 43%, respectively (Figure 6).

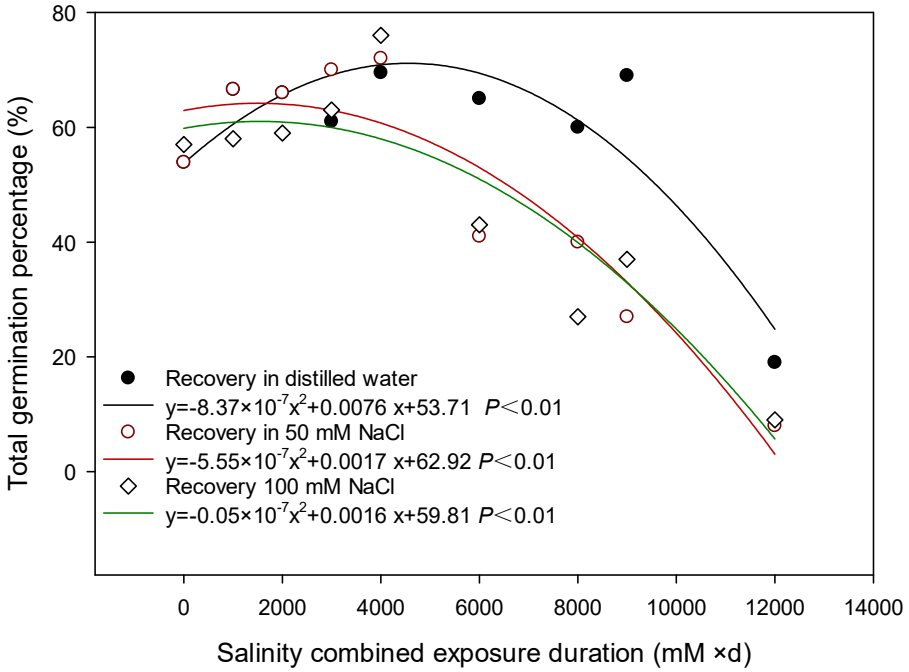

Figure 6. The relationships between total germination percentage and salinity combined exposure duration when *Ch. acuminatum* seeds were subjected to different recovery salt concentrations.

4. Discussion

Our results showed that prolonged exposure duration to high salinity and recovery at low concentrations of NaCl inhibited initial germination and recovery germination of *Ch. acuminatum*, although a high percentage of viable and non-germinated seeds were observed after the recovery experiment, especially those under 300 and 400 mM initial NaCl. Those seeds exhibited healthy features, such as no fungal infection, integrated seed coat, and seeds with a firm white embryo [27]. The tetrazolium test further confirmed their viability. Thus, we suggest that these seeds entered a conditional or secondary dormancy phase prior to recovery treatments, which is induced by prolonged unfavorable conditions [31]. It is widely accepted that salt may induce seeds into a conditional dormancy state [32,33]. The conditional dormant seeds could germinate when the soil salinity is diluted by rain or snow melt. If the salt stress could not be alleviated, the seeds might enter a secondary dormancy in the soil seed bank, such as annual halophytes *Suaeda aralocaspica* (Bunge) Freitag & Schütze [34], *Suaeda corniculata* subsp. *magnolica* Lomon. & Freitag [33], *Eruca sativa* Mill. [35] and *Opuntia ficusindica* (L.) Mill. [36].

Seeds of *Ch. acuminatum* exposed to higher salinity for short duration demonstrated the stimulative effect of salt on recovery germination. Total germination percentages in all salinity for 10 d exposure duration were higher than those of the control, especially 400 mM initial treatment (Figure 3c). This result indicates that the negative water potential of the relatively high NaCl solutions might have caused a water stress priming condition in the *Ch. acuminatum* seeds. When the water stress conditions are alleviated by soaking seeds in distilled water, recovery germination is promoted. Similar increasing trends of germination after experiencing an initial osmotic stress have also been observed in other halophytes such as *Suaeda moquinii* (Torr.) Greene [37], *Atriplex halimus* L. [38], *Cakile maritima* Scop. [39] and *Puccinellia limosa* (Schur) Holmb. [40].

As predicted, not only salinity and exposure duration were critical factors for recovery germination rate, but also the solute concentrations used for subsequent recovery treatments had significant effects on recovery germination and total germination percentages ($p < 0.05$; Table 2). Recovery concentration of 50 mM and 100 mM NaCl solutions decreased the recovery germination percentage and germination rate of *Ch. acuminatum*, especially when they were exposed for a longer duration (20 or 30 d). Based on the relationship

between total germination and duration of combined exposure to salinity, it is observed that the total germination might be 20% greater recovering in distilled water than in 50 or 100 mM NaCl solutions (Figure 6). Thus, the previous studies may have overestimated the recovery germination percentage and rates of halophytes and glycophytes under salt alleviated field conditions, as the recovery germination was only tested in distilled water [10,41–45].

Our study showed that most of the *Ch. acuminatum* seeds could germinate and recovery after salt treatments within two days. This species mainly distribute in arid and semi-arid regions and saline soils, where there are low and irregular rainfall [46]. The rapid seed germination of *Ch. acuminatum* is an adaptive strategy in saline-alleviated environmental conditions experienced during the rainy season to ensure a successful subsequent seedling establishment [42]. Similar research showed a rapid germination pattern of *Ch. acuminatum* germination time to reach 50% germination was 1 d and to reach 90% germination was 3 d [23].

The salt tolerance threshold of halophytes varies widely depending on their respective strategies for adaptation to the environment. For example, seeds of *Atriplex patula* L. could germinate in less than 170 mM NaCl, while *Salicornia rubra* A. Nelsson have a very high salt tolerance of 1000 mM NaCl at the germination stage [47]. In our study, seeds of *Ch. acuminatum* could tolerate up to 300 mM NaCl concentration, with 5% seeds germinated. However, recovery germination of *Ch. acuminatum* seeds was high when they were transferred to distilled water or relatively low salt concentrations. Based on Woodell's classification of halophytes [48,49], *Ch. acuminatum* falls into category one: seed germination decreases with the increase of salinity but has a high recovery germination percentage from the germination perspective of this study.

Plants have the ability to develop adaptive strategies in their particular occupied habitat, and the germination strategy plays a pivotal role in ensuring population stability and prosperity [18,50–53]. Based on our results, *Ch. acuminatum* seeds adopt comprehensive germination strategies in salt stress conditions. At low salinity, a high proportion of seeds germinate immediately when the temperature and relative humidity are optimal, and only a small proportion of seeds remain dormant in the soil seed bank. At median and high salinity, the majority of seeds do not germinate due to hyper-salinity and enter a conditional dormancy state. The recovery germination percentage increases under short exposure scenarios when the salinity level is eased. A small proportion of the seeds also remain dormant in soil seed bank. If the seeds are exposed to medium and high salinity conditions over a month, only a small proportion of seeds can recover germination, even after the salinity levels are subsequently diluted to a very low level. Under these circumstances, part of the seeds permanently failed to germinate. A similar dormancy pattern was found in *Suaeda aralocaspica* (Bunge) Freitag & Schütze [34], *Kalidium capsicum* (L.) Ung.-Sternb. [53]. This strategy has an ecological significance under median and high saline environments. The 'cautious' germination strategy allows seeds of *Ch. acuminatum* to avoid injury due to fairly high salt exposure that can lead to their population extinction in such habitats. These results reflect the seedling survival success of this species in saline environments in arid and semi-arid regions from a germination strategy perspective. Further biochemical experiments to test the effects of the osmotic potential of the salt solutions as a possible cause that leads to the difficulty in imbibition and activation of the metabolism of the embryonic axis and the evaluation of the seedling survival in saline environments will be necessary to confirm this hypothesis.

5. Conclusions

In conclusion, prolonged exposure of *Ch. acuminatum* seeds to medium and high salinity and recover in low concentrations of salt solutions significantly decreased the recovery germination percentage and rate while a short exposure duration of low salinity levels had a stimulative effect on recovery germination and total germination. Generally, the weed species *Ch. acuminatum* germinates fast and adopts a 'cautious' germination

strategy under high salinity levels, which helps this species survive in saline habitats. The overall germination processes involved in these saline habitats are likely to be highly complex, and as shown in our preliminary studies, all these factors seem to interact in a highly ordered manner involving physiology, biochemistry, and gene expression related to *Ch. acuminatum* seed germination.

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