Salt Priming Impacts on Edible Mesembryanthemum Crystallinum L.

Subjects: Horticulture
Contributor: Jie He

Mesembryanthemum crystallinum L. is a nutritious edible facultative halophyte. They were cultivated with different percentages of artificial seawater (ASW). All plants were green and healthy. However, there were reductions in shoot and root productivity, and leaf growth. The concentrations of proline, ascorbic acid (ASC), and total phenolic compounds (TPC) increased as percentages of ASW increased. The salt-primed plants switched from C3 to crassulacean acid metabolism photosynthesis and accumulated the greatest amounts of proline, ASC, and TPC. In conclusion, higher salinities and salt priming enhance nutritional quality of *M. crystallinum* L. but compromises productivity.

Keywords: salinity stress ; salt priming ; phytochemicals

1. Introduction

Native to southern and eastern Africa, *M. crystallinum* L. (common ice plant) is a facultative halophyte, which means saline is not a physical requirement for growth [1]. However, some researchers consider that *M. crystallinum* L. belongs to the group "obligatory" halophytes, which requires saline environments for optimal growth [2]. It has high economical value as it has many important uses. Its leaves and stems can be used as human food [3]. It also has antioxidant and antimicrobial properties that helps to reduce inflammation of the mucous membranes in respiratory and urinary systems [4]. The maintenance of food security, in terms of quantity and quality, is an increasing challenge for Singapore due to limited land. In Singapore, almost 90% of food is imported from an increasingly disrupted world resulting from the COVID-19 pandemic. Furthermore, major food production areas are expected to face reduced water availability and increased drought frequency due to climate change [5].

According to Flowers et al. [6], halophytes are plants that are able to complete their lifecycle in a salt concentration of at least 200 mM NaCl under conditions similar to those that might be encountered in the natural environment. Halophytes can tolerate salinity stress as they possess salt responsive genes and proteins to counter the adverse effects of salinity [7][8]. However, tolerance to salinity stress varies among halophyte species [9][10]. Halophytes that are less tolerant to salinity normally reduce their growth in saline environment [11]. Reduced growth under salinity conditions helps the plants to conserve energy for the production of osmolytes, which protect halophytes against hyperosmotic stress [12]. Osmolytes, such as free proline and soluble sugars, defined as having health-promoting benefits, can potentially be used in functional food [13][14]. Soluble sugars and proline could be used by plants in osmotic adjustments [15]. However, it has been reported that halophytes may not be able to survive and thrive under extremely saline conditions [16]. For protection against the oxidative stress caused by salinity, antioxidants such as ascorbic acid (ASC) and phenolic compounds are produced [17][18]. Given that these antioxidants are also beneficial for human health [19], the awareness of a healthier diet and halophytes with high nutritional values may promote additional markets for some halophytic vegetables [20].

Sivritepe et al. [21] reported that seed salt priming is a useful technique to improve the salt tolerance of plants because seeds that have been primed are better able to adjust osmotically. This is because primed seeds have high levels of Na and Cl in their roots as well as high concentrations of soluble sugars and organic acids in their leaves compared to those non-primed seeds [22]. Memory of the first stress (priming) and retrieval of the remembered information upon encounter with the later stress are necessary to improve stress tolerance [22]. Salt-priming treatments have been mainly applied to seeds, and the possible impacts of seed priming on plant growth and development and different physiological processes were monitored during seed germination and seedling stage [23][24][25]. It was reported that NaCl priming improved the germination and seedling growth of canola (*Brassica napus*) [23] and pepper (*Capsicum annuum* L.) [24]. NaCl priming resulted in better cell membrane stability compared to untreated seedlings [23][24]. Farhoudi [25] reported that seed priming improved antioxidant activity and compatible solute content such as sugars and proline in Muskmelon (*Cucumis melo* L.) under salt stress. However, there is very little research on salt priming during the vegetative stage.

M. Crystallinum L. grown under 500 mM NaCl decreased leaf growth, biomass accumulation and leaf water content compared to those grown under lower concentration of NaCl. However, all plants were healthy with similar maximal efficiency of photosystem II (PS II) photochemistry. Plants grown under 500 mM NaCl switched from C_3 photosynthesis to CAM photosynthesis in order to tolerate salinity stress. CAM is characterized by nocturnal CO_2 uptake, which increased water-use efficiency when compared to C_3 plants [26][27]. Phytochemicals such as proline, total soluble sugar (TSS), ASC and total phenolic compounds (TPC) were significantly higher in plants grown under higher salinity compared to those grown under lower salinity [27].

2. Productivity

Figure 1 shows that all *M. crystallinum* L. grew healthily after transferring them to different salinities. Compared to the 10-day-old plants grown in 10% ASW (salinity condition I), all other plants transferred to higher percentages of ASW (salinity conditions II to VII) continued to grow bigger (**Figure 1**) as supported by their higher shoot and root FW and DW after another 10 days of growth (**Figure 2**A,B,D,E). Plants that were transferred from 10% ASW to 20% ASW for 10 days had similar shoot FW as those that remained growing in 10% ASW for another 10 days. However, after changing the salinities from 10% ASW to higher percentages of ASW (salinity conditions III to VI), shoot and root productivity significantly declined. Furthermore, plants that were gradually transferred from 10% ASW to 100% ASW (condition VII, defined as salt-primed plants) had the lower shoot FW (**Figure 2**A) but the highest shoot and root DW (**Figure 2**B,E). It was noticed that the root FW of *M. crystallinum* L. grown in 10% ASW for 10 days (condition I, **Figure 2**D) was less than half of those grown in higher concentrations of ASW (conditions V, VI, VII) for 20 days. However, due to the large standard errors, there were no significant differences in root FW detected among these plants. A similar situation was also seen in root DW (**Figure 2**E). There were generally no significant differences in the shoot/root ratio (FW) and shoot/root ratio (DW) of *M. crystallinum* L. after changing to higher salinities (**Figure 2**C,F).

Figure 1. *M. crystallinum* L. grown indoor hydroponically for 10 days (I) and 20 days (II to VII). I: 10% artificial seawater (ASW) for 10 days; II: 10% ASW for 20 days; III: 10% ASW, 10 days ⟹ 20% ASW, 10 days; IV: 10% ASW, 10 days ⟹ 30% ASW, 10 days; V: 10% ASW, 10 days ⟹ 40% ASW, 10 days; VI: 10% ASW, 10 days ⟹ 50% ASW, 10 days; VII: 10% ASW, 10 days ⟹ 20% ASW, 2 days ⟹ 40% ASW, 2 days ⟹ 60% ASW, 2 days ⟹ 80% ASW, 2 days ⟹ 100% ASW, 2 days (salt-primed).

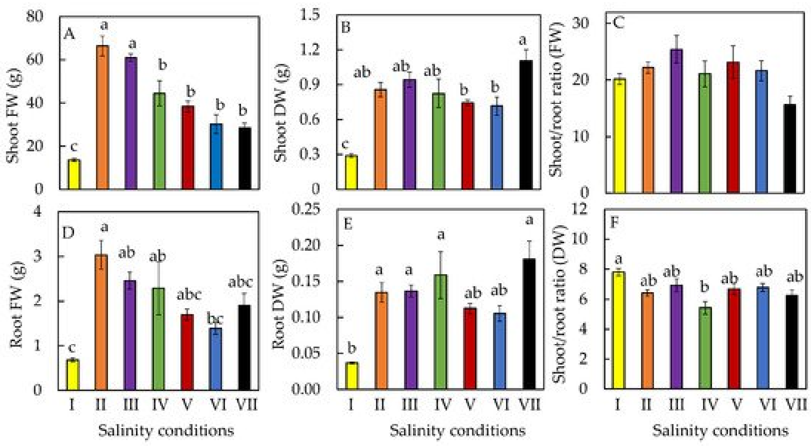

Figure 2. Shoot FW and DW (**A**,**B**), root FW and DW (**D**,**E**), and shoot/root ratio FW and DW (**C**,**F**) of *M. crystallinum* L. grown under different salinity conditions for 10 or 20 days. Values are means (±S.E) of four replicates from four different plants, and different letters indicate significant differences at $p < 0.05$. When letters are absent, there were no significant differences between the treatments. Refer to **Figure 1** legend for different salinity conditions of I, II, III, IV, V, VI, and VII.

3. Leaf Growth

Generally, total leaf number and total leaf area were smaller after the plants were transferred from 10% ASW to higher salinity conditions in ASW ≥30% (**Figure 3**A,B). However, total leaf number and total leaf area of plants that were transferred from 10% ASW to 20% ASW were statistically similar to the plants that remained growing in 10% ASW. Plants grown in 10% ASW for 20 days (salinity condition II) had the highest specific leaf area (SLA), while salt-primed plants (salinity condition VII) had a significantly lower SLA compared to those of the rest of the plants (**Figure 3**C).

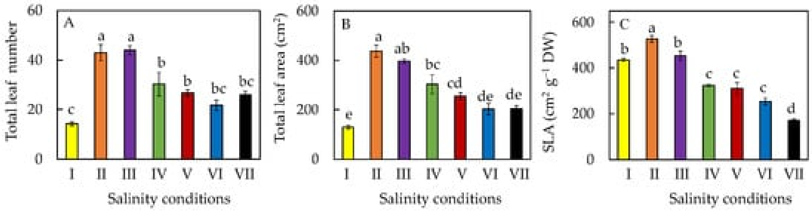

Figure 3. Total leaf number (**A**), total leaf area (**B**), and SLA (**C**) of *M. crystallinum* L. grown under different salinity conditions for 10 or 20 days. Values are means (±S.E) of four replicates from four different plants, and different letters indicate significant differences at $p < 0.05$. Refer to **Figure 1** legend for different salinity conditions of I, II, III, IV, V, VI, and VII.

4. Accumulation of Phytochemicals

Proline concentration increased after salinity conditions were changed from 10% ASW to ≥20% ASW (**Figure 4**A). The salt-primed plants had the highest proline concentration followed by those transferred from 10% ASW to 50% ASW, and then by 40% ASW and 30% ASW. Statistically, there were no significant differences in proline concentration between plants grown in 10% ASW for 10 and 20 days and those transferred from 10% ASW to 20% ASW (**Figure 4**A), which were significantly lower than those grown under higher salinity conditions. However, all plants had similar amounts of TSS (**Figure 4**B). Similar increasing trends were observed for the concentrations of ASC (**Figure 4**C) and TPC (**Figure 4**D). The salt-primed plants had the highest ASC and TPC concentrations compared to those of plants grown in the other salinity conditions (**Figure 4**C,D).

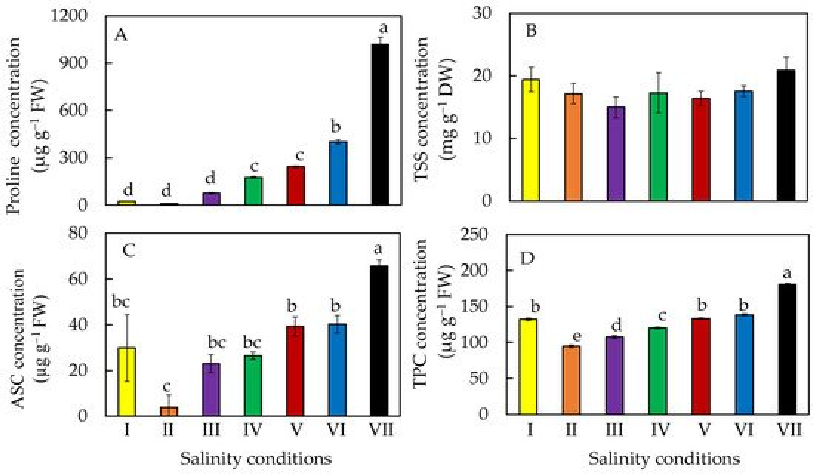

Figure 4. Proline (**A**), TSS (**B**), ASC (**C**), and TPC (**D**) concentrations of *M. crystallinum* L. grown under different salinity conditions for 10 or 20 days. Values are means (±S.E) of four replicates from four different plants, and different letters indicate significant differences at $p < 0.05$. When letters are absent, there were no significant differences between the treatments. Refer to **Figure 1** legend for different salinity conditions of I, II, III, IV, V, VI, and VII.

5. Researches and Findings

All *M. crystallinum* L. plants were first grown in 10% ASW for 10 days and then transferred to different salinities with higher percentages of ASW for another 10 days. All plants continued to grow after salinity conditions were changed (**Figure 1**). *M. crystallinum* L. grown in 10% ASW for the whole growth cycle of 20 days and those first grown in 10% ASW for the first 10 days followed by another 10 days in 20% ASW exhibited the best growth. This was supported by their highest shoot and root FW (**Figure 2**A,D). The high shoot FW is mainly due to the fact that plants grown in these two conditions had the greatest total leaf number and largest total leaf area compared to those grown in the other salinity conditions (**Figure 3**A,B). It was reported that, for plants subjected to salt stress, a general decrease in plant FW is often observed due to a reduction in the number of leaves or leaf abscissions [28]. The reduction in the leaf area for plants grown at higher salinity conditions may be an avoidance mechanism used by the plant to minimize water loss during transpiration [28][29][30]. However, the shoot and root DW were the highest in plants gradually transferred from 10% ASW to 100% ASW (**Figure 2**B,D) because they had the lowest LWC amongst the other plants. Similar results were also obtained where spinach was grown in different concentrations of salt [29]. It was reported that a linear increase in DW and a linear decrease in water content with increasing salinity stress could be due to the Na^+ accrual [31]. Furthermore, LDMC was the highest in salt-primed *M. crystallinum* L., accounting for the lowest SLA (**Figure 3**C) and thicker leaves. A similar trend was also observed in spinach *Spinacia oleracea* (L.), where the increased thickness may be associated with an increase in cell size [31]. Generally, no significant differences were observed in the shoot/root ratio (FW or DW) of *M. crystallinum* L. after changing to higher salinities (**Figure 2**C,F). These results indicate that the changes in salinity do not alter the resource allocation in *M. crystallinum* L., thus, photoassimilate partitioning between root and shoot remains constant. However, contradictory results were reported by another team, who found that the shoot/root ratio increased when *M. crystallinum* L. were grown under salinity [32]. An increased shoot/root ratio implies that the carbohydrate demands of CAM in the photosynthetic shoot take priority over root growth under water-limited conditions [32]. There were no significant differences in LS after the *M. crystallinum* L. plants were transferred from 10% ASW to different higher percentages of ASW. These results imply that the salt-primed *M. crystallinum* L. in this study switched to CAM under high salinity conditions and increased water-use efficiency and thus maintained LS as high as those *M. crystallinum* L. that perform C_3 photosynthesis under non-stressful lower salinity conditions [33]. Similar results were also obtained in our previous work, which reported that salinity did not affect the leaf succulence (LS) of *M. crystallinum* L. [34]. However, LS was significantly higher for all the plants grown in higher salinities for 20 days compared to those grown in 10% ASW for only 10 days. Plants may increase LS to dilute salts [34]. It was found that the LS was significantly lower in salt-primed *M. crystallinum* L. compared to those grown in 10% ASW for 20 days, which could be due to its greater decrease in LWC. Lower LS and LWC in salt-primed *M. crystallinum* L. grown with 100% ASW could be attributed to the stunted root architecture, which might have limited water uptake [35].

Hsouna et al. [36] have recently suggested that plants accumulate osmolytes such as proline as one of the strategies to avoid the consequences of stress caused by high salinity. In this study, proline concentration in *M. crystallinum* L. increased after transferring plants to higher percentages of ASW (**Figure 4**A). He et al. [35] also reported that *M. crystallinum* L. grown in 250 mM and 500 mM of NaCl had a higher proline accumulation compared to the plants grown in 100 mM of NaCl. Salt-primed *M. crystallinum* grown in 100% ASW had the highest proline concentration (**Figure 4**A), suggesting that salt priming could further enhance proline accumulation. Halophytes are able to tolerate salt and maintain their growth through osmotic adjustment, which is achieved by accumulating compatible solutes such as proline or TSS [37]. However, all plants had similar TSS concentrations regardless of the salinity under which *M. crystallinum* L. were grown (**Figure 4**B). Salt stress is known to enhance the production of ROS in plants, which can cause oxidative damage to lipids, proteins, and nucleic acids [38]. It is well known that ASC alleviates the oxidative stress in plants subjected to salinity stress by deactivating the ROS. As *M. crystallinum* L. was gradually transferred from 10% ASW to 100% ASW, the greatest amount of ASC was accumulated (**Figure 4**C). This result suggests that salt priming increases plant protection against oxidative stress. Cayuela et al. [22] reported that phenolic compounds have antioxidant properties and can confer various physiological responses to stresses in plants. This further supports the result of this study with the greatest amount of TPC found in salt-primed *M. crystallinum* L. (**Figure 4**D).

In conclusion, grown in higher salinity or under salt-priming conditions, *M. crystallinum* L. exhibited a high level of salt tolerance, with survival up to 100% ASW. At lower salinity conditions, *M. crystallinum* L. were more productive but had lower nutrition qualities. There were increases in the concentrations of phytochemicals such as proline, ASC, and TPC with increasing salinities. High accumulations of proline, ASC, and TPC in the shoot, which is mainly made up of leaves, increased the protection of *M. crystallinum* L. again salinity stress and enhanced the nutritional quality of edible *M. crystallinum* L. However, the productivity of *M. crystallinum* L. was compromised at higher salinity or salt-priming conditions. Although salt-primed *M. crystallinum* L. grown in 100% ASW had the lowest shoot productivity in this study, they had a greater yield compared to those grown in 500 mM NaCl (salinity similar to 100% ASW). The results of this study provide *M. crystallinum* L. growers a better understanding of the optimal conditions under which plants should grow to achieve specific results, such as high nutritional quality, without substantial yield reduction.

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