Growth and salt accumulation capacity of the common ice plant in the tsunami-affected soil

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ABSTRACT
Halophytes are salt-tolerant plant that grows naturally in saline areas where almost all conventional crops die due to NaCl toxicity. The common ice plant, \textit{Mesembryanthemum crystallinum} L., an annual halophyte native to South Africa, tolerates high salinity levels and accumulates NaCl in a shoot at a high level. To check the availability of the ice plant for desalinization of soils, we cultured the ice plant in soils collected from 16 sites located along coastal regions in the prefectures of Miyagi and Iwate, where were attacked by the tsunami disaster in the wake of the 2011 earthquake off the Pacific coast of Tohoku on 11 March 2011. In the soils obtained from some tsunami affected areas, the growth was better than that in the non-contaminated soil. The factors associated with growth inhibition were suggested to be water ratio (an index of water content) and soil water permeability. The ice plant’s estimated biological yield ranged from 0.33 to 14.6 kg m\textsuperscript{-2}, equivalent to 2.3 to 101.7 t ha\textsuperscript{-1}. The sum of Na\textsuperscript{+} and Cl\textsuperscript{−} was about 9.5 g in the shoot (31.8\% on a dry weight basis), and the estimated total amount of these ions removed from salinized soil was 2.38 t ha\textsuperscript{-1}. These results indicated that the common ice plant could be used as a crop under salinity and a tool for ameliorating NaCl from salinized soils.

Introduction
Salinity is one of the most critical environmental factors causing a reduction in agricultural productivity. The FAO (2008) estimated that over 6\% of the world’s land area is affected by salinity, which occupies more than 800 million ha of land in the world. Salinization is classified into primary and secondary salinization caused by natural force and anthropogenic activity, respectively (Boesch et al., 1994; Rogers & McCarty, 2000). The cause of primary salinization is a saltwater intrusion and wind-borne salt deposition in the land. The Asia-Pacific region is one of the most disaster-prone regions globally, with frequently occurring natural disasters such as earthquakes, tsunamis, and tropical storms, the...
leading cause of seawater intrusion. Global warming makes the situation worse, leading to an increase in the opportunity of massive typhoon attacks.

Most crop and forage plants are salt-sensitive glyco-

phyles and cannot handle a high salt concentration. Once salinity in the soil solution exceeds a certain level, productivity is reduced to an extent becoming commercially unviable. To increase crop production to meet the increased food demand in the future, we might need to use the deteriorated lands to produce more food. Even though numerous efforts have been conducted to improve salt tolerance of crops, such as conventional breeding and genetic engineering approaches, no cultivars for practical use in farmland have been produced (see, Flowers, 2004; Panta et al., 2014 and references therein). One relatively rapid approach is salt-tolerant plants’ use as a valuable crop (Glenn et al., 1999). Some salt-tolerant plants, halophytes, have been cultured for commercial use, e. g. Aster tripolium, Batis maritime, Crambe maritime, Portulaca oleracea, or Salicornia bige-

lovii (see, Shannon & Grieve, 1999 and therein). They represent 0.14% of terrestrial plant species (Flowers & Colmer, 2015). They can complete their life cycle in a NaCl-rich environment, even beyond seawater concentration (ca. 500 mM NaCl), where almost 99% of glycophytes, including crops, die due to NaCl toxicity (Glenn et al., 1999).

The growth of halophytes varies under salinity, but the species that can produce high biomass production, are thus expected to be used to rehabilitate salt-affected land by extracting significant amounts of salt from the soil. Several halophytes have been tested for their possi-

bility of reclamation of salt-affected soils (Akhter et al., 2003; Gul et al., 2000; Ravindran et al., 2007; De Villiers et al., 1995; Zhao et al., 2005). Mesembryanthemum crys-

tallinum L., the common ice plant, is an annual halophyte that can survive in the soil that contains NaCl up to about 800 mM, which is equivalent to about 1.5 times that in the seawater. In the previous study that the ice plant was cultured hydroponically under different NaCl ranged from 50–400 mM, the ice plant accumulated NaCl to shoot up to 14 g per single plant (Agarie, 2004). The ice plant also has been evaluated as a new functional vegetable (Agarie et al., 2009).

On 11 March 2011, a massive tsunami generated by an earthquake off the Pacific coast of Tohoku struck northeastern Japan. In the disaster, 23,600 ha of farmland in the six prefectures (Aomori, Fukushima, Iwate, Miyagi, Ibaraki, and Chiba) face the Pacific Ocean (MAFF, 2013). In the present study, to check the ice plant’s availability as a crop and a tool for desalinization in the salt-contaminated soil, we cultured the ice plant in the tsunami-affected soils. We collected soils from 16 sites located along coastal regions in Miyagi and Iwate, salt contaminated by seawater inundation. These soils are of upland fields and paddy fields which were under-
taken various treatments, such as removing surface soil layer and sludge using heavy machinery after the tsu-

nami. We speculated that the soil properties might have been changed to be unsuitable for cultivation by tsunami intrusion and artificial treatment. The investiga-
tion of soil quality would give us helpful information for cultivating halophytes or salt-tolerant crops in tsunami-affected soil. Therefore, we first analysed the physicochemical properties of each soil, and then conducted plant cultivation tests. In some tsunami-affected soils, the ice plant’s growth was better than that of plants grown in the non-contaminated soil. We discussed the factors that positively and negatively affect the growth, limiting salt amounts removed from the salinized land.

Materials and methods

1. Soils, plant, and culture conditions

The common ice plant (Mesembryanthemum crystallinum L.) was cultured in a greenhouse in an experimental field of Kagawa University (Kagawa, Japan). The soils were collected from late November to late December 2011, and the experiment was conducted from 14 December 2011, to 10 April 2012. Soils were stored at 4°C in the dark until the start of the experiment. We first analysed the physicochemical properties of each soil, and then tested growth performance in the soils. We conducted the experiment under natural sunlight in a greenhouse at the Faculty of Agriculture, Kagawa University, Miki-Cho, Kida-gun, Kagawa Prefecture, Japan. Figure 1 and Table 1 show the locations where soils were collected and the treatment of soils. We obtained the surface layer of soils (5–10 cm, ca. 20 kg) and stored them at 0°C. The soils of the experimental fields of Kagawa University, composed of decomposed granite soil and manure compost with a volume ratio of 1:4 was used as a control soil. Seeds were sown on plug trays (200 cells tray⁻¹) filled with a 5:1 mixture of peat moss and crushed coconut shell and irrigated with tap water till germination and irrigated of Otsuka House solution No. 1 and No. 2 (OAT Agrio Co., Ltd, Tokyo, Japan) twice a week after germination till harvesting according to the conventional method. At the fourth leaf growth stage (53 days after sowing), a plant was transferred to a 2.2 L plastic pot of 18 cm diameter filled with the soil. We prepared four replicates for each soil collected from the sites. The fresh weights of the shoot were measured 118 days after sowing.
**Figure 1.** Sampling points of the tsunami-affected soils. The soils were collected from 16 sites of two prefectures along the Pacific Ocean, indicating numbers. The letter E and number on the upper part of this figure and the letter N and number on the light side of this figure indicate the east longitude and the north latitude, respectively.

**Table 1.** Location, types and treatment of the soil.

| Sites | Prefecture | Types of field and treatment | City, District |
|-------|------------|-------------------------------|----------------|
| 1     | Iwate      | Paddy field, no removal of salt | Rikuzentakata, Takata-chou, Nakata |
| 2     | Miyagi     | Paddy field, no removal of salt and sludge | Kesennuma, Saichi, Minamisaiachi |
| 3     | Miyagi     | Upland field, no removal of salt and sludge | Kesennuma, Motoyoshicho, Oya, Motoyoshi-gun, Minamisanrikumachi, Togura |
| 4     | Miyagi     | Paddy field, no removal of salt | Ishinomaki, Minamisanrikumachi, Togura |
| 5     | Miyagi     | Paddy field, removed surface soil layer* | Ishinomaki, Minamisanrikumachi, Togura |
| 6     | Miyagi     | Paddy field, no removal of salt and sludge | Ishinomaki, Kitaichikadai |
| 7     | Miyagi     | Paddy field, no removal of salt and sludge | Ishinomaki, Watanohahashishita |
| 8     | Miyagi     | Upland field, removed sludge* | Ishinomaki, Shinbashi |
| 9     | Miyagi     | Paddy field, mixed with sludge and ploughed | Ishinomaki, Minamizakaitiidei |
| 10    | Miyagi     | Sludge in waterway of a paddy field | Ishinomaki |
| 11    | Miyagi     | Paddy field, no removal of sludge | Ishinomaki, Kadonowaki-shajiki |
| 12    | Miyagi     | Sludge, in front of houses and a park | Higashimatsushima, Omagarishimodai |
| 13    | Miyagi     | Paddy field, no removal of salt and sludge | Higashimatsushima, Yamato-izaidori |
| 14    | Miyagi     | Subsided paddy field, seawater inflowed | Higashimatsushima, Ootsuka Tona |
| 15    | Miyagi     | Upland field, removed surface soil layer* | Sendai, Miyagino-ku, Gamo |
| 16    | Miyagi     | Upland field, removed surface soil layer* | Sendai, Miyagino-ku, Gamo |
| C     | Kagawa     | Granite soil mixed with compost in the ratio of 3:1 | Kagawa University, Experimental Field, Sanuki city |

*using heavy machinery

2. **Water ratio of soils**

The water ratio of soils is water content in the test method of Japanese geotechnical society standards, calculated as the ratio of the mass of water in the soil to the mass of soil particles. We called it the water ratio to avoid confusion. We measured and calculated the water ratio of soils according to Japanese geotechnical society standards (JGS 0121–2009).

3. **Density of soil particles**

The density of soil particles was determined according to the Japanese geotechnical society standards (JGS 0111–2009).

4. **pH and electric conductivity (EC) of soil**

The pH and EC were determined according to the test method for pH (JGS 0211–2009) and EC (JGS 0212–2009) of suspended soils of Japanese geotechnical society standards using a pH meter (BECKMAN 32 pH Meter) and an EC meter (DKK-TOA Corp., CM-31P), respectively.

5. **Water permeability of the soil**

We made a 250 ml funnel-shaped container using the top half of a plastic bottle and filled it with 100 ml of soil. The weight of the container containing the soil was measured, and then 100 ml of water was poured into the soil. The weight, which changed as the water fell, was measured as time passed. There are some methods for measuring soil permeability, such as the falling head permeability test (JIS A1218), which originally evaluated soil permeability by the water table. However, in this study, it was evaluated by weight.

6. **Determination of anions and cations in soils and plant tissues**

The soil sample was dried at 110°C for 24 h in an electric oven (AS ONE Corp., EO-700B) and crushed into a fine powder with a mortar and pestle. The dried soils were put in pure water and incubated at 25°C for 24 h. The solution dissolved in soils was filtered through a 0.2 μm pore size membrane filter (Phenomenex, USA). The filtrate was used for the analysis. The plant tissues were dried at 80°C for 48 h hours and crushed into a fine powder with a pestle and mortar. The dried tissues were dissolved
in pure water and were filtered through the membrane filter. The filtrate was used for the analysis. The ions were measured using an ICS-900 ion chromatography system (Dionex Corporation, Sunnyvale, CA, USA) equipped with an autosampler (model AS-DV), an isocratic column, a D55 conductivity detector, and a suppressor. A Dionex IonPac AS23 analytical column and an AG25 guard column were used to separate anions, and a Dionex IonPac CS12A analytical column and a CG25 guard column were used to separate cations. The eluent consisted of 4.5 mM sodium carbonate and 0.8 mM sodium bicarbonate for anions and 20 mM methanphoric acid for cations at a flow rate for cations and anions of 1 mL min⁻¹. The concentrations of ions were calculated by referring to a standard solution. The recovery rate measured by K₂SO₄ was 86.6 ± 5.7% for anions and 111.1 ± 10.4% cations, respectively.

7. Statistical analysis

BellCurve for Excell (ver 2.15., Social Survey Research Information Co., Ltd.) was used for the statistical analysis (Dunnett’s test).

Results

Water ratio, particle density, pH, and electric conductivity in soil

We analysed the soils’ physical and chemical factors to know the soil characteristics tested in the present study. Figure 2 shows the water ratio, soil particle density, electric conductivity (EC), and pH of the soil solution.

The water ratio of tsunami-affected soils (Figure 2A) was significantly lower in all tsunami-affected soils than that in control, ranging from 26% to 71%. They were higher in sites 9, 10, and 12, in which the growth was inhibited (Figure 3).

The density of soil particles was significantly higher in all tsunami-affected soils than that in control ranging from 2.3 to 2.7 g m⁻³ (Figure 2B). The pattern of differences in the values among soils is not consistent with the trend of differences among sites in growth. The pH ranged from 5.2 to 8.2 (Figure 2C), and the EC ranged from 0.1 to 2.6 (Figure 2D), respectively. The pH was significantly higher in sites 12, 13, 14 and significantly lower in sites 9 and 10 than in control, where growth was lower than in control. However, it was not the case in sites 4 and 15, in which the growth was comparable with those of control soil. The EC was

Figure 2. Physical and chemical properties of the tsunami-affected soils. A: water content; B: panicle density; C: pH; D: electric conductivity. The numbers on the x-axis indicate the sampling points of the tsunami-affected soils as indicated in Figure 1. The letter C indicates control, the soils of the experimental fields of Kagawa University. All data are represented as the mean ± s.e. of four independent replicates. * and **, p < 0.05 and 0.01 compared with control, respectively (Dunnett’s test).
higher in sites 12, 14, and 15, in which the content of Na$^+$ and Cl$^-$ were higher (Figure 4). The pattern of differences in the values among soils is not similar to the trend of differences in growth among sites, indicating that these values were not directly related to the growth.

**Water permeability of soil**

The water permeability was measured by the changes in soils’ weight with time elapsed after adding water (Figure 5).

The values were expressed as weight relative to the initial values of each soil. The patterns of time-course changes in the weight of soils containing water are classified into three ways: 1) it dropped rapidly, then gradually reduced with time elapsed, indicating higher water permeability, e.g., sites 5, 6, 7, and 15, and control reached the relative weight ranging from 18–50%, 2) it reduced gradually and reached similar levels to those in type 1 at the end of measurements, e.g., sites 4 and 8, indicating moderate water permeability of the soil, and 3), it decreased gradually and reached the relative weight of soil ranging from 85–100% of first values at the end of measurements, indicating that those soils have a lower water permeability, e.g., sites 1, 2, 3, 9, 10, 11, 12, 13, 14 and 16. In these soils, except 1 and 3, the plant growth tended to be depressed more severely than in the other soils.

**The ion concentration of the soils**

All soils contained Na$^+$ at a higher level than control soil (Figure 4). Na$^+$ concentration was the highest in site 12, followed by 14, 15, and 16, which were 311, 198, 133, and 95-fold in control soil. In contrast, it was lower in sites 4, 5, 6, 8, and 11, which are 2.6 to 6.2-fold of that in control soil. Cl$^-$ concentration was higher in sites 1, 3, 12, 14, 15, and 16, ranging from 50.5 to 459 times in control soil. Plants grew well in site 15 (Figure 3), but the growth was relatively stunted in the other sites, e.g., sites 1, 3, 12, 14, and 16. NH$_4^+$ concentration was the highest in site 15, followed by 10, which were 1.5 and 1.3 times higher than control soil. PO$_4^{3-}$ concentration in the tsunami-affected soil was lower than control soil. The highest value, of which in site 8, was 4% of that in control soil. K$^+$ concentration was highest in site 14, about two-fold of that in control soil. In sites 10, 12, 15, and 16, K$^+$ was about 1.5-fold of control soil. Ca$^{2+}$ concentration in sites 1, 10, 12, and 15 was similar (sites 1, 10, and 12) to or slightly higher (site 15) than the control soil. Mg$^{2+}$ concentration was higher in site 15, which showed the highest growth value, but higher in sites 12, 14, and 16, which showed lower growth. Mg$^{2+}$ concentration of these sites was almost twice and similar to that of the control soil. The growth was higher in sites 1 and 15, but lower in sites 10 and 12.

**Plant growth**

Figure 3 shows the fresh weight of the ice plant’s shoots, cultured in the tsunami-affected soils for 65 days. The growth of the plant in control was healthy and normal. The plant’s growth in the soils of 8 sites (1, 3, 4, 5, 6, 7, 8, and 15) was higher than or comparable with control soil. The weight of plants in those sites ranged from 260.7 to 405.2 g plant$^{-1}$. The growth was inhibited modestly in sites 2 and 11 and severely in sites 9, 10, 12, 13, 14, and 16. They were about 9.1 to 30.0% of those in control.

**The accumulation of Na$^+$ and Cl$^-$ in the shoot**

Figure 6 shows the concentration of Na$^+$ and Cl$^-$ in the shoot on a dry weight basis. The Na$^+$ concentration ranged from 45.6 to 132.0 mg gDW$^{-1}$, equivalent to 9.1 to 26.3 times in control soil. In sites 12, 14, and 15, Na$^+$ accumulated in the shoot at a higher level, 25.2, 25.1, and 26.3 times higher than in control soil, respectively. The concentration of Cl$^-$ ranged from 7.0 to 241.4 mg gDW$^{-1}$. The value was highest in site 12, followed by sites 15, 14, and 1, which were 141.2, 122.7, 103.1, and 99.2 times higher than control.
Figure 4. The concentration of ions in the tsunami-affected soils. The ions were extracted from the water-soluble soil fractions by incubation at 25°C for 24 h. The quantification of ions was measured using an ICS-900 ion chromatography system. The numbers on the x-axis indicate the sampling points of the tsunami-affected soils as indicated in Figure 1. The letter C indicates control, the soils of the experimental fields of Kagawa University. Vertical bars indicated the standard error of their replicates. All data are represented as the mean ± s.e. of four independent replicates. * and **, p < 0.05 and 0.01 compared with control, respectively (Dunnett’s test).

The Na⁺ and Cl⁻ in shoot per single plant ranged from 0.11–9.5 g (Figure 7A). The highest values were found in sites 15, followed by 1, 7, and 5, ranging from 54.7, 33.9, 26.7, and 26.6-times in control.

The Na⁺ and Cl⁻ content in the shoot depends on the accumulation of Na⁺ and Cl⁻ (Figure 7B) and the growth performance (Figure 5). Figure 7B shows the relationship between the growth performance evaluated as the fresh weight and contents of Na⁺ and Cl⁻ in shoot per single plant. The Na⁺ and Cl⁻ per single plant tended to increase with the increase in biomass. There were three groups in the values: 1) both growth and content of Na⁺ and Cl⁻ were lower than average value (dotted line, sites 2, 9, 10, 11, 12, 13, 14, and 16) (group 1), 2) the growth was medium (ranged from 260.9 g to 287.8 g), and the contents of Na⁺ and Cl⁻ was lower than that of the
not reduce, but the accumulation of NaCl in tissues was lower due to the lower range of Na\(^+\) and Cl\(^-\) in soils. In group 3, the soils of sites 1 and 7, the contents of Na\(^+\) and Cl\(^-\) were relatively low, but the absorption of Na\(^+\) and Cl\(^-\) and the growth were somewhat higher. In site 15, Na\(^+\) and Cl\(^-\) in the tissue and the growth were both more elevated, and consequently, the content of Na\(^+\) and Cl\(^-\) in the shoot of a single plant was the highest among the plants grown in the soils examined in the present study.

**The relationship between soil moisture and plant growth**

Figure 8 shows the relationship between water permeability evaluated as soil weight relative to the initial values of each soil at 60 seconds after adding water to the soils, which is shown in Figure 3 and the shoot’s fresh weight. The soil with lower relative weight has high water permeability. Shoot’s fresh weight grown in the soil with relative weight lower than 81% was comparable to that in control, but in the soils in which relative soil weight was higher than 82%, shoot’s fresh weight reduced up to 3%-71% of control.

**Discussion**

**Regulating the growth of the ice plant in the tsunami-affected soil**

NaCl accumulated in a shoot was determined by shoot biomass and concentration of NaCl in tissues. The shoot’s Na\(^+\) and Cl\(^-\) were likely unrelated to the soil’s
water-soluble Na⁺ and Cl⁻ concentration. Differences in growth might cause this discrepancy. The plant that can grow healthily has a higher capacity to absorb ions even when the water-soluble Na⁺ and Cl⁻ in the soil is low. They also have high biomass, and the amount of Na⁺ and Cl⁻ per shoot, calculated as the product of ion content per unit weight and shoot fresh weight, is high. Conversely, plants with stunted growth have a low capacity to absorb Na⁺ and Cl⁻, and they cannot absorb Na⁺ and Cl⁻ even when the concentration of water-soluble Na⁺ and Cl⁻ in the soil is high. A trend of a positive relationship between the shoot’s fresh weight and content of Na⁺ and Cl⁻ per single shoot (Figure 7) suggests that the shoot’s growth determined the amounts of NaCl removed from salinized soil. We found that the relative amounts of water retained in the soil (water permeability) tend to be related to the shoot growth of ice plant. The growth of plants cultivated in the soils with higher amounts of water in soils was lower (2, 9, 10, 11, 12, 13, 14, and 16; Figure 8), indicating that the soil moisture was one of the factors responsible for the growth of the ice plant. The ice plant is native to the Namibian desert in southern Africa (Bohnert & Cushman, 2000; Winter et al., 1978). The soil types of sandy soil or sandy loam soil with higher water permeability are suitable for growth.

**The capacity of NaCl removal from the tsunami-affected soil in the ice plant**

NaCl in the shoot was highest in the plant grown in site 15. The sodium chloride accumulated in the shoot was about 9.5 g (31.8%) on a dry weight basis; Figure 7). When we culture the ice plant in 20 cm intervals in a field, the estimated NaCl amount that the plant removes is about 2.38 t ha⁻¹. This amount of NaCl is equivalent to 238 g plant⁻¹ m⁻². Assuming that the roots extend 10 cm underground and the specific gravity of the soil is 1, the NaCl per 1 kg of soil is 2.38 g (0.238%). This is almost one-tenth the concentration of NaCl in seawater. Therefore, it is considered effective in reducing salt damage to crops.
and vegetables. When the ice plant was cultured hydroponically for 49 days with 400 mM NaCl, it accumulated NaCl up to 14 g in the shoot (Agarie, 2004). We suggest that this range of NaCl (about 10–14 g) in the shoot might be the maximum capacity for NaCl accumulation in this species. Panta et al. (2014) have reviewed the potential of halophytes for desalination of salinized soils, and they showed that it was ranged from 0.66 to 6.35 t ha⁻¹ year⁻¹. The desalinization ability of the ice plant was comparable to that of Suaeda fruticosa (2.0 t ha⁻¹ year⁻¹; Rabhi et al., 2009), Kaliadium folium (2.79 t ha⁻¹ year⁻¹; Zhao et al., 2005), and Suaeda salsa (2.06 t ha⁻¹ year⁻¹; Ke-Fu, 1991). These results indicated that the ice plant has a high NaCl accumulation ability similar to halophytes used for desalination. The ice plant grows naturally in coastal areas under climatic conditions characterized by short, cool, moist winters and long and dry summers (Bohnert & Cushman, 2000; Winter et al., 1978). NaCl removal capacity would maximize under a condition similar to that of habitat suitable for the growth.

**Potential of the ice plant as a crop in the salinized soil**

The ice plant’s estimated biological yield ranged from 2.3 to 101.7 t ha⁻¹ if the plant was cultured at 20 cm intervals in the field. In the other halophytes such as Atriplex triangularis, which has been used as a vegetable in the Netherlands, Belgium, and Portugal (Leith et al., 2000), the yield was 21.2 t ha⁻¹ on a fresh-weight basis under seawater irrigation (30 g NaCl l⁻¹; Gallagher, 1985). In the field experiment, Salicornia persica and S. fruticosa was grown with seawater irrigation, which contained 100 mM NaCl, showed 15.0 and 28.0 kg m⁻² year⁻¹, respectively (Ventura et al., 2011). The estimated ice plant’s yield ranged from 0.33 to 14.6 kg m⁻², and the productivity of this species would be similar to those of the Atriplex and Salicornia species.

The ice plant’s growth was promoted rather than inhibited in the soils that contained NaCl to some degree. For example, in site 15, the soil had 4.7 g kg⁻¹ (0.47%, 80.5 mM) NaCl, and the shoot’s fresh weight was 1.6-times higher than that in control. In our previous study, the ice plant, cultured hydroponically under the referenced environmental condition, the growth was enhanced by NaCl with the highest value at 100–200 mM NaCl (Agarie, 2004). The ice plant grows well in the salt-containing soil, and the NaCl-enhanced growth, referred to as halophilism, was confirmed in the plants grown in the tsunami-affected soil. The trait mechanisms remain unclear (Tran et al., 2019ab), but the present study indicated that the ice plant’s growth increased in the salinized soils containing NaCl, of which concentration is up to about 1.0%.

Plants sequestrate the excess NaCl into the vacuole and synthesizes compatible solutes to maintain a balance of osmotic pressure between the vacuole and cytosol. The ice plant synthesizes proline (Demmg & Winter, 1986) and pinitol (Agarie et al., 2009) as compatible solutes, which are health-promoted compounds (Davis et al., 2000; Kim et al., 2012; Watanabe et al., 1999). The antioxidant activity is also enhanced in response to oxidative stress (Agarie et al., 2009) by increased activity and amounts of scavenging enzymes (Miszalski et al., 1998) and the antioxidant compounds (Ibdah et al., 2002). These facts indicated that the ice plant could be used as a functional vegetable, synthesizing beneficial compounds and enzymes in a single plant under salinity.

**Acknowledgments**

The authors wish to acknowledge Dr. Akihito Kusutani, Professor of Kagawa University, for advice on experimental design and timely help in the use of apparatus, and we wish to thank the timely advice and help given by Dr. Koji Tanigawa, assistant professor of Tokushima Bunri University.

**Disclosure statement**

No potential conflict of interest was reported by the author(s).

**References**

Agarie, S. (2004). Possibility of desalinization of saline soils by common ice plant (*Mesembryanthemum crystallinum* L.). *Japanese Journal of Tropical Agriculture*, 48, 294–298. https://doi.org/10.11248/jsta1957.48.294

Agarie, S., Kawaguchi, A., Kodera, A., Sunagawa, H., Kojima, H., & Nakahara, T. (2009). Potential of the common ice plant, *Mesembryanthemum crystallinum* as a new high functional food as evaluated by polyol accumulation. *Plant Production Science*, 12, 37–46. https://doi.org/10.1626/pps.12.37

Akhter, J., Mahmood, K., Malik, K.A., Ahmed, S., & Murray, R. (2003). Amelioration of a saline sodic soil through cultivation of a salt tolerant grass *Leptochloa fascsa*. *Environmental Conservation*, 30, 168–174. https://doi.org/10.1017/S0376892903000158

Boesch, D. F., Josselyn, M. N., Mehta, A. J., Morris, J. T., Nuttle, W. K., Simenstad, C. A., & Swift, D. J. P. (1994). Scientific assessment of coastal wetland loss, restoration and management in Louisiana. *Journal of Coastal Research*, 20, 11–103.

Bohnert, H. J. & Cushman, J. C. (2000). The ice plant cometh: Lessons in abiotic stress tolerance. *Journal of Plant Growth Regulation*, 19, 334–346. 3 https://doi.org/10.1007/s003440000033
Davis, A., Christiansen, M., Horowitz, J.F., Klein, S., Hellerstein, M.K., & Ostlund, R.E. Jr. (2000). Effect of pinitol treatment on insulin action in subjects with insulin resistance. *Diabetes Care*, 23, 1000–1005. 7 https://doi.org/10.2337/diacare.23.7.1000

de Villiers, A.J., van Rooyen, M.W., Theron, G.K., & Claassens, A.S. (1995). Removal of sodium and chloride from a saline soil by *Mesembryanthemum barklyi*. *Journal of Arid Environments*, 29, 325–330. 3 https://doi.org/10.1016/S0140-1963(05)80111-9

Demmig, B., & Winter, K. (1986). Sodium, potassium, chloride and proline concentrations of chloroplasts isolated from a halophyte, *Mesembryanthemum crystallinum* L. *Planta*, 168, 421–426. https://doi.org/10.1007/BF00392371

FAO. 2008. *Land and plant nutrition management service*. http://www.fao.org/ag/agl/agll/spush

Flowers, T.J. (2004). Improving crop salt tolerance. *Journal of Experimental Botany*, 55, 307–319. 396 https://doi.org/10.1093/jxb/erh003

Flowers, T.J., & Colmer, T.D. (2015). Plant salt tolerance: Adaptations in halophytes. *Annals of Botany*, 115, 327–331. 3 https://doi.org/10.1093/aob/mcu267

Gallagher, J.L. (1985). Halophytic crops for cultivation at seawater salinity. *Plant and Soil*, 89, 323–336. 1–3 https://doi.org/10.1007/BF02182251

Glenn, E.P., Brown, J.J., & Blumwald, E. (1999). Salt tolerance and crop potential of halophytes. *Critical Reviews in Plant Sciences*, 18, 227–255. 2 https://doi.org/10.1080/0735268991309207

Gul, B., Weber, D. J., & Khan, M. A. (2000). Effect of salinity and planting density on physiological responses of *Allenrolfea occidentalis*. *Western North American Naturalist*, 60, 188–197. https://www.jstor.org/stable/41717029

Ibdah, M., Kims, A., Seidlitz, H.K., Heller, W., Strack, D., & Vogt, T. (2002). Spectral dependence of flavonol and betacyanin accumulation in *Mesembryanthemum crystallinum* under enhanced ultraviolet radiation. *Plant, Cell and Environment*, 25, 1145–1154. https://doi.org/10.1046/j.1365-3040.2002.00895.x

Ke-Fu, Z. (1991). Desalination of saline soils by *Suada salsa*. *Plant and Soil*, 135, 303–305. 2 https://doi.org/10.1007/BF00010921

Kim, H.J., Park, K.S., Lee, S.K., Min, K.W., Han, K.A., Kim, Y.K. & Ku, B.J. (2012). Effects of pinitol on glycemic control, insulin resistance and adipokine levels in patients with type 2 Diabetes Mellitus. *Annals of Nutrition and Metabolism*, 60, 1–5. 1 https://doi.org/10.1159/000334834

Leith, H., Lohmann, M., Guth, M., & Menzel, U. (2000). *Cash crop halophytes for future halophytes growers*. Institute of Environmental System Research, University of Osnabreuck.

MAFF. 2013. *Disaster and management resolution situation of agricultural management body of the Great East Japan Earthquake: Overview of the status of agriculture and forestry census results*. Department of Statistics. March 11, 2013

Miszalski, Z., Ślesak, I., Niewiadomska, E., Baczek-Kwinta, R., Lütte, U. & Ratajczak, R. 1998. Subcellular localization and stress responses of superoxide dismutase isoforms from leaves in the C3-CAM intermediate halophyte *Mesembryanthemum crystallinum* L. *Plant, Cell and Environment*, 21, 169–179. 2 https://doi.org/10.1046/j.1365-3040.1998.00266.x

Panta, S., Flowers, T., Lane, P., Doyle, R., Haros, G., & Shabalala, S. (2014). Halophyte agriculture: Success stories. *Environmental and Experimental Botany*, 107, 71–83. https://doi.org/10.1016/j.envexpbot.2014.05.006

Rabhi, M., Hafsi, C., Lakhdar, A., Hajji, S., Barhoumi, Z., Hammrouni, M.H., Abdelly, C., Smaoui, A. (2009). Evaluation of the capacity of three halophytes to desalinate their rhizosphere as grown on saline soils under non-leaching conditions. *African Journal of Ecology*, 47, 463–468. 4 https://doi.org/10.1111/j.1365-2028.2008.00989.x

Ravindran, K.C., Venkatesan, K., Balakrishnan, V., Chellapappan, K.P., & Balasubramanian, T. (2007). Restoration of saline land by halophytes for Indian soils. *Soil Biology and Biochemistry*, 39, 2661–2664. 10 https://doi.org/10.1016/j.soilbio.2007.02.005

Rogers, C.E. & McCarty, J.P. (2000). Climate change and ecosystems of the Mid-Atlantic Region. *Climate Research*, 14, 235–244. https://doi.org/10.3354/cr014235

Shannon, M.C., & Grieve, C.M. (1999). Tolerance of vegetable crops to salinity. *Scientia Horticulare*, 78, 5–38. 1–4 https://doi.org/10.1016/S0304-4289(98)00189-7

Tran, Q., Konishi, A., Cushman, J.C. Morokuma, M., Toyota, M. & Agarie, S. (2019a). Ion accumulation and expression of ion homeostasis-related genes associated with halophilism, NaCl-promoted growth in a halophyte *Mesembryanthemum crystallinum* L. *Plant Production Science*, 23, 91–102. https://doi.org/10.1080/1343943X.2019.1647788

Tran, Q. D., Konishi, A., Morokuma, M., Toyota, M. & Agarie, S. (2019b). NaCl-stimulated ATP synthesis in mitochondria of a halophyte *Mesembryanthemum crystallinum* L. *Plant Production Science*, 23, 129–135. https://doi.org/10.1080/1343943X.2019.1682462

Ventura, Y., Wuddineh, W.A., Shpigel, M., Samocha, T.M., Klim, B.C., Cohen, S., Shemer, Z., Santos, R., Sagii, M. (2011). Effects of day length on flowering and yield production of *Salicornia* and *Sarcocornia* species. *Scientia Horticulare* 130, 510–516. 3 https://doi.org/10.1016/j.scienta.2011.08.008

Watanabe, M., Sugimura, K. & Yamanoha, B. (1999). Effect of acute deficiency of dietary proline on proline balance in the rat small intestine and liver. *Journal of Animal Physiology and Animal Nutrition*, 82, 294–304. 5 https://doi.org/10.1046/j.1439-0396.1999.00244.x

Winter, K., Lütte, U. & Winter, E. (1978). Seasonal shift from C3 photosynthesis to crassulacean acid metabolism in *Mesembryanthemum crystallinum*, growing in its natural environment. *Oecologia*, 34, 225–237. https://doi.org/10.1007/BF00345168

Zhao, K.-F., Fan, H., Song, J., Sun, M.-X., Wang, B.-Z., Zhang, S.-Q., Ungar, I.A. (2005). Two Na+ and Cl– hyperaccumulators of the Chenopodiaceae. *Journal of Integrative Plant Biology*, 47, 311–318. 3 https://doi.org/10.1111/j.1744-7909.2005.0057.x