

Review

Halophyte Common Ice Plants: A Future Solution to Arable Land Salinization

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Abstract: The problems associated with the salinization of soils and water bodies and the increasing competition for scarce freshwater resources are increasing. Current attempts to adapt to these conditions through sustainable agriculture involves searching for new highly salt-tolerant crops, and wild species that have potential as saline crops are particularly suitable. The common ice plant (*Mesembryanthemum crystallinum* L.) is an edible halophyte member of the *Aizoaceae* family, which switches from C3 photosynthesis to crassulacean acid metabolism (CAM) when exposed to salinity or water stress. The aim of this review was to examine the potential of using the ice plant in both the wild and as a crop, and to describe its ecology and morphology, environmental and agronomic requirements, and physiology. The antioxidant properties and mineral composition of the ice plant are also beneficial to human health and have been extensively examined.

Keywords: *Mesembryanthemum crystallinum*; functional foods; sustainability

1. Introduction

Climate change, the lack of global water resources, and the increase of saline and dry conditions have negatively affected arable lands. By 2050, it is estimated that crop production must increase by 70% to 100% to meet global food demand [1]. As the actual trend is a 1% to 1.5% annual yield increase for major crops, guaranteeing sustainable agriculture in the future is a challenge [2]. Technological progress and the improvement of cultivation techniques are among the key factors determining wellness in contemporary populations, and have led to extensive population growth in recent decades. Increased soil use due to the growth in production has led to a loss of fertility and the phenomena of salinization and desertification, which render soils unsuitable for cultivation. In particular, salinity induces constraints in plants that are associated with a reduction in their primary production, leaf expansion, and biomass losses. Sustainability in terms of water resource preservation, food availability for poor populations, and a reduction in production inputs is thus a major challenge for researchers. The adoption of tolerant species and good agronomic practices, and the reduction of resource waste are, thus, significant research topics. Seawater and coastal lands represent potentially cultivable areas, but they are useless for conventional agriculture. Halophytes are an exception, as they are highly productive under saline conditions [3]. Saline agriculture with halophyte crops could be one solution to the problems of fresh water resource depletion and the increase of salinized soil areas, as they allow for the cultivation of marginal areas and can enable coastal and salt lands to be productive [4]. Halophytic cash crops can be domesticated through conventional breeding programs and thus improve their productivity and salt tolerance [5].

Halophytes are species that are able to complete their life cycles in environments where the concentration of sodium chloride is greater than 200 mM [6]. They are characterized by anatomical changes such as in the bladder cells and the salt glands, through which the excretion of excessive sodium occurs [7]. The leaves of halophytes can be used as human food (i.e., *Chenopodium quinoa* [8]), for fodder (i.e., *Atriplex* spp. [9]), or as oil seeds (i.e., *Salicornia bigelovii* [10]). They can also be sources of secondary metabolites [11] with potential economic value [12]. Wild halophyte domestication is an approach that should therefore be considered. Menzel and Lieth [13] produced a list of over 2600 halophyte species that differ in their degree of tolerance to salinity. Some belong to the group "obligatory halophytes", which require saline environments for optimal growth, such as the common ice plant (*Mesembryanthemum crystallinum* L.). The aim of this review was to assess the potential of adapting the wild ice plant as a crop, describing its ecology and morphology, its environmental and agronomic requirements, and its physiology.

In addition, the ice plant's antioxidant properties and mineral composition were examined, as it is a food crop that can be highly beneficial to human health.

2. Wild Plant

2.1. Origin and Diffusion

M. crystallinum L. ($2n = 18$) (Figure 1) is an annual succulent belonging to the *Aizoaceae* family and is native to South and East Africa, the Sinai, and southern Europe (Spain) [4,14,15]. It is also naturalized in Mediterranean coastal areas, the U.S., Australia, Mexico, Chile, and the Caribbean [16–19]. In Italy it can be found in Apulia (Vieste), Sicily, Sardinia, Lazio, Campania, Liguria, and Tuscany [20,21].



Figure 1. Young *Mesembryanthemum crystallinum* plant.

2.2. Ecology and Morphology

The common ice plant is typically distributed on coastal sand dunes, saline flats, inland saline areas, and roadsides. It is tolerant to low temperatures and accumulations of salt on the top soil, which excludes other species from growing [22,23]. The seeds survive hot dry summers and can germinate after short periods of rain [22,24–26]. The plant is typically heliophile and megatherm [27]. It can grow in sandy and loamy soils that are well-drained, and even nutritionally poor and saline.

It cannot grow in the shade and prefers dry or moist soil. Its suitable temperature range is from 12 to 30 °C, and it can be killed by frost [26].

It is covered with bladder cells (vesicles) (Figure 2), which are appressed during the juvenile phase, that give it a shiny appearance, from which it derives the name common ice plant [22,28]. Its growth form is prostrate and its height ranges between 10–15 cm. The leaves are large oval or paddle shaped with a rosette form, and are light green (3–5 × 5–10 cm) during the juvenile period and then turn dark green and becomes thicker and smaller in the adult phase [28,29] (Figure 3). The flowers are hermaphrodite, white or slightly pink, and are 7–30 mm in diameter. They have five calyx lobes, about 30 staminodes, and white stigmas, and the bladder cells of the receptacle are particularly prominent. The ice plant flowers year-round, but mainly from spring to summer. The flowers open in the morning and close at night, and are insect pollinated [27]. The fruit is a seed capsule. The leaf's red coloration is caused by the presence of water-soluble pigments belonging to the betacyanins group, which are generally produced in response to salinity, anoxia, or thermal stress [30].



Figure 2. Adult stage characterized by the swell of bladder cells.



(a) Juvenile form

(b) Adult form

Figure 3. Comparison between juvenile (a) and adult form (b): differences in color, the presence of bladder cells, thickness, and leaf border shape can be observed.

2.3. Physiology

The transition from the juvenile to the adult phase leads to changes in the ice plant's metabolism: in addition to the development of epidermal bladder cells (already present on the tissues) there is a switch from C3 metabolism to CAM. *M. crystallinum* has also been studied to examine its ability to switch between C3 and CAM as a response to various stress conditions, such as high salinity levels [25,31], drought [22,32], anoxia, low root temperatures [33], and high temperature [34].

When unstressed ice plants enter this phase, CAM metabolism develops slowly [35], and after the induction of environmental stress (salt, low temperature, or drought stress) or mature growth, there is slight decrease in the photosynthetic rate at midday, which gradually intensifies over successive days. At the end of the transition, there is complete stomata closure over the middle part of the day, with intense net photosynthesis at the earlier and latter parts of the photoperiod [35]. Winter and Gademann note that the decrease of turgor in this phase can stimulate CAM induction in *M. crystallinum*, and CO₂ uptake increases after the middle-day photosynthesis depression [35].

It has also been observed that the salinity does not increase antioxidant activity or phenolics concentration, which could be explained by it avoiding reactive oxygen species (ROS) production by switching its C3 metabolism to CAM [36]. The ice plant reacts to stresses such as high temperatures, salinity, and drought conditions through the CAM process [22,33,37–39] so it can cope with abiotic stresses [40].

The ability to switch to CAM allows CO₂ to accumulate during the night-time, which is used for photosynthesis during the daytime, thus increasing its water use efficiency and carbon fixing capacity [39,41].

3. Nursery Production

Very little information is available about the adaption of the ice plant from the wild to cultivation, particularly regarding the environmental and agronomic processes required from nursery to harvest. The cycle can be divided into the five steps of germination: the juvenile phase, the adult phase, flowering, and seed development.

Seed Germination

The seed germination rate depends on both the seed position in the capsule and the size, and larger seeds generally germinate immediately. Similar behavior had been observed in *M. nodiflorum* and in the *Salicornia* genus [10,17]. The period between seed sowing and transplant is about 20 days on average, and ranges from 1 to over 30 days [22]. The germination growing media used was vermiculite with half-strength Hoagland's nutrient solution as fertigation [42]. Two experiments established that an average temperature of 21 °C and a slightly salty environment appear to be the most suitable germination conditions [22,43]. Ice plant seed dormancy can be terminated through exposure to dry heat treatment [44], which is confirmed by Loconsole and colleagues (2019, unpublished), who observed 21 days from sowing to transplant with seeds sown in a growth chamber at 20 °C and 40% RH using a conventional pot growing mix.

4. Crop Production

The ice plant can be easily grown in sandy and loamy soils that are well-drained, and even nutritionally poor and saline. It cannot grow in the shade. It prefers dry or moist soil. Suitable temperature ranges from 12 to 30 °C, and it can be killed by frost [26]. Regarding irrigation, the pot experiments of Tembo-Phiri et al. [26] established that the ice plant can grow with a water level maintained at 25% of pot capacity (a pot volume of 3.4 dm³) with 3 treatments every week. Ice plants were also successfully cultivated by Atzori et al. [4] in soil that was mainly sandy with 3% loam, 2% clay, and 2% organic matter. A daily irrigation of 10.7 mm was provided to keep soil close to the field capacity. The irrigation water's electrical conductivity (EC) was between 2 to 35 dS m⁻¹. Water

was provided using drip irrigation with drippers 30 cm apart. The best results were obtained from 20 to 35 dS m⁻¹. He et al. [39] examined hydroponic cultivation, and seedlings were transplanted after 4 weeks to 4–5 L pots containing half-strength Hoagland's solution that was replaced weekly and the level was maintained by constantly adding water. The photoperiod was 16-h of light at a photosynthetic photon flux density of 350 μmol m⁻² s⁻¹. The temperature and humidity in the growth chamber were maintained at 26°C/28°C (day/night) and 48%/52% (day/night). Plants were harvested after 21 d.

Adams et al. [22] examined soilless culture and after germination the seedlings were transplanted into pots containing a soil mixture (1:1:1, quartz sand:vermiculite:potting compost, v:v:v) and fluorescent lamps (300 ± 500 μmol m⁻² s⁻¹) were provided in the cultivation area. To enhance betalain production and development, the light photoperiod was set at 12 h light/dark and with day/night temperatures of 23/17°C. In the first period, the ice plants were irrigated with distilled water (until Week 3), which was then replaced by half-strength Hoagland's solution.

From the moment of transplant, the juvenile phase begins (Figure 4). The plants develop about one pair of primary leaves per week until there are seven pairs of leaves on the primary axis. When the seventh leaf pair appears, the growth of the primary axis terminates [22]. During the juvenile phase, some genes can be activated by salt stress in the juvenile leaves, such as the genes for inositol biosynthesis and the specific *Mesembryanthemum* extension of this pathway, which leads to the synthesis of pinitol [45–48]. Salinity stress in juvenile plants may provide transcripts for enzymes that are involved in ROS scavenging activity [49].

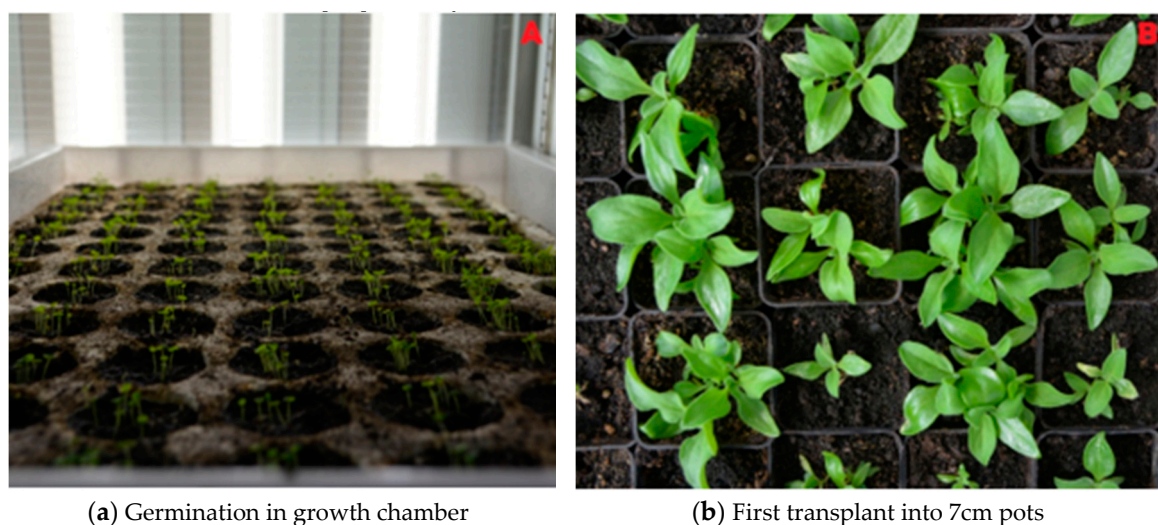


Figure 4. Germination in growth chamber (a) and first transplant into 7cm pots (b).

After the seventh leaf-pair, the adult phase begins. Several secondary axes develop starting from the nodes of the primary axis. On the secondary axis, mature leaves (mentioned above) start to grow. The adult phase is also characterized by the switch from C3 metabolism to CAM; this induction in adult form is constitutive, but juvenile plants can instead switch from CAM to C3 if environmental stress is removed [50]. Another characteristic of the adult stage is the development of bladder cells on secondary leaves and the axis, and primary axis growth is determinate while the secondary axes are indeterminate [22]. The flowering phase generally occurs from late spring to early summer (Mediterranean area) [21].

Flowering is accelerated by salt stress. During the adult period, larger plants produce fewer flowers, while smaller plants produce many flowers at the end of the juvenile growth period. After six weeks of salt stress, the seed capsules generally end their development [22].

In the transition from juvenile to adult phase, salt stress was applied (half-strength Hoagland's solution plus 500 mM NaCl) to plants grown in soil (after five weeks of juvenile growth) [22].

4.1. Light Requirement

All plants are significantly influenced by light intensity and composition, in particular by LED lighting, both in terms of growth and biochemical compound production [51].

Kim (2018) conducted an experiment on ice plants with soilless cultivation, and the leaf number, shoot and root fresh and dry weights, and leaf area were found to increase with increasing light intensity. The best performance was obtained with red light at $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, which gave the best photosynthetic rate at over $120 \mu\text{mol m}^{-2} \text{s}^{-1}$ treatment [52]. However, antioxidant activity and myo-inositol and pinitol concentrations reached the highest levels under blue LEDs [49]. Kim (2018) found that the phenolic concentration was highest under blue LEDs with $120 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD. This suggests that red LEDs influence biomass accumulation, while blue LEDs enhance phytochemical concentrations [52]. This is confirmed by other studies such as that of Weeplian et al. [53], who showed that RW and RB combined with Fr light promoted the reproductive stage and antioxidant activity (the synthesis of phenolic compounds, pinitol, and betacyanins). He et al. suggested that 90% R and 10% B together enhance shoot and root biomass more than R or B alone, in addition to light intensity, and the leaf mass accumulation was found to be higher in *M. crystallinum* grown under red- and blue-LEDs at PPFD of $350 \mu\text{mol m}^{-2} \text{s}^{-1}$ [42]. These results are supported by several other studies that demonstrated how a combination of red and blue light is important for both leaf expansion and biomass accumulation [54–57].

He et al. found that different combinations of BR LED light led to higher chlorophylls and carotenoid accumulation levels than in the 0B condition [39]. This is also reported for other species such as *Rosa hybrida* [58], spinach [59], and cucumber seedlings [54,60].

4.2. PGPR (Plant Growth-Promoting Rhizobacteria) Promotion

Growing plants in limited environmental conditions can be difficult, even with halophytes, but microbe inoculation can help plants to overcome saline conditions, thus resulting in better production [61,62].

Mahmood examined two isolates that are highly tolerant to salinity. The PR-3 and PR-6 isolates showed tolerances up to 1250 mM salinity and indole acetic acid production, and also 1-aminocyclopropane-1- carboxylate deaminase, phosphorus solubilization, and siderophore production [63]. In the same experiment, plants treated with PGPR showed root elongation when compared with the control. This suggests that PGPR can be used to enhance the yield and quality of ice plants [63].

5. Crop and Salt Stress Regulation

Epidermal bladder cells are external vesicles that have a water and NaCl storage function for osmotic adjustments [22,39,64–68], and betacyanins, flavonoids, myoinositol, pinitol, and transcripts for antifungal proteins, which are related to UV protection and/or pathogen defence [69–72]. They are present in the leaves, stem, sepals, and buds, but not on the roots, during all stages of ice plant development. When plants are unstressed and in the juvenile phase, epidermal cell bladders remain appressed, but they swell in volume in stressed plants [28]. Three forms of bladder cell develop in mature tissues: the first along the side shoots; the second are the largest and develop in the seed capsules; and the third develop at the tips of leaves and sepals. This indicates that the bladders could be modified trichomes [22].

Environmental stress, such as salt and drought stress, is known to play an important role in *M. crystallinum* gene expression and development, but some molecules are significant in these gene modifications. Abscisic acid (ABA) for example is considered to be involved in signaling water stress and stimulating stomata closure [72–75], and it has been observed that salt treatment increases the level of ABA and proline [76]. Cytokinins also play an important role in flower initiation and their increase may signal the transition from juvenile form to adult growth and reproduction [77–79].

M. crystallinum demonstrate the typical halophyte behavior of performing best in the presence of NaCl ranging between 50–250 mM NaCl [80]. This is in agreement with Atzori's findings, who observed better production under high salinity levels, suggesting that a saline environment stimulates growth (the FW and DW of juvenile control leaves were lower than in those treated with salt) [4].

Similar experiments have shown that maximum growth was obtained with a 100 mmol L⁻¹ NaCl-solution [81] with a tolerance of up to 300 mmol l⁻¹.

The high photosynthetic activity at high saline concentration could be explained by a general biochemical stimulation of plants, rather than CAM activity induction [81].

As mentioned, the ice plant is not only a saline-tolerant plant, but also has drought resistance: the results of growth response and biomass accumulation recorded in previous studies demonstrate that the ice plant is well adapted to drought and may grow even better with low amounts of water [82–86]. Tembo-Phiri found no difference among several water treatments regarding growth and biomass accumulation, and the stress conditions were mitigated by the CAM metabolism [32,87].

Atzori et al. found differences in the life cycle length between stressed and unstressed plants: senescence in the control plants started in August, while the stressed plants were still in the vegetative phase. Thus, stressed plants may have more time to increase their biomass production [4]. Similar results are reported by Adams et al. [22].

In addition, the Na⁺ storage ability of the epidermal bladder cells enables the ice plant to avoid the saline stress condition, leading to a decrease in antioxidant compounds [36].

M. crystallinum is also able to store Ca²⁺ and Mg²⁺. This is an ability common to the *Caryophyllaceae* family [84–86], in addition to high Zn²⁺ concentrations in shoots. As many people throughout the world are Ca²⁺ deficient in their diets, this could represent a significant finding [88].

Thus, the ice plant can produce a significant amount of biomass through utilizing marginal soils and irrigation water (a height of 0.26 m was reached with a water pot capacity of 80% and 0.23 m with 25%). Accumulation can also increase under saline conditions [26].

6. Secondary Metabolites

The *Mesembryanthemum* genus shows a wide inter-specific variability in terms of antioxidants, radical-scavenging activities, and the abundance of phenolic compounds [89].

An HPLC assay on *M. edule* shoots revealed 12 phenolic compounds, which are mainly flavonoids but with two phenolic acids: avicularin, hyperoside, isoquercetin, isorhamnoside-rutinol, kampherol, phloretin, quercetin, quercitrin, rutin, phloretin xyloglucoside, chlorogenic, and p-coumaroylquinic acid [89]. Falleh found a noticeable presence of tannins [90] and catechin in particular, as also detected by Shu, which can be regarded as a positive standard in different antioxidant bioassays [91]. Other studies confirm higher antioxidant activity in the aerial parts than in shoots activity [92]. The main antioxidant secondary metabolites are betacyanin and flavonol conjugates [93].

The ice plant accumulates betalains instead of anthocyanins [94], and the accumulation of these compounds is also found to be light-dependent. Vogt found that high levels of light intensity and UV influence the synthesis and accumulation of these compounds, and reported a higher accumulation of betacyanins and flavonol conjugates in the bladder cells of the upper epidermis in plants treated with high light radiation (500 μmol m⁻² s⁻¹) than in those treated with 150 μmol m⁻² s⁻¹ [70]. UV-A radiation alone may also lead to the accumulation of these secondary metabolites [70]. Last, an important functional compound in ice plants is d-pinitol, which can act against diabetes and memory impairment [95–97]. Studies have shown that pinitol production in plants can be induced by environmental stresses such as temperature, water deficit, and salinity [98–100]. Inositols, which are known to promote health, are also abundant in the African ice plant [101].

7. Phytoremediation Ability

The increase in pollution and arable land depletion means that different methods of recovering pollutants from soils are required. Plants with this ability have been investigated by several researchers [102–105].

Phytoremediation, used to treat metal pollution, has also been introduced to overcome the problem of salinity, and salt-removing species have been used to control salinity and decrease NaCl concentrations [103,104,106]. Phytoremediation is defined as the use of plants to remove pollutants from the environment and to render them harmless [107]. Plants used for phytoremediation can be commercially produced, thus providing an income to farmers. Several halophytic plant species have been tested for their salt phytoremediation ability [82,106,108,109], and species such as *M. crystallinum* [110] were found to be able to survive in contaminated soils without any metal and salt toxicity effects, and reduce soil salinity and metal contamination [26,111]. *M. crystallinum* have a high Cd concentration in their shoots ($700 \mu\text{g g}^{-1}$ DM) [110], possibly due to the accumulation of these compounds into vegetal tissues [112–114]. This suggests halophytes can be used for saline soil detoxification [115–117].

In an experiment conducted by Amari et al. into the nickel tolerance of ice plants, nickel-induced chlorosis was not observed at concentrations higher than $465 \mu\text{g g}^{-1}$ dry mass, but production was reduced [118].

The ability to maintain photosynthetic activity and PSII integrity in the presence of excess Ni is another interesting characteristic. Data on chlorophyll fluorescence has demonstrated only slight differences in the photochemical activity of Ni-treated plants compared to the control. F_0 was almost constant during the nickel treatment and PSII light efficiency appeared to be unaffected by Ni-exposure (F_v/F_m was close to 0.80, even at $100 \mu\text{M NiCl}_2$). From the experiments mentioned above, we can conclude that ice plants are suitable for the metal phytostabilization of polluted sites [118].

8. Human Health

This ability to overcome difficult environment conditions can be attributed to antioxidant activity, derived mainly from phenolic compounds [119–121]. Halophytes are thus of interest both for therapeutic cosmetics and food [122,123]. *M. crystallinum* and *M. nodiflorum* were used in Tunisian folkloric medical treatments against ocular infection [124], and the leaf extracts are traditionally used as preservatives, as a remedy against throat and mouth infections [125], in soap-making [126] (Figure 5), and to treat several cancers [127,128]. The juice from the leaves can be used to treat several fungal and bacterial diseases, sinusitis, diarrhea, infantile eczema, tuberculosis, and other disorders such as diabetes or obesity [122,126,129]. It is also used to treat inflammation of the respiratory or urinary systems, water retention, and painful urination, and for soothing lung inflammation [130] and spider and tick bites [131]. The leaf juice also demonstrates antimicrobial activity, particularly against *Staphylococcus aureus* and *Pseudomonas aeruginosa* [92], a noticeable resistance against insect, fungal, bacterial, or viral based diseases [32], and antiseptic properties [131]. The resistance level appears to be related to the concentration of antimicrobial compounds [132].

A major functional compound found in *M. crystallinum* is pinitol. Lee et al. found a positive effect of D-pinitol of *M. crystallinum* extracts on blood glucose levels (diabetes), neural protection, and memory ability in a rat model [95–97].

In terms of cosmetic uses, dermatological effects were found from an extract of *M. crystallinum* by Raak et al., and they demonstrated a significant increase in hydration when using ice plant-based cream compared to untreated skin [133]. It has also been reported to delay skin ageing [134].

The ice plant can be used in salads, juiced, and can enhance the flavor of fish and seafood [26]. It has a crunchy texture and a fresh, salty, lemony flavor [135–137]. On its own it tastes like water with salt, and the crystallization of the salt is somewhat reminiscent of the taste of an oyster. It is used as a food in India, California, Australia, and New Zealand, and in some European countries [106], such as Germany and the Netherlands [138].



Figure 5. Ice plant leaf extract and body care lotion, an example of several uses of this plant (Dr. Hauschka—https://www.dr.hauschka.com/it_IT/).

9. Conclusions

Salinization of both soil and water and the high competition for scarce freshwater resources are increasing problems. Sustainable agriculture is required to adapt to these conditions, and new highly salt-tolerant crops are sought. Particularly suitable are wild species that have potential as saline crops. They have a remarkable capacity for acclimation and flexibility in their development, which is lacking in glycophytic plants. The high salt tolerance and content in the bioactive compounds, in addition to the excellent capacity for phytoremediation, makes the ice plant an important candidate for use in several areas, such as human food and medical care, and in the decontamination of polluted sites. By improving the cultivation system of ice plants, future large-scale production can be developed.

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